THE ECOLOGY OF VENOM USE IN THE JAVAN SLOW LORIS (*NYCTICEBUS JAVANICUS*) AND ITS IMPLICATIONS FOR CONSERVATION

EVA JOHANNA RODE-MARGONO

2015

THE ECOLOGY OF VENOM USE IN THE JAVAN SLOW LORIS (*NYCTICEBUS JAVANICUS*) AND ITS IMPLICATIONS FOR CONSERVATION

Author:

Eva Johanna Rode-Margono

Supervision team:

Director of Studies: Prof. Nekaris K.A.I.

Co-Supervisor: Prof. Nijman V.

OXFORD BROOKES UNIVERSITY

Thesis is submitted in partial fulfilment of the requirements of the award
of
Doctor of Philosophy

May 2015

ABSTRACT

The slow loris *Nycticebus* spp. belongs to the few venomous mammals. I aimed to explore sources for venom sequestration and the ecological function of slow loris venom, which has never been studied before. I examined the hypotheses that venom is used for intraspecific competition, predator defence and/or (ecto-) parasite avoidance. From April 2012 to June 2013 I observed 12 radio-collared and several uncollared wild Javan slow lorises (*N. javanicus*) at the rural agricultural field site Cipaganti in West Java, Indonesia. I collected behavioural observations including feeding and ranging data, examined faecal samples for diet remains and parasites, and regularly checked animals for ectoparasites. I also captured arthropods over five months. I monitored the coexistence with potential predator species using camera traps and by conducting forest surveys throughout Java. Venom may be sequestered from secondary plant metabolites and noxious arthropods, as the latter were abundant at the study site. Javan slow lorises fed extensively on gum (56 %) and 95 % of faecal samples contained arthropod remains. With regard to the ecological function, ranging patterns and social interactions indicated that the social system, with a monogamous social organisation and mating system with promiscuous tendencies, has potential for high sexual and non-sexual intraspecific competition. Camera trapping and forest surveys revealed the coexistence of Javan slow lorises with potential predators. However, predator avoidance could not explain the detected lunarphobia in Javan slow lorises. Additionally, animals were surprisingly ectoparasite-free. My results support all three hypotheses explaining the ecological function but should be enforced by analysing the venom composition in relation to various dietary and environmental factors, aided by (behavioural) experiments with potential predator and parasites. Finally, I applied my results to conservation of the Critically Endangered Javan slow loris, providing recommendations for the conservation of wild populations, husbandry of captive animals and reintroduction.

ACKNOWLEDGEMENTS

I am deeply grateful to my supervisor Prof. Anna Nekaris who has given me the opportunity to study an amazing primate, the Javan slow loris. Without her and my co-supervisor Prof. Vincent Nijman's guidance, advice, patience and constant encouragement this project would not have been possible. Thank you for believing in me.

I would like to thank the Indonesian authorities Riset and Teknologi (Ristek), Balai Konservasi Sumber Daya Alam Bandung (BKSDA Bandung), Research Center for Biology, Indonesian Institute of Sciences (LIPI) and Konservasi Sumber Daya Alam Garut (KSDA Garut) for their support in this project. Special thanks goes to my research counterpart Mrs Wirdateti from LIPI. She and Dr Gono Semiadi from LIPI, and Mr Teguh and Mr Rakim from KSDA Garut helped me with endless advice and support.

The field work was funded by the Leverhulme Trust (RPG-084), Mohamed bin Zayed Species Conservation Fund, People's Trust for Endangered Species, Conservation International Primate Action Fund, Cleveland Zoological Society and Cleveland Metroparks Zoo, Chicago Zoological Society/ Chicago Board of Trade (CBOT) Endangered Species Fund, Primate Society of Great Britain Conservation Working Party, Columbus Zoo, Amersfoort Zoo, Primate Conservation Inc., the International Primate Protection League and Brookes University.

Hatturnuhun ke tracker dan teman-teman saya Dendi Rustandi Pondiana (Mr Dendi), Dede Ahmad (Kang Aconk), Adin Sopian (Mr Adin), Mr Ade, dan Wawan Tarniwan. Proyek penelitian saya tidak bisa berkembang atau berkelanjutan untuk jangka waktu yang lama dan sukses tanpa bantuan, semangat mereka dan tentu saja dukungan dari pemerintah dan juga seluruh masyarakat setempat.

I would like to thank all my volunteers and students for their help: Alke Voskamp, Matthew Ward, Marlies Albers, Prescillia Rindang Putri, Vanessa Reithinger, Patrick Demus, Helene Wendt, Daisy Fox Maryon, Sarah Lundregan, Mark Rademaker and Sophie Bader.

Several people have contributed to the success of the project and the finalization of the thesis. I am very grateful to the members of staff of LAHUKA company who have facilitated the complicated process of permit applications. Whenever I needed advice with capturing, rescuing and treating slow lorises in the field, I could count on the instant help by the staff of Cikananga Wildlife Center, International Animal Rescue (IAR) Indonesia and Jakarta Animal Aid Network (JAAN). Especially the emergency support by the director of Cikananga Wildlife Center, Resit Soezer, and the steady and trustful help of my friend Iing Iryantoro gave me the strength to pull through difficult field times. Magdalena Svensson, Graham Toon and Andy Field at Brookes University provided technical support; Dr Guiseppe Donati helped with statistics. Emerson Tan assisted me with endless support. My friends Shun Deng Fam, Grace Fuller and other anonymous reviewers of early stage drafts of this thesis have enormously helped to improve the quality of my dissertation.

Finally, I want to express my deepest thank to my whole family, who always have supported me in my dream to study primates in the wild and have helped me to get through difficult times. Apart from the tremendous experience resulting from this project, the most precious outcome of my time in Indonesia is my wonderful husband Hendra Margono who always stood by me, and our new family.

TABLE OF CONTENTS

General methods

Basic ethology and ecology of the Javan slow loris and potential sources for the sequestration of slow loris venom

Take up your arms! Intraspecific competition, territoriality and social system in Javan slow lorises

LIST OF TABLES

LIST OF FIGURES

ABBREVIATIONS

AN	K. Anne-Isola Nekaris
ASL	above sea level
BGE	Brachial gland exudates
BKSDA	Natural Resources Conservation Office (*Balai Konservasi Sumber Daya Alam*)
CITES	Convention on International Trade of Endangered Species
CR	Critically Endangered
DD	Data Deficient
EN	Endangered
GDP	Gross Domestic Product
GPS	Geographic Position System
IAR	International Animal Rescue
IUCN	International Union for the Conservation of Nature
kDa	Kilodalton
KHR	Kernel Home Range
LAHUKA company	Company Lautan Hutan Kayu - Indonesian Expedition Services
LC	Least Concern
LFP	Little Fireface Project
LIPI	Indonesian Institute of Sciences (*Lembaga Ilmu Pengetahuan Indonesia*)
MCP	Minimum Convex Polygon
NGO	Non-governmental organisation
PA	Protected Area
RISTEK	Research and Technology (*Riset dan Teknologi*)
SIMAKSI	Entrance Permit for Protected Areas (*Surat Izin Masuk Kawasan Konservasi*)
UNEP	United Nations Environment Programme
UNESCO-MAB	United Nations Educational, Scientific and Cultural Organization - Man and the Biosphere
VDA	Venom delivery apparatus
VDS	Venom delivery system
VN	Vincent Nijman
VU	Vulnerable

CHAPTER 1

GENERAL INTRODUCTION

1. Brief overview of theoretical background, aims and objectives

Fry et al. (2009a, p. 501) define venom as “a secretion, produced in a specialized tissue (generally encapsulated in a gland) in one animal and delivered into a target animal through the infliction of a wound (regardless how tiny it is). Venom must further contain molecules that disrupt normal physiological or biochemical processes so as to facilitate feeding or defence by/of the producing animal.” In contrast to venomous animals, poisonous animals do not deliver their toxins directly by the use of specialized venom glands and a connected venom delivery apparatus. Instead (parts of) their bodies contain substances that are poisonous when ingested or touched. The term toxin is used to describe biologically produced chemical substances that impact biological functions in other organisms and thus apply to both venom and poison. Venom has evolved multiple times independently by convergent evolution in the animal kingdom (Fry et al. 2009a, Wong & Belov 2012, Casewell et al. 2013). While many or even most members of certain lineages such as toxicoferan reptiles, spiders, scorpions or centipedes are venomous, few mammals have developed this trait (Dufton 1992, Ligabue-Brown et al. 2012). With the exception of the platypus (*Ornithorhynchus anatinus)*, only few studies have been conducted on venomous mammals. As a result there are knowledge gaps in the venom composition, venom delivery system, and ecological function of venom. Due to the phylogenetic closeness of humans and other mammals, details of venom in mammals would be helpful in pharmacological discovery and development and in molecular studies, evolution and ecology (Dufton 1992, Fry et al. 2008, Dutertre & Lewis 2010, Harrison et al. 2011, King 2011, Casewell et al. 2013). Detailed studies have been impossible due to the small quantities of available gland material in small species, difficulties in maintaining animals in captivity and the protection and conservation regulations and status of several species (Dufton 1992, Ligabue-Brown et al. 2012). Furthermore, scientists may be unaware of this venomous mammal or focus on more popular species such as snakes. Slow lorises[1] ***Nycticebus*** spp. are amongst the few venomous mammals and the only venomous primates. By licking their brachial gland in the flexor area of the elbow, slow lorises mix the gland secretion with saliva and the toxin is delivered by their bite (Hagey et al. 2007). Reactions of prey animals, conspecifics and humans can be extreme, even lethal (Wilde 1972, Streicher 2004, Klotz et al. 2009, Nekaris et al. 2013a). Apart from being unique as venomous primates, all species of slow lorises are threatened by habitat loss and the trade for pets and traditional medicine (IUCN 2014). The Javan slow loris (***N. javanicus***) is assessed as Critically Endangered on the IUCN Red List (Nekaris et al. 2013b), and has been listed as one of the 25 Most Endangered Primates in the World (Mittermeier 2009, 2012, Schwitzer et al. 2014). Although studies

---

[1] The term “slow loris” used in this thesis refers to slow and pygmy lorises (*Nycticebus* spp.)

of wild populations have intensified since the start of the new millennium, only two long-term studies that involve radio-tracking have been conducted on wild slow lorises (greater slow loris ***N. coucang***, Wiens 2002; pygmy slow loris ***N. pygmaeus***, Starr 2011). Apart from short habitat surveys, a distribution survey and a post-monitoring project of animals rescued from the pet trade (Winarti 2003, 2011, Moore 2012, Wirdateti 2012, Nekaris et al. 2014a), no detailed long-term study on wild Javan slow lorises had been conducted until now.

This background leads to the two main aims of this thesis. I wanted to investigate the ecological function of venom in wild slow lorises by exploring intraspecific competition, predator avoidance and parasite defence in the Javan slow loris. Furthermore, I wanted to use the ecological data gathered, such as natural diet, habitat preferences, social system, predator avoidance and parasitology to assist in the development of conservation strategies and plans for slow lorises in captivity and in the wild.

The specific hypotheses of this project were:

- To explore the source of slow loris venom by collecting feeding data of at least ten wild Javan slow lorises, and examine the hypotheses:
    1) Slow loris brachial gland exudates and saliva, and subsequently their bite are not toxic/venomous (null hypothesis)
    2) Slow loris brachial gland exudates is produced ***de novo***
    3) Slow loris brachial gland exudate comes from components of the slow loris diet, such as secondary plant compounds and noxious prey

    The toxicity of slow loris bites and the possibility of production ***de novo*** are discussed in section 5.3, but not examined in the rest of the thesis.
- To explore the ecological function of slow loris venom by collecting ecological and behavioural data of at least ten wild Javan slow lorises and their potential predators for a full year, and analysing them in relation to four research hypotheses:
    0) Slow loris venom has no function (null hypothesis)
    1) Slow loris venom is used in intraspecific competition
    2) Slow loris venom plays a role in anti-predator strategies, as a venomous bite, concealment or deceit, or mimicry
    3) Slow loris venom is used to reduce (ecto-) parasite load

    Three more potential functions are intraspecific signalling (“perfuming”), prey capture and pre-digestive aid. These functions will be introduced in section 5.4, but are not examined in the rest of the thesis. Except for the null hypothesis the proposed functions are non-exclusive.

- To provide the first detailed behavioural and ecological data of wild Javan slow lorises for a full year
- To assess the distribution, abundance and conservation status of Javan slow lorises and to assess presence absence of the small- to medium-sized mammal fauna of Javan slow habitats by conducting forest surveys throughout Java. This can help to assess whether the Javan slow loris can act as a flagship, or even umbrella, species for conservation.
- To generate recommendations for conservation strategies and plans, and directions for future research, based on my findings
- To lay the foundation for the first long-term conservation and research field project on the Javan slow loris

2. Thesis structure

2.1 Framework and limitations

The PhD research was part of a project funded by the Leverhulme Trust received by AN in 2011, with the title "The only poisonous primates: ecological context and function of slow loris venom". Originally the PhD project aimed to (1) determine the composition of slow loris venom by determining if its components suggest the sequestration by noxious plants and (2) which (or what combination) of the hypotheses about the ecological function could be supported by the evidence, considering the behaviour and ecology of animals in the wild. Explicitly answering both questions required the analysis of the venom, including correlating the quantity or quality of venom with sex, age, season, variations in diet, predator presence, ectoparasite infestation and mating activities. To reach these goals, I collected samples of brachial gland exudate (BGE), saliva and faeces every three months during health checks of the slow lorises. While collection and storing of the samples worked well, I was not successful in gaining the final permits to export the samples to our collaborator Bryan Fry, at the University of Queensland, Australia, in time for the inclusion of results into the PhD dissertation. The inclusion of the data would have led to unpredictable and unacceptable delays in my thesis submission. The lack of export permits has led to a situation where results rely completely on field observations of the behaviour and ecology of the Javan slow loris, but not on chemical details of venom components and composition. Nevertheless, I have compiled information that gives preliminary clues about the ecological function of venom in slow lorises which can serve as a starting point for further field studies and complement conclusions drawn from ongoing behaviour experiments in captivity. The export of samples was recently successful (April 2015) and venom analyses will eventually be done by Bryan Fry. The analyses are planned for mid-2015, with results becoming available soon after, and publications planned in peer-reviewed journals depending on the quality of the results.

The conservation part of the project was tackled by integrating the ecological and behavioural research on venom use with a set of conservation activities in the field such as visiting schools. One of the major achievements of the overall project was to establish a field station for the long-term research and conservation project, the “Little Fireface Project” (LFP, Nekaris et al. 2012b) in the village Cipaganti, Garut regency, West Java (Figure 2.2). The field station included trained field staff, basic equipment and emphasised good relations with the local community. The (preliminary) results of the PhD research were also reported and presented to various Indonesian authorities, the research counterpart LIPI, the local community, two rescue centres that care for confiscated slow lorises, and various international scientific and conservation meetings and conferences.

2.2 Chapter Layout

This thesis consists of eight chapters. CHAPTER 1 is a general introduction in which I first state the aims. I then give a background of venom systems including the current definition of venom. I go on to describe the few extant venomous mammals, whose venom systems are not well known due to difficulties of studying them. Then I introduce the study species – the Javan slow loris – whose ecology has never been studied in the wild before. Next, I explain what is known about their venom system. Although a handful studies have been conducted on the composition of venom and their effects on laboratory animals, the adaptive significance of venom is far from being understood. I subsequently go through all potential ecological functions of slow loris venom and discuss whether according to the current state of knowledge they are likely to explain venom use in slow lorises. Finally I list conservation applications of this thesis. The general methods chapter (CHAPTER 2) first explains the framework of the project by providing a time-line, and introduce the study country and preparations of the field work. Secondly, it explains the field methods that were relevant for the subsequent chapters. CHAPTERS 3 to 7 of this thesis may refer back to this chapter in order to avoid repetition. CHAPTER 3 deals with the potential source of venom in slow lorises. It presents data on the diet of Javan slow lorises during the first months of the study and compares them to the few studies on wild animals of other slow loris species. I discuss whether secondary plant metabolites and noxious arthropods in the diet can be used for sequestration of venom. As direct observations and faecal samples were limited, I give information about noxious arthropods in the field site as potential prey items. As a general foundation, I also present data of the activity budget, social behaviour and habitat use. CHAPTER 4 explores the possibility that slow lorises use venom for intraspecific competition. I present the first study of the social system of the Javan slow loris, including information on their social organisation as inferred from ranging patterns, their mating system and their social structure, as well as characteristics of territoriality and social behaviour. I discuss whether the social system bears a high potential of sexual and non-sexual competition. In CHAPTER 5 I present data on the mammal community living in the Javan slow loris habitat, including potential predators, based on surveys throughout Java and long-term study site Cipaganti. This serves the purpose to discover which potential predator species coexist with Javan slow lorises in order to create a foundation for investigating the hypothesis that slow lorises use venom as predator defence. As predator-prey relations are difficult to study, the identification of further locations with respective species may assist future studies. Factors influencing the detection of species at study sites are presented. To give more information about small to medium sized carnivores and other mammals on Java, that in general are not well studied, I present data on their presence, distribution and behaviour. CHAPTER 6 further investigates the role that predator defence may play in the use of slow loris venom. In this chapter I explore the effect of lunar illumination and climate factors on the activity of the Javan slow loris. I examine whether the reaction to moon light can be explained by a predator avoidance strategy by looking at whether predators show a similar variation in reaction to those variables as slow lorises. CHAPTER 7 examines the potential ecological function of slow loris venom in (ecto-) parasite avoidance by looking at the prevalence and intensity of endo- and ectoparasites in Javan slow lorises. The parasitology of wild Javan slow lorises has not been reported so far. CHAPTER 8 provides the general discussion by summarising the likely roles that each of the hypothesised functions could play in slow loris ecology. I discuss the novelty and significance of my data, the contribution to the scientific body of knowledge and give recommendations for future projects. Finally, I integrate the conservation implications of my study, and give practical recommendations and future directions for the conservation of slow lorises, other mammal species and conservation project management in general.

3. Venom and its use in the animal kingdom

3.1 Definition

The widely accepted definition by Fry et al. (2009a,b, section 1) is based on biological function (section 3.3) that for example acknowledges that venom of specialized predators may be very target-specific (e.g. birds, Pawlak et al. 2006, 2009) or some native prey can become resistant to predator venom, and thus not show any reaction. The authors caution against a traditional, anthropocentric view of toxicity that acknowledges toxicity only if there is proof of medical significance or effects on humans or laboratory animals. As a result, the modern definition of venom also includes animal clades that have not previously been regarded as venomous by traditional definitions, such as the haematophagus clades fleas, ticks, leeches, and vampire bats (Low et al. 2013), whose venom does not kill prey but just facilitates feeding. Venom may thus also include anticoagulants as they disrupt normal physiological processes in the target animal.

3.2 The venom system

Components of the “venom system” are the venom delivery apparatus (VDA), the venom gland and the venom itself – the secreted toxins (Fry et al. 2009b). The VDA, the venom gland(s) including the connecting ducts and possible muscles involved in the delivery of the venom are referred to as the “venom delivery system” (VDS).

Venom is a highly complex mixture of bioactive compounds. These are combinations of proteins (ranging from multi-unit globular enzymes to small peptides), and may include other compounds such as salts, organic molecules, amino acids and neurotransmitters (Casewell et al. 2013, Fry et al. 2009a). Venom has evolved via the duplication of a gene encoding for a normal body protein that is usually involved in key regulatory processes or bioactivity (Casewell et al. 2013). The copy of the gene is then “recruited” by a selective expression in the venom gland (Fry et al. 2009a, 2012). Additional gene duplications may lead to neofunctionalisation (a new function is acquired) or subfunctionalisation (additional functions develop while the original function is retained, which buffers against deleterious effects and facilitates further mutations). The resulting multilocus gene families usually encode several toxins with many different functions and potencies (Wong & Belov 2012). Several protein groups have been convergently recruited in multiple animal lineages (reviewed in Fry et al. 2009a). Fry et al. (2012) give an overview of normal body protein type, their derived toxin classes, the function of the non-toxic normal physiological body proteins, the derived basal toxicity of the ancestral venom protein, and the toxicity of the final venom proteins in reptiles. Venom can be informally classified according to the effects of envenomation. Hematoxic venoms affect the cardiovascular system and heart and can cause haemolysis, disrupt blood clotting, further tissue damage and organ failure, as it breaks down proteins. It acts rather slowly, is often painful, and may also aid digestion. Neurotoxic venoms affect the nervous system and brain. They can block or activate ion channels and membrane receptors and cause paralysis, muscle weakness, epilepsy and cramps, reduced motor coordination, asphyxiation, followed by nausea, vomiting, diarrhoea, fever, headache, blurred vision, swollen lymph nodes, dizziness, and others. Cytotoxic venoms have more localized and cellular effects, such as necrosis and apoptosis with subsequent cell lysis, with symptoms such as local pain, swelling, blisters, or rashes (Sitprija & Suteparak 2008, Wong & Belov 2012). Envenomation can also lead to immunological responses such as allergic reactions and anaphylactic shock (Sitprija & Suteparak 2008). All types of venoms can lead to organ injury and death. As venoms are complex protein and enzyme cocktails they can cause more than one of the listed reactions. The composition and effect of venom on the target animal is related to the behavioural context (Casewell et al. 2013). Defensive venoms, like in echinoderm or fishes, cause immediate and extreme localized pain while predatory venoms are more variable in their composition and effect.

In the animal kingdom many different VDSs have evolved to facilitate the delivery of venom into the target animal. The VDA can be fangs, or modified teeth, spines, spurs, stingers, pincers, spays, and others (Smith & Wheeler 2006, Fry et al. 2009a, Casewell et al. 2013). For each VDA type a variety of forms may have evolved. Tooth morphology in reptiles ranges from ungrooved teeth with smooth surface, to teeth with grooves of different length and depth, to fully enclosed tubular venom canals (Jackson 2003, Fry et al. 2008). Venom glands can have a manifold of different positions in the body, can have several compartments (e.g. one per tooth) and are connected to the VDA either directly or via one or several ducts. All components of the venom glands, such as the gland itself, its compartments, ducts, and secretory epithelia can be of different types, sizes, length and location (Fry et al. 2008, Dugon & Wallace 2012). The dichotomous evolution of snakes and anguimorph lizards is demonstrated by the extensive diversification of maxillary venom glands in snakes, and the mandibular venom glands in lizards, while in some species other gland degenerated respectively (Fry et al. 2012). Specialised muscles may help to deliver venom quickly, and efficiency and speed are increased by venom gland compressor systems. Amongst vertebrates, the VDAs reach an extreme level of sophistication, efficiency and diversity (Jackson 2003).

3.3 The ecological function of venom

Venom can serve five different functions. Most commonly it helps in foraging or defending against predators, but also can assist in intraspecific conflicts (Casewell et al. 2013, Fry et al. 2009a,b, Whittington & Belov 2007, Wong & Below 2012). Venom thus perfectly fits the definition of a weapon. Venom functions are not mutually exclusive and therefore venom can have more than one function. Spitting cobras for instance are one of the rarer reptile species that use venom for both defensive purposes and prey capture (Arbuckle 2009). Some additional functions of venom can involve the facilitation of digestion or maintenance of oral hygiene (Blaylock 2000, Arbuckle 2009). Pit vipers feed on relatively large prey and their venom immobilizes and helps to digest.

3.4 Evolution of venomous animals

Venom has evolved multiple times independently by convergent evolution in the animal kingdom, and occurs in centipedes, cephalopods, echinoderms, cone snails, fish, several insect orders, scorpions, spiders, toxicoferan reptiles (lizards and snakes), sea anemones and even some mammals (Figure 1.1; Fry et al. 2009a,b, Wong & Belov 2012, Casewell et al. 2013). The most common ecological function of venom in the animal kingdom is prey acquisition (Caswell et al. 2013). Optimization of venom to prey is believed to be the strongest driver of adaptive selection (Casewell et al. 2013). The diversification of the monophyletic venomous reptile clade toxicofera is particularly well studied (Fry et al. 2005). This clade shows that the venom system can also be secondarily lost in evolution (Fry et al. 2009b, 2012), e.g. if snakes shift their prey capture technique to constriction or their prey type to defenceless prey such as eggs, worms or snails (Fry et al. 2008, 2009b, 2012). Differences in venoms between closely related species, populations, sexual differences in the same species, or even ontogenetic shifts within the same individuals can be explained by diet (Daltry et al. 1996, Andrade & Abe 1999, Mackessy et al. 2003, Guércio et al. 2006, Arbuckle 2009).

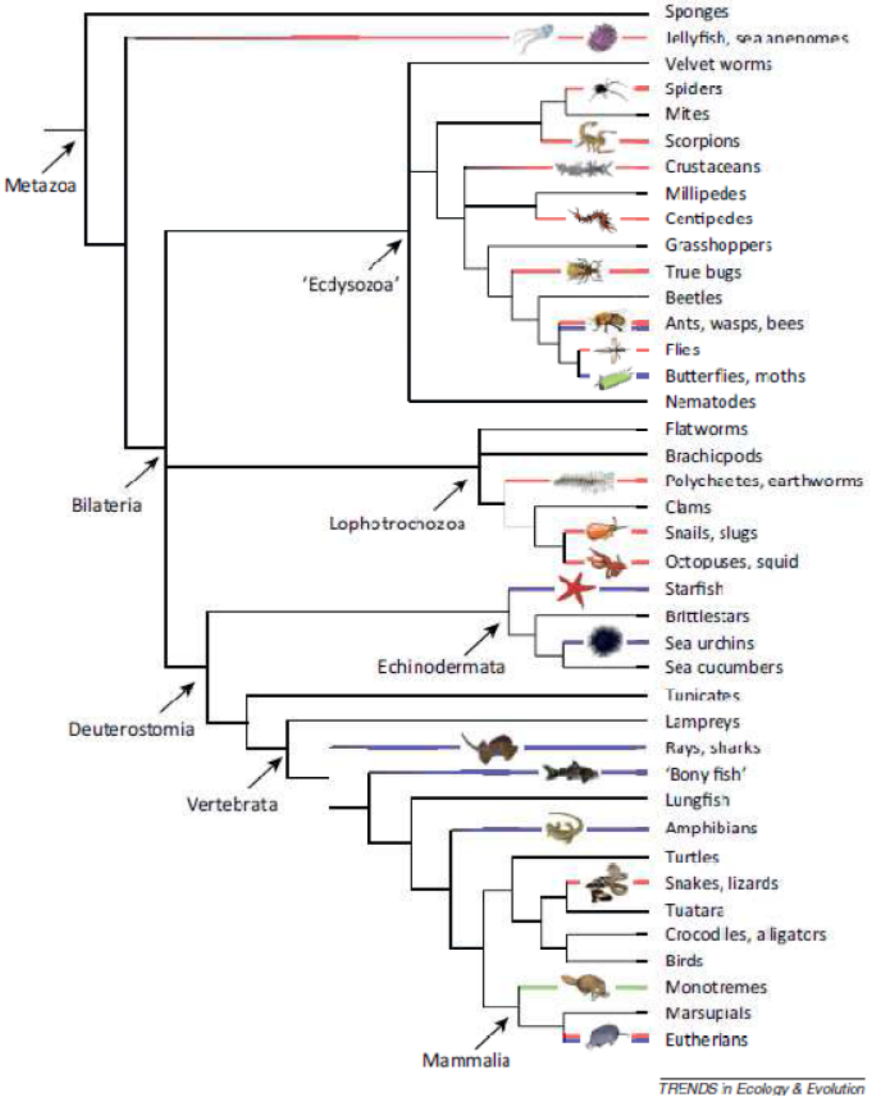


Figure 1.1: Schematic tree of venomous life in the animal kingdom. Coloured branches highlight major animal lineages that include members with venom systems and code for the ecological function. Red: prey capture. Blue: predator defence. Green: intraspecific competition (Figure reproduced from Casewell et al. 2013)

The energetic cost of venom synthesis and use leads to a certain level of venom economy in many species. In some rattlesnakes the amount of venom injected seems to depend on the size of the prey (Hayes et al. 1995) and the behavioural context (Young & Zahn 2001). The duration of venom flow, maximum venom flow rate and total venom volume in western diamondback rattlesnakes *Crotalus atrox* were all significantly lower in predatory than in defensive strikes (Young & Zahn 2001). Scorpions have evolved two kinds of venom that differ in the metabolic cost: an inexpensive pre-venom readily used in defensive low threat encounters, and more expensive, protein-rich main venom (Inceoglu et al. 2013, Nisani & Hayes 2011). Spiders meter venom by injecting more venom when intensity and duration of prey movement is high or high threat situations occur (Malli et al. 1999, Kuhn-Nentwig et al. 2004). The selection on venom and prey can be compared to evolutionary arms races (Dawkins & Krebs 1979) where the evolution of venom resistance in prey and novel venom compositions, production and metering in predators put reciprocal adaptive pressures on each other (Caswell et al. 2013).

Although the ecological function of predator defence is not regarded as highly adaptive especially if prey-predator encounters are infrequent or predators are taxonomically and physiologically diverse (Casewell et al. 2013), venom may shape the evolution in communities by offering protection of non-venomous, vulnerable species via mimicry. In Batesian mimicry the harmless species mimics a venomous or otherwise dangerous species (Balogh et al. 2008). Muellerian mimicry occurs where two or more harmful species mimic each other for the mutual benefit of being confused with each other and both gain protective advantages (Sherrat 2008).

3.5. The application of venom studies

The study of venom has interdisciplinary use. It can help in the discovery and development of pharmacological products (e. g. pain killers, anaesthetics, treatment of cardiovascular or autoimmune diseases, and others), the development of therapies, the study of protein functioning, and the study of evolution at community level (prey predator interactions), species level, and even molecular level (proteins) (Dufton 1992, Fry et al. 2008, Dutertre & Lewis 2010, Harrison et al. 2011, King 2011, Casewell et al. 2013). Due to the traditional definition of "venomous", and studies generally tend towards the well-known, more dangerous and dramatic species, the use of venom as a bio resource is still under-utilized (Fry et al. 2008, Low et al. 2013). Due to the closer phylogenetic relatedness the study of venomous mammals and primates is interesting and important for the understanding of protein functioning, and applications in medicine and pharmacy.

4. Venomous mammals

Venom systems in mammals (Table 1.1, Figure 1.2, primates in section 5) are relatively rare and comparatively little known. Although traditional folklore and myths point to the possibility of venomous mammals (Dufton 1992, Nekaris et al. 2013a, Nijman & Nekaris 2014), the venomous members of this animal class have long been neglected by scientists. Only the venom systems of the platypus, shrews and more recently slow lorises are studied more in detail (Dufton 1992, Ligabue-Brown et al. 2012). The question of why venom systems are so rare in mammals and whether they were more widespread in the earliest mammals, due to them being small and imperfectly homothermous with a selective pressure of high foraging efficiency, remains speculative. It is difficult to reconstruct soft tissue structure and function from bones and teeth (Orr et al. 2007). Two studies for instance claimed to have discovered venomous extinct mammals from the Pleistocene and late Palaeocene (*Beremendia*, *Bisonalveus browni* and an unidentified species). The assumption that these fossils were venomous was based on grooves running along their teeth, which potentially could aid in venom delivery as is common in snakes (Fox & Scott 2005, Cuenca-Bescós & Juan Rofes 2007). This conclusion was criticized by Folinsbee et al. (2007) and Orr et al. (2007) who showed that several non-venomous mammals have grooved teeth and most of the venomous mammals except for solenodons have non-grooved teeth. They explain the presence of grooves in mammals by structural support of teeth, e. g. as a form of tooth buttress, because the holes of grooves accommodate the sharp opposite teeth or general structural strength.

Table 1.1: Venomous mammals and their venom systems. PC = prey capture, IC = intraspecific competition, PD = predator defence

Order, family	English name	Scientific name	VDA	Venom gland position	Ecological function	References
Chiroptera, Phyllostomidae	Hairy-legged vampire bat, white-winged vampire bat, common vampire bat	*Diphylla ecaudata, Diaemus youngi, Desmodus rotundus*	Razor-like upper and lower incisors	Principal submaxillary gland	Facilitation of feeding	Low et al. 2013
Soricomorpha, Soricidae	American short-tailed Shrew, European water shrew, Mediterranean water shrew	*Blarina brevicauda, Neomys fodiens, N. anomalus*	Sharp and large incisors and canines	Significantly enlarged and granular submaxillary salivary glands	Unclear Possible: PC, prey immobilising agent, digestive aid	Tomasi et al. 1978, Martin 1981, Dufton 1992, Lopez-Jurado & Mateo 1996, Kita et al. 2004
Soricomorpha, Solenodontidae	Hispaniolan solenodon, Cuban solenodon	*Solenodon paradoxus, S. cubanus*	Enlarged and modified lower second incisors with almost tube-like deep groove	Submaxillary glands near base of the tubular lower second incisors	Unclear Possible: PC, IC	Folinsbee et al. 2007, Orr 2007
Monotremata, Ornithorhynchidae	Platypus	*Ornithorhynchus anatinus*	“Crural system”: hollow keratinised spurs on hindlegs connected by a duct to the venom gland	“Crural glands”: specialised venom glands in thigh area	IC (sexual competition during mating season), PD	Temple-Smith 1973, Grant & Temple-Smith 1998, Whittington & Belov 2007, Krause 2009
Primata, Lorisidae (section 5)	Slow and pygmy lorises	*Nycticebus* spp.	Needle-like toothcomb (incisors and canines of lower jaw)	“Brachial gland”: venom gland on the ventral side of the elbow; submaxillary saliva gland	Unclear Possible: PC, PD, IC and/or ectoparasite defence	Alterman 1995 , Krane et al. 2003, Hagey et al. 2007, Nekaris et al. 2013a

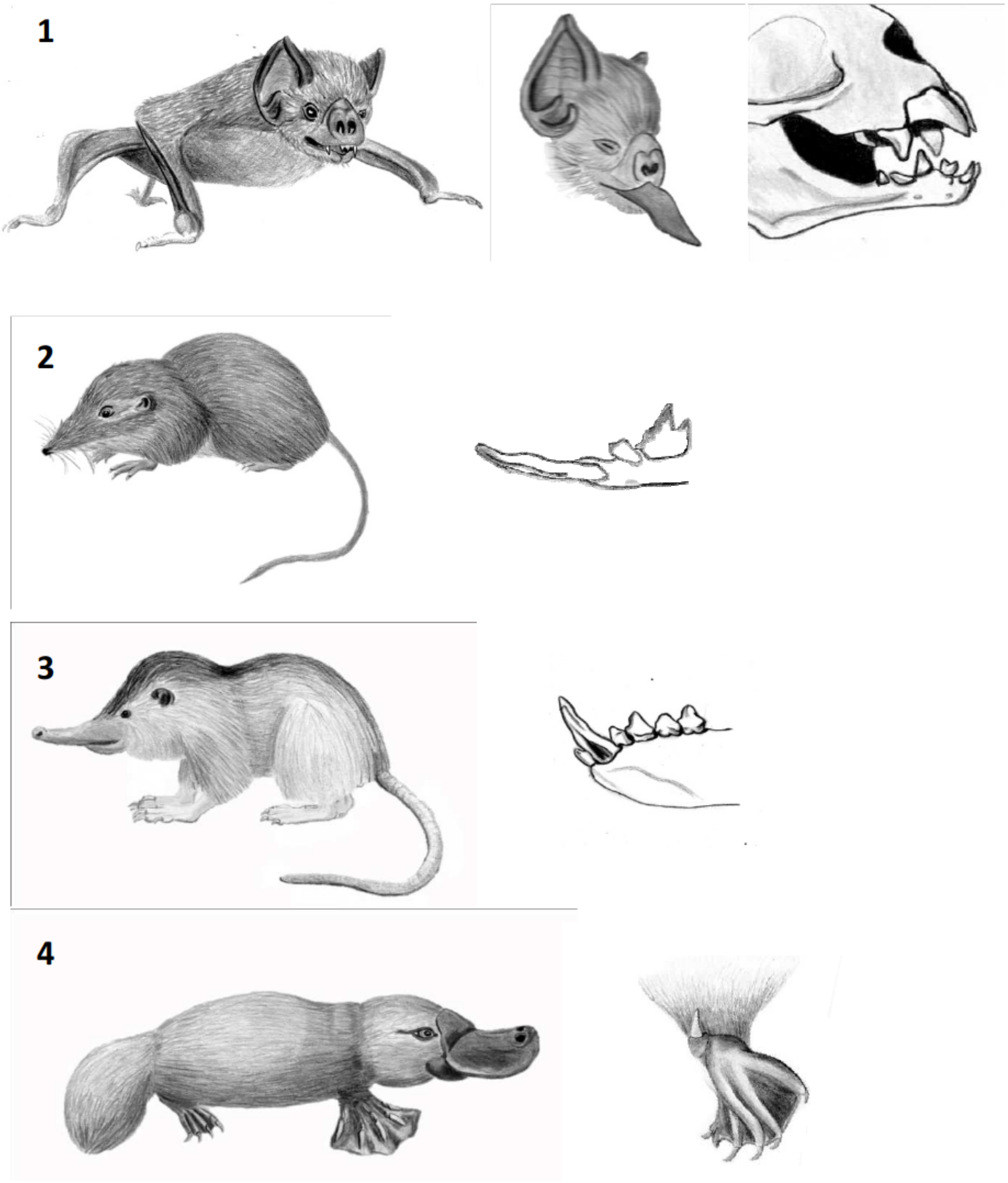


Figure 1.2: Venomous mammals and their venom systems: 1. Common vampire bat with tongue and specialized teeth; 2. European water shrew and teeth; 3. Hispaniolan solenodon and deeply grooved teeth; 4. Platypus with crural spur; 5a. Javan slow loris; 5b. Juvenile displaying defence position; 5c. Brachial gland (arrow); 5d. Toothcomb. All drawings by Kathleen Reinhardt, slow loris photos from Little Fireface Project (A. Walmsley, W. Tarniwan, M. Williams)

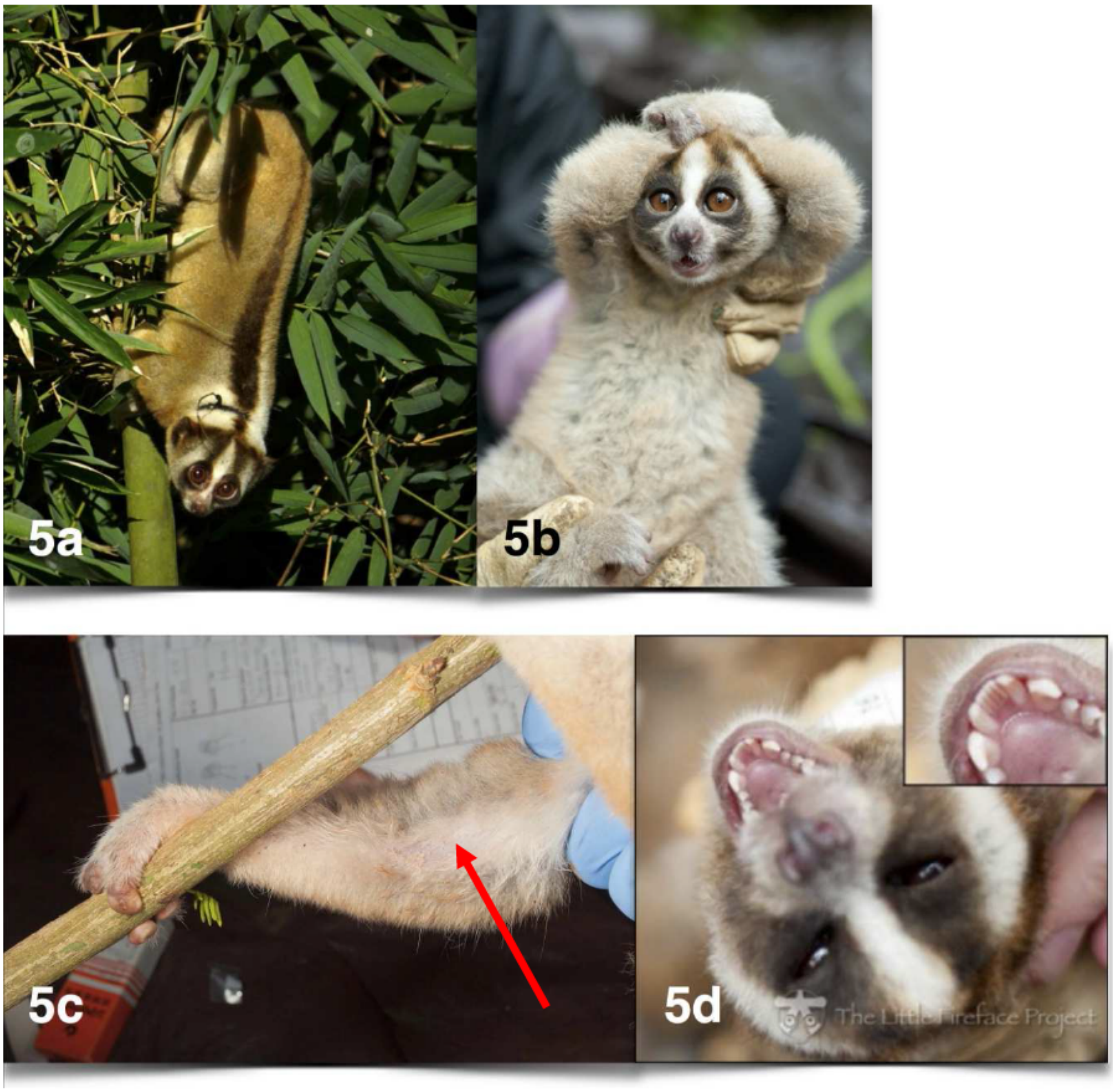


Figure 1.2: Continued

In only a few mammal species the venom components have been identified (American short-tailed shrew, platypus, slow loris [section 5]; Ligabue-Brown et al. 2012) and more studies are needed to confirm toxicity in other species. Although new protein characterisation techniques are available, laboratory tests are still restricted due to small quantities of available gland material, difficulties in maintaining animals in captivity, and the endangered and protected status of solenodons, slow lorises and platypuses (IUCN 2014). Finally, many older studies have tested venom on laboratory animals instead of natural prey species (Dufton 1992).

4.1 Chiroptera

Vampire bats belong to the subfamily Desmodotinae. They are highly specialized for a haematophagus lifestyle with sensory sensitivity to locate prey and the position of capillaries, and strong limbs for approaching prey on the ground (Greenhall & Smith 1988, Schondube et al. 2001). Their venom system has developed to serve the ecological function of feeding. A normal haemostatic response after a wound is inflicted would be the fast production of a fibrin clot that prevents further blood loss. The venom of vampire bats however possesses strong anticoagulant and proteolytic activity that delays blood clotting for several hours (Ligabue-Brown et al. 2012). The VDS consists of modified large and sharp incisors that inflict crater-like wounds to the prey animal, submaxillary venom glands and a tongue that darts in and out the wound and delivers venom from its sides (Greenhall & Smith 1988; Figure 1.2). The bat sucks the blood up through two ducts on either side of the tongue (Greenhall & Smith 1988). Target animals are usually cattle, horses, goats, pigs, sheep, or birds. Bats prefer sleeping prey and they approach them carefully. Their bite is described as painless. Target animals normally do not die. The relationship to the target animal is more that of a parasite that ensures the continuous survival of the host animal (Delpietro & Russo 2009). Prey animals develop an immune response with resistance to anticoagulants, with regularly exposed animals showing shorter blood-clotting and bleeding times (Delpietro & Russo 2009).

4.2 Eulipotyphla

Formerly known as Insectivora, this order includes three species of shrews and two species of solenodons and is the order with the greatest number of known venomous mammal species (Table 1.1). One of the toxic components of the venom of the American short-tailed shrew is the blarina toxin (BLTX), which can be extracted from the sublingual and submaxillary glands (Kita et al. 2004). This neurotoxic protein is responsible for the main effects on tested target animals (mice, rabbits, cats and insects) such as general depression, breathing disturbance, paralysis and convulsions, especially if injected intravenously (Tomasi 1978, Martin 1981, Dufton 1992, Kita et al. 2004). Similar effects have been observed for *Neomys* spp. and solenodon venom (Pucek 1968, Rabb 1958), but these toxins have not been purified yet. In all species the VDS involves enlarged and granular submaxillary glands where toxic saliva is produced. The animals inject the venom with their teeth. Shrews have sharp and large incisors and canines as typical for insectivores. The teeth are ungrooved but incisors have concave inner surfaces (Folinsbee et al. 2007). Solenodons in contrast possess lower enlarged canines that are deeply grooved (Folinsbee et al. 2007; Figure 1.2 [3]). In shrews the glands are ducted towards the front of the lower jaw (Dufton 1992), but in solenodons pockets hold the venom glands inferior to the base of the teeth (Folinsbee et al. 2007). There are still debates about the ecological function of venom in shrews and solenodons (Ligabue-Brown et al. 2012). Due to their small size and high metabolism shrews need constant food supply and consume more than their body weight within 24 hours (Dufton 1992). They are known to immobilise and cache their prey (especially earthworms, insects, snails, small mammals) for later consumption. This hoarding of alive but paralysed prey may especially be advantageous in cold seasons with infrequent and lower quantity or quality food supply (Martin 1981, Merrit 1986). Others state that the possession of venom would enable shrews to overcome larger prey by adding to their power to weight ratio (Dufton 1992, Furió et al. 2010). Although shrews are very fast and fierce hunters venomous bites in the occipital region of the head of fishes, frogs, mice and voles may help to save energy when overcoming such difficult prey (Dufton 1992). Due to the relatively high food intake in shrews, Dufton (1992) also discussed a possible digestive aid by venom. It is not yet clear if the tooth canals in solenodons have specifically evolved to facilitate venom injection or if they merely serve structural stability (Folinsbee et al. 2007). Finally, Rabb (1959) observed that Hispaniolan solenodons kept together in enclosures had high death rates despite the only visible wounds being bite marks by conspecifics on the feet. Thus, a function as a weapon in intraspecific competition cannot be ruled out for solenodons.

It is still unclear if the Canarian shrew *Crocidura canariensis* (Lopez-Jurado & Mateo 1996), the American shrew *Sorex cinereus*, and the European mole *Talpa europaea* are venomous (Lopez-Jurado & Mateo 1996, Ligabue-Brown et al. 2012). Lopez-Jurado and Mateo (1996) showed that Canarian shrews were able to paralyse lizards with their bites. Moles are known to cache paralysed worms in their burrows, similar to shrews, and have large and granular maxillary glands (Dufton 1992). These species have however not yet been tested for venom (Ligabue-Brown et al. 2012).

4.3 Monotremata

The platypus lives in fresh water rivers and streams at the east coast of Australia (Grant & Temple-Smith 1998). In adults, the VDS is only present in males that possess hollow keratinised spurs on their hindlegs that are connected to the venom-producing crural glands (Figure 1.2). Spurs and glands together are called the crural system. The spurs can be erected with the help of strong muscles and small articulating bones, and driven into the target animal (Grant 1995, Whittington & Belov 2007). To attack, animals wrap their hind legs around the target animal, drive their spurs into it and inject venom (Fenner et al. 1992). Spurs and muscles are so strong that extraction of the platypus by the victim is difficult. Both sexes are born with spurs, but females lose them during ontogeny (Grant 1995). Components of platypus venom are a complex mixture of peptide fractions and proteins (reviewed in Ligabue-Brown et al. 2012). Rabbits tested with platypus venom exhibited oedema, hypotension, respiratory problems and some individuals died (Kellaway & LeMessurier 1935, Martin & Tidswell 1895), while envenomated people describe intensive pain and swellings lasting for weeks or even months with no effect from pain killers such as morphine (Fenner et al. 1992). It is believed that the venom system has its function in sexual competition for females (Whittington & Belov 2007, Ligabue-Brown et al. 2012) as venom glands are only active in the mating season (Temple-Smith 1973). Males generally avoid each other and become highly territorial and aggressive during the mating season (Temple-Smith 1973). Platypus venom may also have defensive functions. When the platypus was still hunted for their fur, and still today, envenomation of people and (hunting) dogs occurs. The related long-beaked echidna (*Zaglossus* sp.) also has spurs like the platypus, but they cannot be erected (Wong et al. 2013). A milky substance is secreted in the breeding season, which may act as communication (Wong et al. 2013).

4.4 Arguably venomous species

The European hedgehog ***Erinaceus europaeus*** was suggested to anoint its spines with toxic saliva mixed with toad (*Bufo*) toxins as a predator defence strategy, but tests have not yet verify toxic substances (Brodie 1977, Dufton 1992, Mebs 1999). A very similar behaviour was recently described for the African crested rat ***Lophiomys imhausi*** (Kingdon et al. 2012). Animals chew roots and bark of poison arrow trees ***Acokanthera schimperi*** (Apocynaceae) trees and then apply the saliva onto their VDA that consists of specialised lateral-line hairs. The sponge-like structure of the hairs allows the saturation with toxic liquid aided by capillary forces. Upon being attacked, the animal parts a layer of long, covering hair with specialised muscles so that the toxin-loaded hair is exposed. Venom is likely to be the "ouabain" that can be extracted from the *Acokanthera* tree and is traditionally used in Africa for elephant hunting. The toxin seems to be effective in deterring predators like domestic dogs. The mucous membranes of dogs that try to bite an African crested rat come in contact with the rat's toxin-loaded hairs which can cause lack of coordination, mouth frothing and distress, but may even lead to collapse and death. Physiological effects include heart failure, defective blood-clotting and generalised internal bleeding. White blood cells with toxic granules were found. Venom in African crested rats would thus serve a predator defence function (Kingdon et al. 2012). As the definition of venom by Fry et al. (2009a) requires the production of venom by specialised tissue (gland), the African crested rat and the European hedgehog would not qualify as venomous animals, despite an effective venom delivery apparatus. They would thus hold a special position between truly venomous and poisonous animals. However, Kingdon et al. (2012) speculate that unusually large salivary glands may help to produce saliva that augments ouabain, and thus would play an active role in processing toxins.

5. Slow lorises and their venom system

5.1 The biology and ecology of slow lorises

Slow lorises belong to the primate infraorder Strepsirhini. Strepsirhine primates are united by the traits of having a moist nose, a single grooming claw on the second digit of each hind foot and a toothcomb that consists of the procumbent lower incisors and canines (Martin 1990, Nekaris & Bearder 2011). Strepsirhines are further divided into Lemuriformes and Lorisiformes. The only family of Lorisiformes is Lorisidae with three sub-families: Galaginae (***Galagoides*** spp., ***Galago*** spp., ***Euoticus*** spp., ***Sciurocheirus*** spp., ***Otolemur*** spp.), Perodicticinae (***Perodicticus*** spp., ***Arctocebus*** spp.), both occurring in Africa, and Lorisinae (***Loris*** spp., ***Nycticebus*** spp.), occurring in Asia (Rasmussen & Nekaris 1998, Grubb et al. 2003, Roos 2003, Nekaris & Bearder 2011). The sub-family Lorisinae includes the slender lorises ***Loris*** spp. with two recognised species and the slow lorises ***Nycticebus*** spp. with eight recognised species. The geographic range of slow lorises and their IUCN Red List status are listed in Table 1.2 and Figure 1.3.

Table 1.2: Overview of the currently recognized eight species of slow loris, their geographic range and their IUCN Red List status (IUCN 2014)

Species	Common name	Authority	Body mass (wild)	Geographic range	IUCN Red List status
Nycticebus bancanus	Sody's slow loris	Lyon 1906	?	Indonesia (Bangka, Belitung)	Not assessed
Nycticebus bengalensis	Bengal slow loris	Lacépède, 1800	1140-2100	Bangladesh, Burma, Bhutan, Cambodia, China, India, Laos, Thailand, Vietnam	Vulnerable A2acd+3cd+4acd, trend decreasing
Nycticebus borneanus	Bornean slow loris	Lyon 1906	360-580	Indonesia (Borneo)	Not assessed
Nycticebus coucang	Greater slow loris	Boddaert, 1785	635-850	Indonesia (Sumatra, peninsular Malaysia, Thailand, Singapore	Vulnerable A2cd, trend decreasing
Nycticebus javanicus	Javan slow loris	Geoffroy, 1812	750-1150	Indonesia (Java)	Critically Endangered A2cd+4cd, trend decreasing
Nycticebus kayan	Kayan slow loris	Munds et al. 2013a	500-700	Indonesia (Borneo), Malaysia (Borneo)	Not assessed
Nycticebus menagensis	Philippine slow loris	Lydekker 1893	265-800	Brunei, Indonesia, Malaysia, Philippines	Vulnerable A2cd+3cd, trend decreasing
Nycticebus pygmaeus	Pygmy loris	Bonhote, 1907	360-580	Cambodia, China, Laos, Vietnam	Vulnerable A2cd, trend decreasing

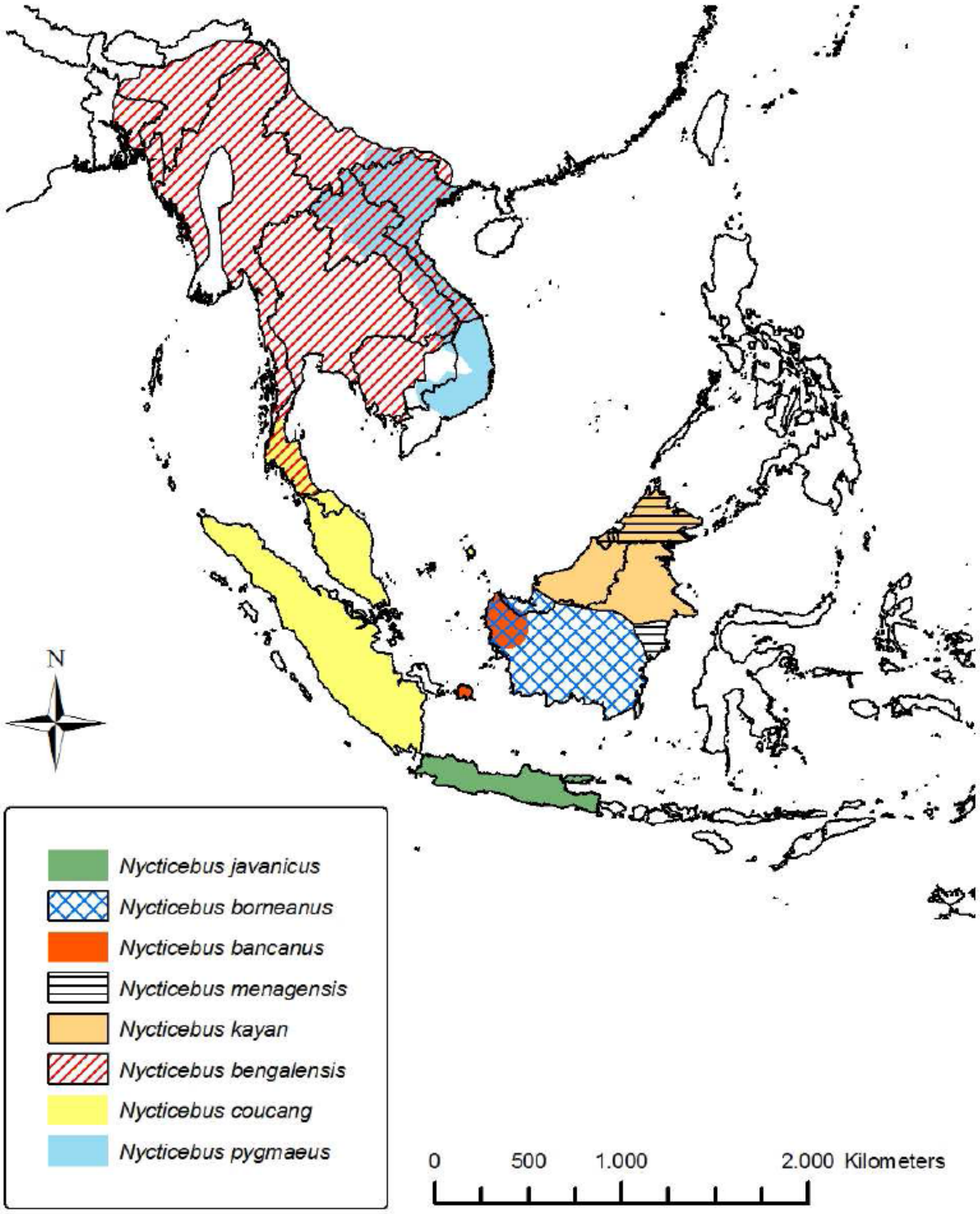


Figure 1.3: Geographic distribution of currently eight recognized species of slow loris *Nycticebus*. The shown distribution on Borneo is based on museum specimens (Munds et al. 2013a) and exact distribution and sympatric overlap still needs to be refined. Map produced with shapefiles from IUCN (2014), adapted to the current knowledge of species distribution of Bornean species (Munds et al. 2013a) and Javan slow loris (Voskamp et al. 2014, this study).

In contrast to the gracile slender lorises (*Loris* spp.) slow lorises are more robust (Nekaris & Bearder 2011). All Lorisinae species move rather deliberately and smoothly. Although animals spend most of their time in trees they are able to cross between disconnected trees on the ground (Wiens 2002, Appendix 4, section 6). They can speed up considerably when walking and climbing but cannot leap. Instead they bridge canopy gaps by cantilevering (Walker 1969, Ishida et al. 1992, Sellers 1996, Nekaris & Stevens 2007). Their hands and feet are highly adapted to suit the arboreal lifestyle, with high grasping force, reduced manual second digits and specialized vascular bundles that allows blood flow during extended periods of immobility (*retia mirabilia*) (Hill 1953, Gebo 1986, O'Dea 1990, Rasmussen & Nekaris 1998). The latter helps to ensure the availability of nutrients and oxygen in the limbs when circulation is restricted due to lengthy muscular contractions (O'Dea 1990). Additionally, cooling effects of the vascular bundles may reduce the requirement for oxygen and nutrients in the limb tissues, especially important for mammal species in colder climates where the metabolic cost of warming the limbs are further reduced this way (O'Dea 1990). 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 loris occurs, can be close to freezing (Streicher 2004). Slow lorises weigh between app. 300g and 2 kg, have a short muzzle, large forward-facing eyes, small ears, and the tail is short or absent (Martin 1990, Nekaris & Bearder 2011). Like all other strepsirhine primates except the Tarsier *Tarsius* spp., slow lorises possess the *tapetum lucidum*, an extra layer in the retina that improves the animal's ability to see at night and causes the orange reflection of the eyes when an external light is directed towards the animal (Fleagle 2013). The coat pattern includes a dorsal stripe and a typical fork-shaped facial pattern that varies between species. The Javan slow loris (Figure 1.2 and CHAPTER 2 Figure 2.5) usually has thick fur with dark markings, including a black dorsal stripe that is enclosed by a whitish lateral stripe, a distinct white diamond between the eyes extending to the forehead and circumocular patches extending to the cheeks (Nekaris & Jaffe 2007).

Nekaris and Bearder (2011) have reviewed numerous studies about the life history and reproduction of slow lorises in captivity (Ehrlich & Musicant 1977, Rasmussen 1986, Rasmussen & Izard 1988, Ehrlich & Macbride 1989, Nash 1993, Weisenseel et al. 1998, Fitch-Snyder & Schulze 2001, Fitch-Snyder & Ehrlich 2003, Fuller et al. 2014). Most slow lorises give birth to singletons, but pygmy slow lorises often have twins (Weisenseel et al. 1998). In contrast to the other slow lorises, in captivity pygmy lorises reproduce strictly seasonally with a mating peak in July and September and most births occurring in February and March (Jurke et al. 1997, Fitch-Snyder & Jurke 2003, Streicher 2004). Newborns of slow lorises are tiny and depend entirely on the mother. Like in all Lorisinae (Ehrlich 1974, Charles-Dominique 1977, Rasmussen 1986, Zimmermann 1989, Nekaris 2000, Nekaris & Bearder 2011) slow lorises are parked during the night when the mother is foraging actively (Fitch-Snyder & Schulze 2001, Nekaris & Bearder 2011). They can be parked from the first day on, with the duration of time being parked gradually increasing (Fitch-Snyder & Schulze 2001). Slow lorises have among the longest life histories of all primates for their body size with long interbirth intervals, gestation and lactation periods, and offspring dependency (Rasmussen & Izard 1988, Martin 1990). Stud books exist for captive populations of greater and pygmy slow lorises, while other slow loris species are rarely held in captivity. Although the highest age recorded for slow lorises in captivity are 22 and 24.5 years for pygmy and greater slow lorises respectively, mean age at death is considerably lower at 6.5 and 9.5 years (Fuller et al. 2014). This emphasises the difficulty to keep these animals in captivity (Nekaris & Campbell 2012, Fuller et al. 2014) and leads to the assumption that maximum ages recorded are extremes and longevity in the wild is considerably lower.

Although slow lorises generally seem to rely on forested habitat they are found in various habitats such as disturbed forests, relatively open savannah grasslands, forest plantations and rural agriculture areas (Wiens 2002, Nekaris et al. 2009, Nekaris & Bearder 2011, Rogers & Nekaris 2011, CHAPTER 3). Bamboo seems to play a role for the suitability of habitat (Voskamp et al. 2014), especially as animals seem to require dense vegetation for their sleeping sites (Winarti 2003, 2011, Dahrudin & Wirdateti 2008, Rogers & Nekaris 2011).

Slow lorises occur at altitudes of up to 1700m ASL (Nekaris et al. 2014a). With very low encounter rates of 0.02 to 0.20 animals per km (Nekaris et al. 2008, Nekaris & Nijman 2008, Winarti 2008), Javan slow lorises fit into the generally low encounter rates found for slow lorises (Nekaris et al. 2008). Others have found that encounter rates are highly variable (Nekaris et al. 2014a, Voskamp et al. 2014).

Until the beginning of the new millennium detailed studies on slow lorises were restricted to animals in captivity. Since then the interest in slow lorises has increased, with numerous published studies on wild animals, investigating the distribution, abundance and habitat use (e. g. Wiens 2002, Winarti 2003, 2011, Wiens & Zitzmann 2003, Streicher 2004, Radhakrishna et al. 2006, 2010, Wiens et al. 2006, Collins 2007, Swapna 2008, Swapna et al. 2008, 2010, Das et al. 2009, 2014, Pliosungnoen et al. 2010, Rogers & Nekaris 2011, Starr 2011, Starr et al. 2011, Moore 2012, Wirdateti 2012, Lehtinen 2013, Munds et al. 2013b, Starr & Nekaris 2013, Streicher et al. 2013, Nekaris et al. 2014a, Voskamp et al. 2014, this study). Until now however, only one long-term radio-tracking study had been conducted on wild slow lorises, focusing on greater slow lorises in West Malaysia (Wiens 2002). Three further radio-tracking studies in natural habitat have been conducted on reintroduced, previously rescued pygmy slow lorises in Vietnam (Streicher 2004, Kenyon et al. 2014) and Javan slow lorises in West Java (Moore 2012).

5.2 Venom system in slow lorises

My null hypothesis is that the brachial gland exudates and the saliva of slow lorises are not toxic and thus its bite not venomous. Various research (Alterman 1995, Krane et al. 2003, Hagey et al. 2007) and reports from slow loris bites (Wilde 1972, Medani & Nekaris 2014) show however that in deed slow lorises are the only primates known to be venomous. The VDS consists of the brachial gland that is located in a relatively hair-free, slightly raised area in the flexor region of the elbow (Hagey et al. 2007), and the needle-like toothcomb (Figure 1.2 [5cd]). When threatened, the slow loris can "charge" its VDA by quickly raising its arms over the head and combing BGE with saliva (Hagey et al. 2007). The toothcomb is believed to aid in feeding and grooming (Nekaris & Bearder 2011) but has been shown to allow venom to travel upwards to the tip of the tooth by capillary forces and thus aid venom delivery (Alterman 1995).

In the first study of slow loris venom composition, Alterman (1995) injected BGE extracted with formid acid into mice, resulting in 2 of 10 slow lorises had lethal bites, and with methylene chloride, resulting in four of seven slow lorises being lethal to mice. When he incubated BGE with saliva, all mice died. He suggested that the toxic protein in the BGE must be activated by enzymes in the saliva. This two-stage venom would be unique in vertebrates. Krane et al. (2003) extracted BGE from a single captive animal, probably Bengal slow loris ***N. bengalensis***, and used high performance liquid chromatography to identify organic compounds in the venom sample. They found that the BGE protein had a high sequence similarity to the cat allergen Fel-d1 and suggested that the similarity to an allergen might explain the variable reactions to slow loris bites in humans. Hagey et al. (2007) further examined this major component and identified it as a new member of the secretoglobin family. Secretoglobins are only found in mammals, especially in their secretions such as saliva, but also fluids of the lung, prostate or uterus (Jackson et al. 2011). Biological activities include immune response, tissue repair and cell signalling, while in mice they play a role in mate selection via the coding for androgen-binding proteins (Jackson et al. 2011). This heterodimeric BGE protein with 17.6 kDa has an α-chain and a β-chain that have high sequence similarity with the two chains of Fel-d1, as suggested by Krane et al. (2003). All three slow lorises species tested (greater slow loris, Bengal slow loris, pygmy slow loris) have two protein isoforms (Krane et al. 2003, Hagey et al. 2007). Wounds inflicted from slow loris bites are very painful, slow healing, can cause oedema, local loss of feeling, fester, and leave scarring and loss of fur (Wilde 1972, Streicher 2004, Klotz et al. 2009). Reactions in humans range from little effects to severe anaphylactic shock, including hypotension, tachycardia, backache, poor organ perfusion and peripheral shut down that may even lead to death (Wilde 1972, Nekaris et al. 2013a, Madani & Nekaris 2014).

5.3 The source of venom

I have proposed two hypotheses that would explain how toxicity in slow lorises is acquired. Toxins in both poisonous and venomous species can be either synthesised by the animal itself (*de novo*) or sequestered from other plant or animal sources (Daly et al. 1994, Daly 1995, Hutchinson 2007). Sequestration is informally defined as “the deposition of secondary phytochemicals into specialised tissues or glands of an insect” (Duffey 1980, p. 447). The word sequester however is also used for higher trophic levels, such as the sequestration of arthropod chemicals into tissues or glands of arthropod-feeding animals (Daly 1995).

Most plant families produce secondary metabolites as defence against herbivores, to either become toxic or to reduce digestibility (Glander 1982, Opitz & Mueller 2009). Some plant-feeding animals such as many arthropods developed different adaptations to deal with plant defences. They can either avoid feeding on toxic plant parts, their guts may be impermeable for the toxins which are quickly excreted, they may detoxify toxins with the help of specialised metabolic mechanisms or microorganisms, they may tolerate toxins, or they may accumulate, modify or concentrate toxins for their own benefit (reviewed in Opitz & Mueller 2009). The same is possible at higher trophic levels. Species that sequester chemical compounds usually use them against predators or as antimicrobials (Daly 1995). The terms “noxious” and “poisonous” describe the extremes of a continuum dependent on the effect of the stored chemicals ranging from slightly irritating to lethal. Arthropods have been reported to sequester compounds from a number of plant families, such as Fabaceae (Wiens et al. 2006, Ortitz & Mueller 2009). Many plant parts that form components of primates’ diets such as leaves, plant exudates (gum, sap, resin) or nectar may contain secondary metabolites (Bearder & Martin 1980, Glander 1982, Nekaris et al. 2010a). As will be reported in CHAPTER 3, the main diet of slow lorises comprises gum and nectar; for the Javan slow loris these are exclusively from Fabaceae species. Glucose in sugary diets such as nectar can help primates to detoxify secondary plant compounds (Smith 2010), and may sustain the combination of gum and nectar feeding in slow lorises.

A second route of sequestration of toxins for slow lorises would be via the ingestion of noxious arthropods. This route has been well studied for many amphibians such as dendrobatids (poison-dart frogs) that sequester toxins from a variety of alkaloid-containing arthropods such as myrmicine ants, mites, occinellid beetles or siphonotid millipedes (Dumbacher et al. 2004, Saporito et al. 2004, 2007, 2009, 2012), and other amphibians including toads and salamanders (reviewed in Daly 1995). Other vertebrate classes also sequester toxins, such as pitohui birds (***Pitohui*** sp.), which, like frogs, sequester toxins of the batrachotoxin family from melyrid beetles (genus ***Choresine***, family Melyridae) (Dumbacher et al. 2009), or the Asian tiger snake species ***Rhabdophis tigrinus*** that sequesters toxins from toads (Hutchinson et al. 2012). Coleoptera, Lepidoptera, Heteroptera, Hymenoptera, Orthoptera and Sternorrhyncha predominantly sequester secondary plant exudates (reviewed in Opitz & Mueller 2009) and can, together with other noxious or toxic arthropods like millipedes, centipedes and spiders, serve as sources for venom sequestration in slow lorises. The sympatric occurrence of noxious members of these taxa with slow lorises is reported in CHAPTER 3.

If toxins are sequestered from noxious animals or plants instead of produced ***de novo*** there should be variation in toxin quantity and quality between species, populations and even individuals due to geographically different availability of toxin sources (Daly et al. 1992, Dumbacher et al. 2004, 2009), which is the case for pitohuis (Dumbacher et al. 2009). Dendrobatid frogs raised in captivity on crickets and fruit flies for example do not produce detectable skin alkaloids (Daly et al. 1992).

Toxic substances in poisonous or venomous animals may even be a combination of sequestered and synthesised toxins. While amines, peptides, proteins and steroids stored in the granual skin glands of amphibians and serve predator or microbial defence functions, are produced ***de novo***, alkaloids such as batrachotoxins in poison arrow frogs are sequestered (Daly 1995). Slow lorises thus may synthesise some components of their venom but sequester others. As opposed to ***de novo*** production of toxin, toxicity acquired from the uptake of secondary metabolites such as alkaloids from arthropods or plants varies according to the nature and availability of those items. The variation in human response to loris bites indicates that at least some parts of the venom in slow lorises may be sequestered. Just as in poison dart frogs, slow lorises in captivity do not seem to be (that) venomous, possibly due to the lack of natural diet. So far a combination of protection and conservation status of slow lorises and strict export permits have prohibited detailed examination of all body tissue and a higher sample size that could show clear seasonal, age-related, geographical or other variations.

5.4 Ecological function of slow loris venom

Although several hypotheses have been proposed to explain the ecological function of slow loris venom, and this and related studies led by AN have revealed hints, the exact function still remains unsolved. The six hypotheses proposed are the following.

0) Slow loris venom has no function (null hypothesis)

Slow lorises use venom:

a) to compete with conspecifics (CHAPTER 4)
b) as intraspecific signalling (“perfuming”) (not studied in this thesis)
c) to avoid or defend predators (CHAPTER 5 and 6)
d) to avoid or defend (ecto-) parasites (CHAPTER 7)
e) capture prey (not studied in this thesis)
f) as pre-digestive aid (not studied in this thesis)

a) Intraspecific competition

There are only a few species that are reported to use venom in intraspecific competition (CHAPTER 4). Bite wounds are very common in the wild, captivity (zoos and recue centres) and wildlife markets. While in captivity and markets bites must stem from conspecifics, in the wild may also result from predator attacks. However, as I have never observed a predator attack during 14 months of field work, indicating the rarity of predation events, and the characteristics of bites point to conspecifics (Wiens 2002), most of the wounds are likely to stem from other slow lorises. Bites are followed severe health consequences such as necrosis, septicaemia, pulmonary oedema, cellulitis, that are chronically non-healing and often lead to death (Sutherland-Smith & Stalis 2001, Wiens et al. 2006, Fuller et al. 2014, Nekaris et al. 2013a). Slow lorises seem to be territorial (Nekaris & Bearder 2011). The anaphylactic shock in a human reported by Wilde (1972) followed after the owner wanted to separate two fighting lorises. Although animals are usually relatively peaceful with low frequencies of agonistic encounters (Ehrlich & Musicant

1977, Wiens & Zitzmann 2003, Nekaris et al. 2013a), males seem to compete intensively for mating opportunities (Nekaris et al. 2013a). Males seem to anoint themselves before and during these agonistic encounters (Nekaris et al. 2013a). Hagey et al. (2007) found that the BGE is a unique and complex oil and contains more than 68 (Bengal slow loris) and 200 (pygmy loris) volatile and semi-volatile components and proposed the function to be a warning signal for conspecifics.

b) Intraspecific signalling

Olfactory signalling is used in intrasexual competition and intersexual mate choice in many primates (Heymann 2006). In order to be effective in intraspecific communication, the odors must bear an individual signature (Knapp et al 2006). Many studies show that profiles of scent markings by urine, saliva or special scent glands can code for individuals, sex, age, nutritional status, health, dominance of the sender, group identity and kin recognition (Charles-Dominique 1977, Clark 1982a,b, Scordato et al. 2007, Fisher et al. 2003a,b, Colquhoun 2011). At least some olfactory cues are determined by the individual's genes of the major histocompatibility complex (MHC). Knapp et al. (2006) showed that for instance in Ring-tailed lemurs (***Lemur catta***), a lemur species that possesses highly developed scent glands and adopts a variety of scent-marking displays (Scordato et al. 2007), there is a relationship between the highly variable MHC and concentrations of volatile compounds. The high number of volatile and semi-volatile compounds in slow loris BGE could similarly code for detailed information of the sender and thus aid in social communication (Hagey et al. 2007). The planned analysis of BGE and saliva gland samples by using gas chromatography and mass spectrometry will expand on the findings of Hagey et al. (2007) and maybe showing a relationship between details of the sender and combinations and concentrations of the glands' volatile compounds.

c) Predator avoidance

Although slow lorises can walk and climb relatively quickly, they cannot rely on hasty escape like other more agile species, because they cannot leap (Crompton et al. 1993, Nekaris & Bearder 2011) and have a slow metabolism of only 40 % of the predicted basal metabolic rate for eutherian mammals, which is comparable to sloths (Whittow et al. 1977, Mueller 1997). Instead, slow lorises avoid predators by crypsis (Charles-Dominique 1977, Nekaris et al. 2007). They possess morphological adaptation that allows them to remain still for long times such as highly mobile wrists and ankles, or ***retia mirabilia,*** a special network of arteries in arms and legs that ensure the exchange of oxygen and waste material even when the animal is not moving (Whittow et al. 1977, Mueller 1979, Nekaris & Bearder 2011). The fur colouration and the dorsal stripe in slow lorises provide camouflage on tree trunks (Nekaris et al. 2010a). An additional defensive feature such as venom would be advantageous. Several effects are possible. It was suggested that slow lorises use venom directly against predators by biting (Alterman 1995), or indirectly by warning conspecifics through the smell of increased BGE secretion, by deterring predators with olfactory cues in the slow loris' gland exudates (Muellerian mimicry) (Hagey et al. 2007) or by anointing to conceal adults and their offspring (olfactory crypsis) (Alterman 1995). The latter two would especially be useful in cold weather periods and periods of food scarcity when animals go into torpor (Streicher 2004). Slow loris mother also park their young from the age of six weeks while foraging during the night (Ehrlich & MacBride 1989, Nekaris & Bearder 2011). The anointment could repel predators (Alterman 1995). This repellent effect could be due to a smell advertising unpalatability, a camouflaging smell or even a chemical warning signal of the actual venom. Many species chew plant material with secondary metabolites and rub it on their fur (Weldon 2004, Clucas et al. 2008), or ingest material and accumulate toxins in their skin, fur or feathers to make themselves unpalatable (pitohui: Dumbacher et al. 2009; poison dart frogs: Dumbacher et al. 2004, Saporito et al. 2012; rough-skinned newt ***Taricha granulose***: Williams et al. 2003). As toxins in many animals are acquired from secondary metabolites in natural food plants and arthropods that may not be available to animals in captivity, this mechanism may not be detectable ***ex situ*** (e.g. poison dart frogs: Dumbacher et al. 2004, Saporito et al. 2012). Ground squirrels (***Spermophilus beecheyi***, ***S. variegates***) are reported to chew snake skins of their major predator, rattlesnakes ***Crotalus*** spp., and anoint themselves to deter exactly these (Clucas et al. 2008). Females and juveniles engaged in longer application bouts than males (Clucas et al. 2008). In the typical defence position, slow lorises also smear the strong smelling, clear and oily BGE to their heads and necks.

Although Nekaris et al. (2013a) only observed one event where a mother anointed a parked infant in 18 months of field observation, the prediction that the venom would at least repel olfactory-oriented predator species seems to be supported. In behavioural experiments, the mix of BGE and saliva effectively repelled cats (leopard ***Panthera pardis***, tiger ***P. tigris***, clouded leopard ***Neofelis nebulosa***), sun bears (***Helarctos malayanus***) and civets (common palm civet ***Paradoxurus hemaphroditus***, binturong ***Arctitis binturong***); but has not repelled visually-oriented Bornean orangutans ***Pongo pygmaeus*** (Alterman 1995, Nekaris et al. 2013a). Slow lorises show little or no response to potential predators such as olfactory-oriented common palm civets and leopard cats which suggests a lack of concern by adult and young slow lorises that move in close distance of less than 5 meters of the predators (CHAPTER 6).

Confirmed predators only include orangutans ***Pongo*** spp. (Utami & van Hooff 1997), snakes (Wiens & Zitzmann 1999), hawk eagles (Hagey et al. 2007) and monitor lizard ***Varanus*** spp. (Kenyon et al. 2014). While orangutans are visually-oriented and raptors have a weak sense of smell, snakes and monitor lizards have a good sense of smell due to the vomeronasal or Jacobson's organ. The hypothesis that visually-oriented predators are not or less affected by slow loris venom as compared to olfactory-oriented predators should be examined further in behavioural experiments.

In support of the hypothesis of protection of parked and defenceless young, severe reactions of humans bitten by juvenile slow lorises have been reported. The account of a herpetologist reveals that he had a severe anaphylactic shock upon a bite of a slow loris juvenile, with extreme swellings in the face, hypotension and other typical allergic reactions (Madani & Nekaris 2014). All immature slow lorises that were captured in this study had a certain amount of venom secretion visible (CHAPTER 4).

Casewell et al. (2013) question the adaptive significance of venom as a predator defence strategy if predator encounters are relatively rare and predators diverse. Nekaris et al. (2013a) postulate that the evolution of venom may have been an adaptive strategy against predators used by slow lorises as a form of Muellerian mimicry with spectacled cobras. Muellerian mimicry traditionally is defined as a convergent resemblance between two defended species (Sherratt 2008, Balogh et al. 2009). During the Miocene, when both slow lorises and cobras migrated throughout Southeast Asia, land bridges formed between Africa and Asia, and drier and seasonal woodland, and savannah-like landscapes occurred (Heaney 1991, Voris 2000, Bird et al. 2005). Although arboreal, slow lorises can and do venture to the ground to travel considerable distances if no other arboreal alternative are available (Rogers & Nekaris 2011, Wiens & Zitzmann 1999). This can be seen especially in lorises that live in savannah-like or open agricultural landscapes (Wiens & Zitzmann 2003, CHAPTER 3). This situation has made the animals vulnerable, especially to aerial predators. Consequently predation pressure may have favoured the development of snakelike features as a form of Muellerian mimicry: slow lorises possess extra vertebra in the spine permitting to snake-like movement, a long dark dorsal stripe that increases this appearance from above, have aggressive vocalisations (pant-growl) that resemble cobra-hisses (in slender loris), facial markings that reminiscent of the eye-spots of spectacled cobras, and the possession of venom (Elliot & Elliot 1967, Shapiro et al. 2001, Daschbach et al. 1981, Zimmermann 1985, Nekaris & Bearder 2011). Although mimicry is rare in vertebrates (especially mammals) compared to invertebrates (Pough et al. 1988), this combination of aposematic, auditory and possibly olfactory similarity may have given slow lorises an adaptive advantage. Whether the venom was included in the first set of mimicry traits, or just as an olfactory signal without toxic compounds, remains speculative. There is a continuous mimicry spectrum between extreme forms of Batesian mimicry (a harmless species mimicking a defended species) and Muellerian mimicry (both species are defended) (Balogh 2008). Furthermore, Sherratt (2008) suggests that not all Muellerian forms of mimicry are mutualistic relationships, as the rarer species often is the benefiting one.

d) (Ecto-) Parasite avoidance and defence

Ectoparasites negatively affect success in reproduction and survival (Combes 2001). While in gregarious primates grooming functions to reduce parasite load (Spruijt et al. 1992), species that have solitary or dispersed social organisations lack this service by conspecifics and individuals are not able to clean their fur in inaccessible body regions (Douglas 2008). This is especially the case when species like slow lorises go into solitary torpor or park their young during active foraging periods. Many species reduce parasite load with the help of secondary metabolites (Forbey et al. 2009). Several bird and mammal species including primates are known for anting (letting ants walk over their fur or plumage) or anointing themselves with other plants and animals (e.g. millipedes, lime fruits ***Citrus***, leaves and stems of vines, resins) which have bioactive compounds (reviewed in Huffman 1997, Lozano 1998, Forbey et al. 2009). Many species first chew plant parts to release the active compounds and mix them with saliva for easier application. These treatments are believed to have an antiparasitic effect (Huffman 1997). Several bird species are known to add fresh leaves with insecticidal and antibacterial properties into their nests (Lozano 1998).

The venom of slow lorises may have a similar repellent effect on ectoparasites (Nekaris et al. 2013a). Prevalence and intensity of ectoparasite infestation among Lorisidae is extremely low compared to other primates (Rode & Nekaris 2012). While eight of nine wild studies of six taxa revealed no or very few ectoparasites (slender lorises ***Loris tardigradus***, ***L. lydekkerianus lydekkerianus***, ***L. l. nordicus***, Bengal slow loris, Javan slow loris, pygmy slow loris), only one study of greater slow loris conducted during the wet season found a small amount of ticks in all animals (Wiens 2002, Rode & Nekaris 2011, 2012). All twelve leeches used in a preliminary test died upon coming into contact with BGE combined with saliva (Nekaris et al. 2013a). A recent study tested the effect of BGE on arthropods and found 78 % of arachnids, the order ticks belong to, died within one hour after the mixture of BGE and saliva was applied (Grow et al. 2015). As ectoparasite infection varies across season (Wright et al. 2009) a covarying toxicity of venom may indicate that slow lorises use venom for ectoparasite avoidance and defence.

While I focus on the defence of ectoparasite, another possible function of venom in slow lorises could also be the defence of endoparasites. The ingestion of secondary metabolites has been associated to treatment of endoparasites (Lisonbee 2008, Forbey et al. 2009). Especially secondary plant metabolites with low absorption such as tannins may help in the treatment of endoparasites as they are only ingested but not absorbed and thus are less toxic for the body (Forbey et al. 2009). A mixed diet of secondary plant metabolites may protect better against endoparasites due to arising parasite resistance (Villalba & Provenza 2009). It is thus possible that venom with its complex combination of proteins may have evolved to treat internal parasites in slow lorises.

e) Prey capture

In Alterman's (1995) early experiments BGE combined with saliva was lethal to mice. Yet, although slow lorises feed on large insects and small vertebrates (birds, frogs, lizards, mice, bats, tarsiers), in contrast to shrews, prey is still relatively small compared to the predator's body size. Slow lorises catch and consume prey rapidly and efficiently with the help of their powerful jaws and sharp teeth, and there is no indication of paralysis in prey or caching behaviour in slow lorises (Nekaris et al. 2013a). A few behavioural experiments in rescue centres have been performed, but all report that slow lorises are highly capable in killing prey, and do not seem to use venom for killing (Gray 2013, Reithinger 2013). Experiments that involve the application of BGE and saliva on arthropods showed that in 84 % of the trials maggots were initially impaired but only 42 % died after one hour (Grow et al. 2015). This is in contrast to the results for arachnids, where 78 % died.

f) Pre-digestive aid

A last possible function of slow loris venom is the aid in pre-digestion. Slow lorises have specialized hindgut morphology with an enlarged caecum and a short duodenum (Hill 1953). This anatomy of their digestive tract may help to breakdown carbohydrates in gum and arthropods (Fleagle 1999). This diet additionally may contain toxic compounds or digestive deterrents (Wiens et al. 2006). In contrast to bushbabies that digest gum in their large caecum with the help of symbiotic bacteria (Charles-Domonique 1977, Hladik 1979), slow lorises lack a chambered site for microbial fermentation (Hill 1953). Wiens et al. (2006) propose that slow lorises rely on conjugates, such as glucuronic acid derived from glucose, to detoxify their diet. This energy demand may account for their slow life style (Wiens et al. 2006). Components of slow loris venom may help in digestion, as it was suggested for the primary venom function in monitor lizards (*Varanus* spp.) (Arbuckle 2009), in such a way that salivary amylases can work more efficiently on carbohydrates, and may even assist in the detoxification process. This may also explain why BGE is combined with saliva. However, to test this hypothesis venom must be analysed, which is planned for the future.

6. Relevance to conservation

6.1 Conservation status of the Javan slow loris

The model species used in this study is the Javan slow loris. The Javan slow loris was designated as Critically Endangered on the IUCN Red List in 2013 based on a combination of historic forest loss, continued degradation (meaning that less than 20 % of habitat suitable for Javan slow lorises remains), extreme fragmentation of suitable habitat, and heavy exploitation for the pet trade (Thorn et al. 2009, Nekaris et al. 2013b). These factors led to a suspected decline of at least 80 % over the last three generations (Nekaris et al. 2013b). The Javan slow loris has also been listed amongst the Top 25 Most Endangered Primates in the World since 2008 (Mittermeier et al. 2009, 2012, Schwitzer et al. 2014).

6.2 Threats

The factors that have led to the Red-Listing of the Javan slow loris in the highest category are persistent and ongoing. Extensive habitat loss and fragmentation put Javan slow loris populations in danger of local extinctions without the possibility of migrating from isolated habitat patches. Like other slow lorises in Indonesia, the Javan slow loris is caught for the pet trade and to a lesser extent for traditional medicines (Shepherd et al. 2004, Nekaris et al. 2010b). Slow lorises are amongst the most frequently encountered protected primates in animal markets in Java (Shepherd et al. 2004, Nekaris & Nijman 2007). Despite being venomous, slow lorises are easy to catch due to their relatively slow movements, especially when detected during the day. Although the majority of the trade is to satisfy a large domestic demand, smaller proportions are smuggled abroad to destinations like the Middle East and Japan. Confiscations often reveal animals with high mortality due to transport conditions, and difficulties in the immediate appropriate care of rescued animals (Nekaris et al. 2009, Moore 2012). Even if animals survive, in the majority of cases they are not viable candidates for reintroductions due to having their teeth removed by traders (Moore et al. 2014).

As the main trade hub is illegal wildlife markets in Jakarta, rescue centres on Java receive high amounts of animals of all Indonesian slow loris species. Unfortunately, in many cases animals have been released into the wild without proper consideration of the IUCN reintroduction guidelines; animals are released without post-monitoring, proper habitat assessments to ensure habitat suitability, or surveys to clarify the existence and density of extant wild populations (Kumar et al. 2014). A big problem is that the origin of confiscated animals is almost never known. As a result, released animals may not be adapted to the local conditions and have difficulties feeding, finding shelter, and establishing a home range. Additionally to this welfare issue, morphological similarity of slow lorises leads to frequent species misidentification (Navarro-Montes et al. 2009). Some taxa of slow loris are known to hybridize in zoos and could potentially hybridize in the wild as well (Schulze & Groves 2004, Nekaris et al. 2009).

The desire to own a slow loris as a pet is fuelled internationally by the use of Web 2.0 sites (Nekaris et al. 2013c). Web 2.0 sites are different to normal web sites, because users can generate the contents actively, and get into a social media dialogue in a virtual community. Examples of Web 2.0 sites are YouTube where users can upload videos, or Facebook, where users can share stories, photos, videos and more. Although these websites can also be used for conservation purposes, very often “cute” videos of wild animals belonging to threatened and protected species, go viral and generate attention from people who would like to own a slow loris as a pet (Nekaris et al. 2013c). Considering that Asian countries are using the internet intensively with, for instance, Indonesia having one of the biggest number of Facebook users in the world in 2012 (more than 50 million users, ca. 93 % of the internet users; Internet World Stats 2014), this can lead to an increase in the trade of slow lorises locally, nationally and internationally. Related to this new threat is the use of primates including slow lorises as photo props, especially in tourist areas like Thailand, and photos being uploaded onto social media websites (Cannon et al. 2013, Nekaris et al. 2013c, Osterberg & Nekaris 2015).

6.3 Protection of the Javan slow loris

On an international level, all slow lorises have been listed on Appendix I of CITES since 2007. In Indonesia all slow lorises are protected by the Indonesian Law 5/1990 (***Lampiran Peraturan Pemerintah Nomor 7 tahun 1999 & Undang-Undang No. 5 Tahun 1990***). As species identification is difficult, especially for untrained staff, law enforcement often becomes difficult (Schulze & Groves 2004, Shepherd et al. 2004, Lee et al. 2005, Navarro-Montes et al. 2009).

6.4. Conservation aspects of this thesis

Even though this PhD thesis mainly focuses on the ecological and behavioural significance of venom in slow lorises, the study species Javan slow loris is highly threatened and protected in Indonesia (section 6). I constantly had to monitor data collection activities to minimise the risk of disturbance that may lead to changed natural behaviour including reproductive and dispersal related activities. The conservation implications of this study are manifold. Although increasing numbers of researchers are working on the different slow loris species (section 5.1), only one detailed long-term study on wild animals has been done (Wiens 2002), and knowledge about slow loris behaviour, ecology and distribution is still very limited, due to their nocturnal and cryptic character that makes detailed studies difficult. All my results are of considerable importance for conservation planning (Table 1.3) and should be included in the first IUCN / SSC Conservation Action Plan for the Asian Slow Loris. Although venom is one of the reasons why traders clip and cut out the teeth of slow lorises before selling them (Nekaris et al. 2009, 2010b, Moore 2012, Nekaris & Campbell 2012), the fact that bites can indeed be very dangerous (Wilde 1972, Nekaris et al. 2013a, Madani & Nekaris 2014) may deter a person who wants to purchase a cute pet or hunters and middlemen from catching and trading animals. Traditional myths and beliefs seem to be effective in preventing hunting of slow lorises (Nijman & Nekaris 2014). Reinforcing them may thus be an effective community-based conservation tool. To ensure the effective use of the results I try to make my findings as widely available as possible, also to field conservationists and practitioners.

Table 1.3: Aspects of this thesis and their relevance to the main study focus venom and to conservation

Aspect of this thesis	Relevance to venom research	Relevance to conservation
General behaviour, feeding behaviour, habitat use	Source and acquisition of venom Prey capture hypothesis	Protection of crucial resources, designation of appropriate protected areas, selection of suitable habitat for release of translocated animals, husbandry of captive animals
Social organisation, mating system, social behaviour, territoriality	Intraspecific competition hypothesis	Husbandry of captive animals, design of release schemes
Ranging behaviour	Intraspecific competition hypothesis	Assessment of population densities, space requirements in translocation programmes
Distribution, density and ecology of potential predator species	Predator avoidance hypothesis	Selection of suitable habitats and animal communities for release of translocated animals, training of release candidates, assessment of natural threats to animals, conservation planning for carnivores and other sympatric mammal species
Parasites of slow lorises	Parasite defence hypothesis	Medical care and husbandry of captive animals
Factors influencing survey effort	N/A	Effective design of geographical distribution surveys

CHAPTER 2

GENERAL METHODS

1. Brief overview

Although this thesis focuses on the venom of slow lorises, the whole project should be seen in the light of studying a threatened species. This is why this chapter goes beyond the explanation of the mere field methods. It explains the general framework of the field work, as I want to make my experience as helpful as possible for future (conservation) projects. Thus the general methods include:

- A general framework (section 2) including an overview of the study country (2.1) and preparations of the field work such as gaining permission for doing research and the decision for a study site (2.2)
- Introduction to the study sites (section 3)
- Overview of field work methods (section 4)

The PhD study took three years and included a preparation phase, the actual field work and an analysis phase. The different activities are shown in Table 2.1.

Table 2.1: Timeline of activities during the three years PhD study

July 2011 – Jan. 2012 **7 months**	**Feb. 2012 – June 2013** **17 months**	**July 2013 – June 2014** **12 months**
- Proposal writing - Grant applications - Preparation	- Preparation at the rescue centre International Animal Rescue, Indonesia - Field work in Indonesia	- Analysis - Writing up thesis

Feb	**Mar**	**Apr**	**May**	**Jun**	**July 2012 – January 2013**	**Feb**	**Mar**	**Apr**	**May**	**Jun**
Preparation 2 months										
	Forest surveys 4 months									
		Field work Cipaganti, including camera trapping 14 months								
						Arthropod sampling 5 months				

2. General framework

2.1 Java, Indonesia

2.1.1 Biogeography and climate of Indonesia

The Republic of Indonesia (latitudes 11°S to 6°N, longitudes 95°E to 141°E) consists of an archipelago with over 17,000 islands (Iskandar & Erdelen 2006). The islands lie on the edges of the Pacific, Eurasian, and Australian tectonic plates. This geographic location makes Indonesia the country with the highest number of active volcanoes in the world (78 active volcanoes) and causes numerous earthquakes and eruptions (Siebert et al. 2010). Flora and fauna are very diverse as Indonesia spreads over three major biogeographical regions (van Welzen et al. 2011). Sundaland is a biogeographical region of Southeast Asia and comprises the Malay Peninsula and the Indonesian islands Sumatra, Borneo, Java and Bali and their surrounding islands. Between the islands Bali and Lombok runs the "Wallace line" that divides the Indomalayan ecozones in the west and Wallacea transitional zone in the east, according to the distribution of birds (Wallace 1860). The phytogeographical boundary follows the "Huxley Line" running in the west of Java, making Java part of Wallacea (van Welzen et al. 2011). While the fauna and flora of Sundaland is more similar to East of Asia, the Wallacea transitional region is inhabited by more marsupials and birds, and holds a mixture of flora and fauna of Asia and Australia. Wallacea comprises all islands between the Wallacea line or Huxley line, and the "Lydekker Line" running in the west of the island New Guinea whose fauna is considered to be more similar to Australia (van Welzen et al. 2011). West Papua and Papua administratively belong to Indonesia. While both, Sundaland and Wallacea are listed as biodiversity hotspots of the world, Sundaland is listed amongst the top biodiversity hotspots based on the number of endemic species and habitat loss, ranking second in terms of endemic plants, fifth in terms of endemic vertebrates and seventh in terms of remaining primary vegetation (Myers et al. 2000, Brooks et al. 2002).

Java is approximately 139,000 km^2 large with ecologically distinct zones and high levels of endemism (Whitten et al. 1996). Precipitation varies from over 6,000 mm per year in parts of west and central Java to less than 1,500 mm in parts of east Java and along the north coast (van Welzen et al. 2011). Monthly low temperatures for instance vary between 11 °C and 16 °C and high temperature between 21 °C and

23° C for Bandung, West Java, the nearest city to my study site (CHAPTER 2, section 3.1) but vary throughout Java (World Weather Online 2014). Java is largely of volcanic origin and altitudes vary between 0 to 3676 m above sea level (Siswowidjoyo et al. 1997). While the western part of Java is characterised by a tropical wet climate favouring rainforest, the eastern part of Java has a more seasonal climate resulting in drier forest types, including deciduous forests and even savannah (Heaney 1991, Sémah & Sémah 2012).

2.1.2 Administration and demography of Java

Indonesia has approximately 240 million inhabitants, resulting in a population density of 136 people per km^2 (Worldbank 2014). The 143 million people inhabitants of Java make a population density of about 1117 people per km^2. This makes the island Java one of the most densely populated islands in the world. Java has six administrative regions, the provinces Banten, West Java, Central Java and East Java, and the two special regions Jakarta and Yogyakarta. A province is divided into regencies and cities (*Kabupaten* and *Kota*, e.g. 17 regencies and 9 cities West Java), then districts (*Kecamatan*, e.g. 620 districts for West Java) and finally urban villages (*Desa*). The three major languages spoken on Java are Javanese, Sundanese and Madurese, three of the more than 700 living languages spoken in Indonesia (Lewis 2009). Ninety percent of the Javan population are Muslim, the rest consists of Christians, Hindu and Buddhists. Regarding its development status, Indonesia is placed into the few “newly industrialized countries”, nations with economies more advanced and developed than those in the developing world, but not yet with the full signs of a developed country. This is mainly based on the Human Development Index (HDI), which is a combination of life expectancy, education, and income indices. According to the CIA World Factbook (2013) the gross domestic product (GDP) per capita at nominal values (the value of all final goods and services produced within a nation in a given year) of Indonesia ranks 119 in the world with a GDP of US$ 3500 (for comparison UK ranks 26, with a GDP of US$ 39,600). Literacy (people of age 15 and above who can read and write) is high at 92.8 % (UNESCO Institute for Statistics 2013). Life expectancy lies at 69 for men and 73 for women (World Health Organization 2013).

2.1.3 Habitat destruction and conservation on Java

Java’s high human population accounts for just 7 % of the land area, but 67 % of the human population of Indonesia (Lavigne & Gunnell 2006) resulting in enormous pressure on biodiversity (Smiet 1990, Sodhi et al. 2004, Miettinen et al. 2011). Indonesia faces some of the highest deforestation rates in the world (Sodhi et al. 2004, Santilli et al. 2005) with more than 90 % of Java's natural vegetation having been lost due to conversion to agriculture, development, and large-scale palm oil plantations (Sodhi et al. 2004). The good conditions for growing crops are partly explained by the high fertility of volcanic soil. The native primary or secondary forest that remains is predominately located in areas difficult to access such as in mountains (Smiet 1992, Lavigne & Gunnell 2006; Figure 2.1). This has triggered the near extinction of many larger mammals or caused highly fragmented distribution (e.g. Javan rhino ***Rhinoceros sondaicus***, Javan tiger ***Panthera tigris sondaica***, Javan subspecies of the leopard ***Panthera pardus melas***) (Santiapillai & Ramono 1992, Whitten et al. 1996, Fernando et al. 2006, Corlett 2007). Threats to fauna include forest decline (Sodhi et al. 2004, Santilli et al. 2005), but also trade in wild animals for pets, traditional medicine or other economic uses (Shepherd et al. 2004, Corlett 2007, Shepherd 2009, 2012a,b, Nijman 2010).

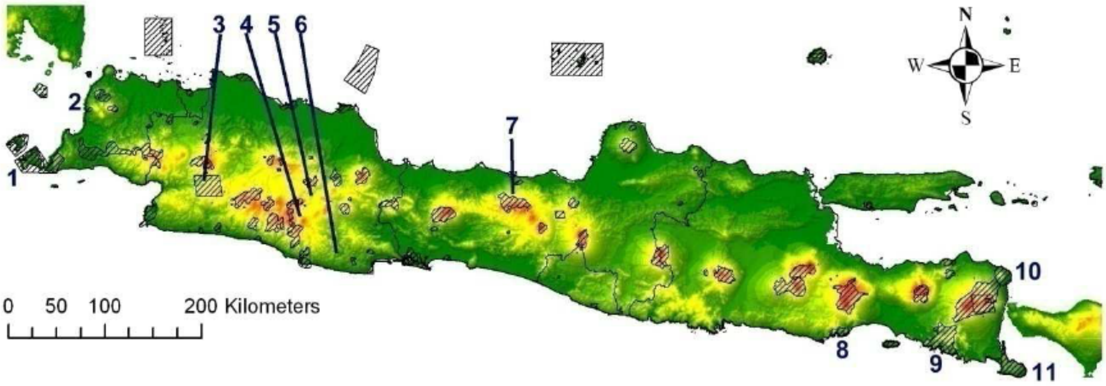


Figure 2.1: Position of protected areas on Java in relation to altitude. Dark green indicates 0m asl, and increase towards red indicates an increase in altitude. Locations of protected areas retrieved from IUCN & UNEP (2014). The long-term study site was located in Cipaganti (indicated by number 4). Other study sites were 1 = Ujung Kulon; 2 = Carita; 3 = Mount Gede Pangrango and Cimungkat*; 4 = Cipaganti* and Pangalengan*, adjacent to Mount Papandayan; 5 = Sumedang*; 6 = Tasikmalaya* and Limbangan; 7 = Dieng Plateau; 8 = Mount Bromo; 9 = Meru Betiri; 10 = Ijen Plateau; 11 = Alas Purwo. * = unprotected area.

There are 751 Protected Areas (PAs) recognised in Indonesia by the IUCN (IUCN & UNEP 2014). 167 of these PAs are located on the island of Java, summing up to roughly 20,000 km^2 (excluding marine PAs) and about 7 % of Java being protected (Figure 2.1). They include 100 Nature Reserves (IUCN category I, total 3519 km^2) and 16 National Parks (IUCN category II, total 5606 km^2). Other PAs with no applicable IUCN category are for instance one World Heritage Site (Ujung Kulon National Park, 1231 km^2, number 1 on Figure 2.1) and one UNESCO-MAB Biosphere Reserve (Cibodas Biosphere Reserve, part of Mount Gede Pangrango, 575 km^2, number 3 on Figure 2.1).

2.1.4 Protected area management on Java: case example Mount Papandayan

Mount Papandayan (number 4 on Figure 2.1) is an active volcano in the regency Garut and regency Bandung, province of West Java, with its peak located at 7°19’42’’S and 107°44’00’’E and an elevation of 2,675 m ASL. Almost all forested areas are covered by Mount Papandayan Nature Reserve (***Cager Alam***; IUCN category Ia, 66.2 km^2, assigned in 1924), and are surrounded by tea plantations and production forest of pines ***Pinus*** spp., ***Altingia exelsa*** and ***Agathis damara*** (Sulistyawati et al. 2008). The three major vegetation types of the Nature Reserve are mixed forest, grassland and crater vegetation, with an occurrence of 185 species of plants (trees, shrubs, herbs, climbers), and 72 bird species of 26 families, including the two endangered species Javan hawk-eagle (***Spizaetus bartelsi***) and blue-tailed trogon (***Harpactes reinwardtii***) (Sulistyawati et al. 2008). Full lists of species can be found in Sulistyawati et al. (2005).

Several management problems in the conservation of the PA Mount Papandayan were identified by Zuhri & Sulistyawati (2007) and Sulistyawati et al. (2008), and are representative of most PAs on Java:

a) Decrease in biodiversity due to forest clearing and conversion to agricultural land due to poverty and land scarcity. Due to deforestation the size of the forested area decreased from 10,283 ha (1994) to 7,581 ha (2001) (Sulistyawati et al. 2008);
b) Area instability resulting from the PA’s location, which is surrounded by built areas, its small size, its un-compact shape resulting from on-going loss of forest and the presence of enclave and roads crossing the PA;
c) Presence of natural resource exploitation (poaching, channelling water resources for irrigating fields, collecting honey, fuel woods, mushrooms, and livestock feeds) inside the PA boundary due to ineffective protection management and poverty;
d) Ineffectiveness of PA management in general due to weakness in the organization structure, number and quality of the staff, limited equipment, lack of law enforcement, and limited utilization of the reserve for research and education.

Sustainable management strategies with a strong involvement of stakeholders including local communities have been proposed (Zuhri & Sulistyawati 2007, Sulistyawati et al. 2008). In 1978 an area adjacent to the Nature Reserve has been declared as Mount Papandayan Recreation Park (IUCN category V, 2.2 km^2) that potentially offers opportunities for sustainable ecotourism.

The management problems for the Nature Reserve Mount Papandayan as indicated by Zuhri & Sulistyawati (2007) and Sulistyawati et al. (2008) are characteristic for most of Indonesia's PAs that in many cases are "paper parks" with on-going resource exploitation and forest clearing (Curran et al. 2004). One of the main problems is that biologists often ignore the social and cultural context, but on the other hand effective conservation of PAs requires the absence of excessive anthropogenic disturbance. Modern conservation often sees stewardship by local communities as the solution to many problems. However, community-based conservation schemes often do not work in practice, as problems are passed to local communities without giving them the knowledge and tools to effectively manage their own natural heritage (Wells 1999, MacKinnon & Wardojo 2001). Bickford et al. (2007) suggest several points for the effective conservation of PAs in Indonesia. Management of the parks must be decentralised to promote stewardship, but go hand in hand with sufficient funds, training and equipment to ensure enforcement of park management and regulations. Multi-stakeholders must be included in protection schemes, such as the government, non-governmental NGOs, the public sector such as ecotourism companies, the public school system and religious groups. Protection measures must be supported by environmental education, awareness projects, incentives for local communities adjacent to the park, and sustainable land-use policies. As strict and abrupt boundaries of PAs are often ineffectively protected, Bickford et al. (2007) advocate the establishment of PA buffer zones and corridors between PAs that allow the sustainable use of certain natural resources and thus balance the constraints of conservation on rural development.

2.2. Preparation of the field work

2.2.1 International Animal Rescue Indonesia

After arriving on Java early February 2012, I spent the first two months at the rescue centre of International Animal Rescue (IAR) Indonesia in Ciapus, Bogor, West Java. During this time period I prepared the main part of my study. The proximity to Jakarta enabled me to organise permits there during the first week (APPENDIX 1). The rescue centre is specialised on the care of confiscated and rescued macaques and slow lorises. At the time of arrival approximately 100 Indonesian slow loris specimens were housed there; most were greater and Javan slow lorises, and a few Bornean slow lorises ***N. menagensis***. The animals are in different stages of the reintroduction process: in quarantine, in socialisation cages where they are introduced to conspecifics or in pre-release cages that are furnished intensively with natural vegetation. By observing the animals, I could make my own detailed behaviour ethogram, test my observation methods, and practice observing the different behaviours of slow lorises. As the health of slow lorises was checked routinely every seven weeks, I could learn about the handling of the animals and how to take BGE and saliva samples (section 4.1.1). Two animals had been released on Mount Salak, in approximately one hour walking distance from the centre, and were followed using radio-tracking to monitor their release. I joined the staff of IAR for several days to experience the difference between observing animals in cages and in the wild, and practiced the use of a reduced ethogram for wild observations (section 4.1.3). Finally, I was able to practice my Indonesian language, get used to the culture and climate, and finalise my own research proposal on the basis of my experience at IAR. In these two months I also started the first forest surveys (section 4.1.6).

2.2.2 Permits

The process of applying and processing research permits in Indonesia is complicated and time-consuming. Details of pre-arrival, post-arrival and export permit application processes are explained in APPENDIX 1. As one original aim of my PhD study required the analysis of the gland exudates and saliva samples in the laboratory of our collaborator Bryan Fry at Brisbane, Australia, University of Queensland, I needed export and CITES permits additionally to the normal research permit. The application process for the CITES export permit required the organisation of many different letters and permits (APPENDIX 1). Export of samples from Indonesia is always difficult and it is almost certain that the application for export permits may take longer than the indicated time. The issue of the final permits was heavily delayed and took almost three years.

2.2.3 Forest surveys

I conducted forest surveys for the reasons: (1) finding an appropriate location for the long-term study of slow lorises, (2) testing of the predator hypothesis and (3) extending the knowledge of the current distribution of Javan slow lorises. In this section I describe the general preparation and conduct of the forest surveys; the detailed methods are described in section 4.1.6.

First, I mapped all protected areas on Java (Figure 2.1). I selected study sites by using information about the presence of slow lorises in unprotected areas by talking to several Indonesian researchers and local people, and a species distribution model (Thorn et al. 2009). A description of study sites can be found in section 3.2. Surveys were conducted in various combinations together with AN, VN and local and international students. Survey results are published in Voskamp et al. (2014) and presented in CHAPTER 5.

For surveys in PAs, the office of the respective BKSDA (***Balai Konservasi Sumber Daya Alam***) must be visited first, the research permit (RISTEK = ***Riset dan Teknologi***, Research and Technology) and the entrance permit for protected areas (SIMAKSI = ***Surat Izin Masuk Kawasan Konservasi***) presented, and entrance fees for the protected area paid. If no contact in the area has been established before, the Regional Natural Resources Conservation Office (BKSDA) is a good place to ask for the contact details of experienced guides. However, BKSDA offices were often relatively far from the actual survey site, which made travelling between sites – especially with local transportation – challenging.

Most of the unprotected areas in the regencies Garut, Tasikmalaya and Ciamis were accompanied by AN and VN, a local guide experienced in slow loris field work, and a former slow loris hunter; they helped to socialise with the local authorities. Upon arrival the team met with the village chief first, to socialise, introduce the purpose of our visit, show permits and get information about the location, as well as possible local guides and accommodation.

2.2.4 Decision for a long-term study site

After surveying several locations in the regencies Garut, Tasikmalaya and Ciamis, together with AN, I decided to establish the field site at Cipaganti village, regency Garut. I made this decision on the basis of several criteria. First, we had several encounters with wild Javan slow lorises at Cipaganti, indicating a healthy study population there. Second, I considered socio-economic aspects of the area. Some areas would have required nocturnal radio-tracking in fragile agriculture areas such as rice fields that can easily be damaged. Third, the goodwill of the village chief and possibly other locally important people was important. Fourth, the habitat at Cipaganti fulfilled a balance between the presence of relatively natural vegetation, manageable terrain and potential for successful captures for radio-collaring. The latter was discussed with the former slow loris hunter Mr Ade who helped and trained us in capturing slow lorises. Finally, I considered practical needs such as proximity to medical care.

3. Study sites

3.1 Long-term study site Cipaganti village

The project team (AN, VN, and I) established the field station in Cipaganti village (***Desa Cipaganti***), Cisurupan (***Kecamatan Cisurupan***), regency Garut (***Kabupaten Garut***), province West Java (***Provinsi Jawa Barat***), at S7°6'6 - 7°7'0& E 107°46'0 - 107°46'5 (Figure 2.2) in April 2012. Cipaganti lies in the foothills of Mount Puntang, which is part of the mountain range containing the active volcano Mount Papandayan. While Mount Papandayan is recognized as a Nature Reserve (section 2.1.4), the partly agricultural areas surrounding the Nature Reserve are not protected. The distance between the edge of the village and the boundary of the protected forest on slopes of the ridges that cannot be cultivated is approximately 1300 m, while the first contiguous forest is about 2000 m away from the village. The land between reaches from c. 1300 m up to 1750 m ASL ranging into Zones that are in Java classified as Sub-montane (1200 m – 1800 m ASL) and Montane Zones (1600 m – 2400 m ASL); at altitudes above 1500 m ASL, ground frost can occur (Nijman 2013). The land is covered with a mosaic of cultivated fields (called ***talun*** by Sundanese people) planted with crops like tea, beans, chilli, tomato, tobacco, potato, cabbage, onion, carrot etc., abandoned fields and bush patches, bamboo patches, tree plantations and forest patches. Fields are often bordered by trees with a more or less connected canopy.

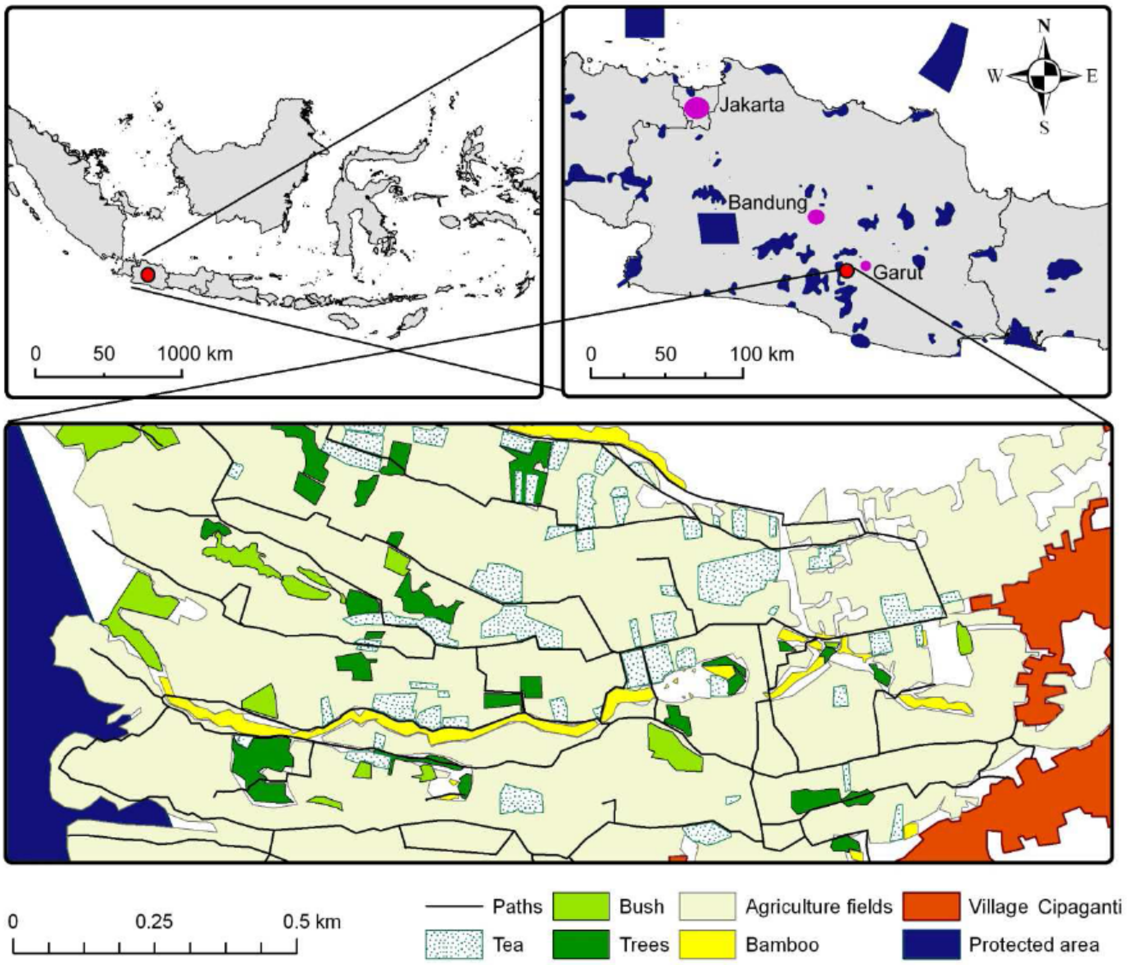


Figure 2.2: Location of the long-term study site Cipaganti bordered by the village Cipaganti in the east (red) and the protected area Mount Papandayan in the west. Blue indicates protected areas on the second and third map. The habitat is characterized by the mosaic-like landscape of agriculture fields, and small patches of bushes, trees and bamboo. Habitat of white areas not assessed.

The climate at the field site varied with respect to temperature and rain fall (Figure 2.3), with daily minimum temperature between 12.4 °C and 20.7 °C, but around 2 degrees lower due to the higher altitude of the study site as compared to the research station (weather station at app. 1300 m ASL). During the dry period monthly precipitation fell below 150 mm per month and monthly minimum temperature were considerably lower (minimum in dry period 12.4 °C in July 2012; maximum in wet period 17.3 °C in January 2013). During dry periods rivers dried out and some trees shed their leaves (e.g. Japanese persimmon *Diospyros kaki*, Indonesian mahogany *Toona sureni)*. One of the important nectar-producing plants for slow lorises, fairy duster or red calliandra *Calliandra calothyrsus*, did not bloom during the dry period.

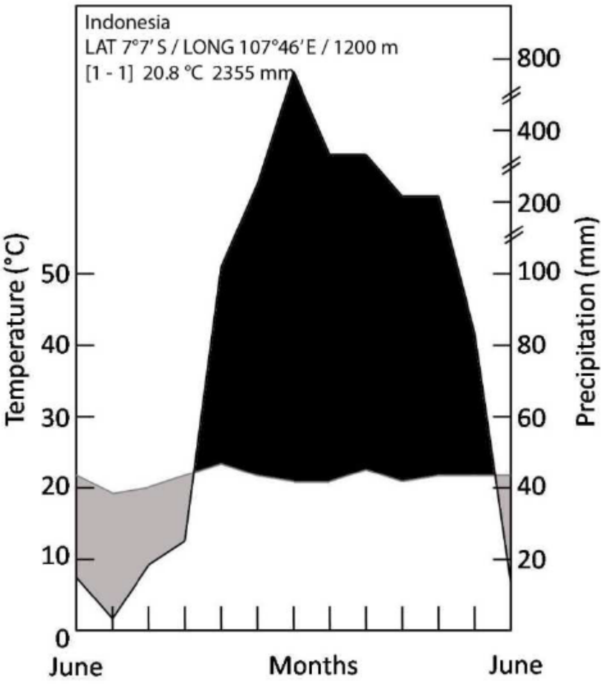


Figure 2.3: Weather diagram based on data from the base camp in Cipaganti village at app. 1300 m ASL for June 2012 to June 2013. The grey line indicates monthly mean temperature (left y-axis), the black line indicates monthly precipitation (right y-axis). According to Walter & Lieth (1967) the grey area indicates a dry weather period and the black area a wet weather period. However, a different definition has been used in order to create periods of same length (see text).

The study site covers about 50 ha and is located between 1300 and 1650 m ASL adjacent to Cipaganti village. Accordingly, the terrain is steep and difficult to traverse. The long-term study site Cipaganti includes several small streams coming from the mountain, typically narrower than 2 m and usually dry from May to July. While observing slow lorises in Cipaganti, I often spotted small rodents (especially mice) in trees that are potential prey for most carnivore species discussed in following chapters. Human presence and disturbance at the study site are high. Many people work in the fields every day starting before dawn at about 5:00. Trees and bushes are regularly cut for wood production or clearance. Furthermore, people set traps for pigs for crop protection and for birds for the pet trade. Hunting or disturbance of pigs (European wild pigs *Sus scrofa*, Javan warty pigs *S. verrucosus*) during the night has been observed, beehives are harvested once per year during the dry season, and landslides are common during the rainy weather period.

3.2 Forest survey sites

Although we primarily looked for slow lorises during forest surveys, we included all levels of vegetation including the ground in order to detect potential predators and understand their sympatric geographical community distribution. I used data from three expeditions, one (April-June 2012) focusing on 14 sites distributed across Java (Voskamp et al. 2014), one (May-July 2013) in East Java, and one (February-May 2014) in West Java. When results of surveys are reported in CHAPTER 5, they always indicate if survey results include data from the long-term study site Cipaganti (section 3.1).

The study sites (Figure 2.4) were at altitudes between sea level and 1,840 m ASL. While protected sites visited during surveys mainly consisted of secondary forest in different stages of growth as well as forest plantations with mainly non-native trees, unprotected sites were mosaic-like landscapes (***talun***) with forest and bamboo fragments, agricultural fields and non-native forest plantations. Survey sites with their protection status are listed in APPENDIX 3.

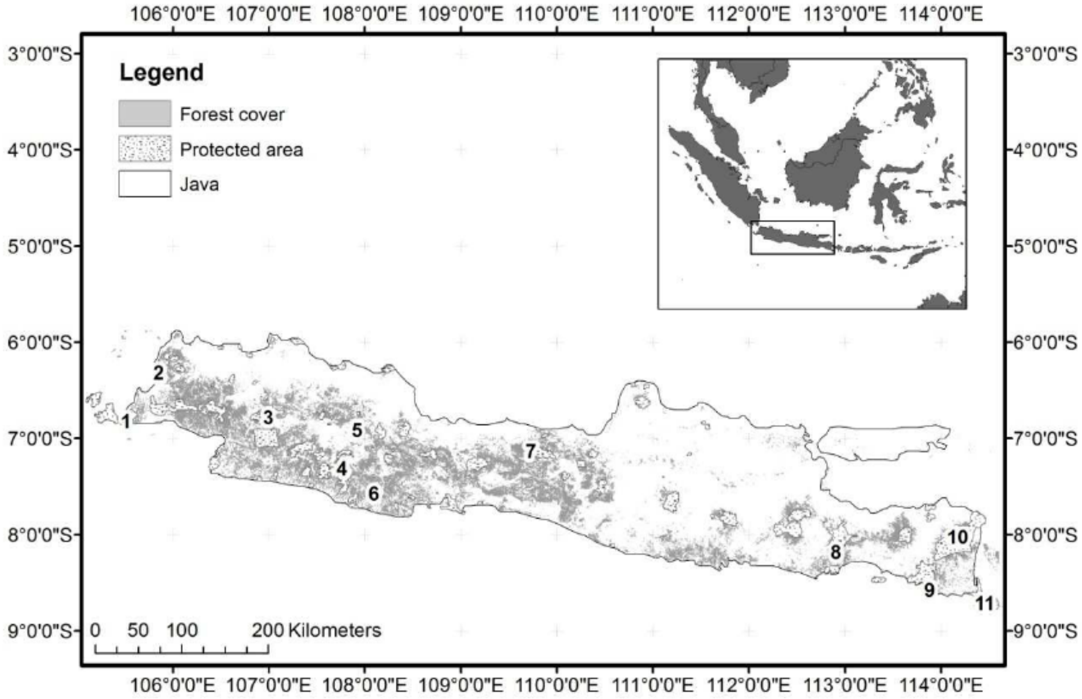


Figure 2.4: Survey sites for forest surveys in Java, Indonesia, in 2012–2014. Nine out of 14 sites are in protected areas. 1 = Ujung Kulon; 2 = Carita; 3 = Mount Gede Pangrango and Cimungkat*; 4 = Cipaganti* and Pangalengan*; 5 = Sumedang*; 6 = Tasikmalaya* and Limbangan; 7 = Dieng Plateau; 8 = Mount Bromo; 9 = Meru Betiri; 10 = Ijen Plateau; 11 = Alas Purwo. * = unprotected area

4. Field work methods

4.1 Data collection

4.1.1 Capturing and handling

As trapping success for slow lorises is low (Wiens & Zitzmann 2003) the team captured animals by hand. An experienced ex-hunter of slow lorises helped in the capture process that usually involved steering the animal to an isolated tree or tree part and then climbing the tree and catching the animal by hand. I did not sedate animals, but processed them immediately at the place of capture, and released them afterwards on the same tree. We used leather gloves for bite protection and rubber gloves for infection control. One person held the loris with a firm grip around the neck and holding the very strong extremities with the other hand. Extremely agile individuals required a second person assisting in holding, as the slow loris would try to grab sampling and measuring equipment. Lorises were very fast in bending the body in a ball-like position, lowering the head towards the chest and trying to bite, making a fast hold under the chin important. After being held tight, most animals assumed the defence position with raised and interlocked arms immediately (Hagey et al. 2007). I re-captured all animals every three months for a general health check and for collecting samples BGE, saliva and faeces.

4.1.2 Venom sampling, morphometrics and preparation of radio-tracking

To ensure minimum time between capture and sampling, I always took samples of BGE and saliva first. I sampled BGE using Sterilin transport swabs with Aimes agar gel medium (Sterilin Limited, UK) by rolling and scraping the cotton tip of the swap on the brachial gland. To take saliva, I used a standard 1ml syringe with detached needle and tried to get saliva from as close to the salivary glands as possible. Both swabs and syringes containing samples were sealed with Parafilm (Bemis Flexible Packaging, US) and put on ice brought to the field. As soon as possible after the return from the field, samples were frozen in a standard freezer with approximately -8 °C. If the animal defecated, faecal samples were collected and stored in 70 % ethanol. I separated small c. 8 g samples that would be stored dry in silica gel after 24 hours in ethanol for venom analysis and potential future genetic analysis. The other part of the faecal samples was kept in 70 % ethanol for future diet analysis. I determined the sex of the animals, checked for pregnancy using abdominal palpation, and assessed stage of the oestrous cycle (Manley 1966, Izard et al. 1988). I also monitored lactation by checking for elongated nipples and milk expression (Wiens & Zitzmann 2003). I weighed animals with spring balances (Pesola®, Canada). Age classes were determined by body mass and pelage pattern and length. Adults had body masses greater than 750 g, juveniles between 250 g and 750 g, and infants below 250 g. As body mass varied substantially, and sub-adults can reach adult size while retaining juvenile pelage coloration and length, mass was considered an inconclusive indicator of adolescence. The pelage of infants and juveniles was fluffy and contained long hairs with white tips which gave the appearance of frosting; the transition between this condition and an adult coat pattern without white tips contributed to the categorization of sub-adults (Figure 2.5). I examined the general condition of captured animals. Head-body length was defined as the distance between the base of the tail and the tip of the nose, and measured using a tape measure. Animals were stretched out as far as the natural body shape allowed and the measurement tape was applied along the middle of the back and head. I took further standard morphometric measurements including tail length, head length and width, ear length and width, hind foot span, hand span, upper and lower hind- and forelimb, muzzle length, chest girth, neck girth, testes length and width, following Schmid & Kappeler (1994) (APPENDIX 4, section 1).

I attached radio collars (17 g, on average 1.9 % of body weight, BioTrack, UK) to adult animals, and marked them individually by fitting one or two coloured stainless steel bead chains (2mm per bead) around their wrists. The observation teams followed the radio-collared lorises in two shifts during the night, from 18:00 to 00:00 and 00:00 to 06:00 (Wiens & Zitzmann 2003), covering one animal per shift. We tracked animals with the aid of an antenna (6 and 8 element flexible Yagi antenna, Biotrack, UK) and receiver (R1000, Communication Specialists, US). If uncollared but identifiable animals were encountered, they were observed as long as possible until they moved away.

Figure 2.5: Javan slow lorises change their coat pattern, colour and fur density as they age. Shown here are a very pale infant (~4 weeks old) with fluffy fur; juvenile with characteristic pale coat with very dark markings and very long fur; and typical brown adult with shorter fur and paler markings

4.1.3 Data collection of behaviour and ranging

If not indicated differently, observation data in this thesis stem from 14 months of field observations from April 2012 to June 2013. I used instantaneous behaviour sampling with 5-minute intervals and took ***ad libitum*** notes (Altmann 1974, Nekaris 2001). The behavioural ethogram is included as APPENDIX 3. At each sample point I also recorded the tree species used by the animal and the distance to the closest slow loris, if present. For the latter I used the categories “in bodily contact” or “less than a body length away”, “less than 5 m distance”, and “within sighting distance”. I also collected data on the posture and locomotion of animals, the position in the tree, substrate type, substrate size and substrate angle (APPENDIX 4). Categories for these variables and illustrations, and basic frequencies can be found in APPENDIX 5.

Every 15 minutes I took a GPS bearing of the animal‘s position. The eye shine of the animals and successful close triangulation were regarded as sufficient for taking GPS fixes. I used Garmin GPS 60 and 62st with an average precision of about 4.3 m. I only took a GPS point if the precision was 8 m or better. If I lost the animal before 15 minutes, I took the GPS point at the next 5-minute interval that the animal was seen.

4.1.4 Camera trapping

Potential nocturnal predators that were known to be present at the field sight were common palm civets and leopard cats (*Prionailurus bengalensis*). Camera traps were used specifically to examine presence of at least partly ground-dwelling ‘potential predators’ of slow lorises in the long-term study site Cipaganti. The one to six cameras traps (Cuddeback Attack IR; Bushnell Trophy cam night vision) were set 0.5 m above the ground in small openings or wildlife trails in otherwise relatively dense vegetation (small trees, undergrowth, bamboo), but not in very open space because of the risk of theft. Camera traps were not baited and were set to operate round the 24-hour cycle. Photographs of the same individual or social group (if identifiable) at the same camera trap station that were less than two hours apart are treated as comprising one record. If identification to species was uncertain, records were excluded. No other location was camera-trapped.

4.1.5 Weather data and lunar illumination

With a TFA Nexus weather station (TFA Dostmann, Germany) located at the field station in Cipaganti, I collected data on temperature, humidity, rain and wind, with one data point every hour. I calculated minimum temperature of the night and rain over the last 24 h. I estimated cloud cover in the field to the nearest 10 %. Luminosity was recorded using the exact percentage of the moon illuminated when above the horizon, using the programme MOONDV version 1 (Thomas 1998). When below the horizon an illumination of 0 was recorded.

4.1.6 Forest surveys

At all forest survey sites the team walked transects along existing paths and roads and I recorded all confirmed nocturnal mammal sightings. Teams of at least two people walked at an average speed of approximately 500 m/hour, scanning all levels of vegetation using headlamps with a combination of either red (Nekaris et al. 2008) or white filters. Transects ran during approximately 18:00 to 02:00. In Cipaganti I recorded incidental sightings of all mammals seen when observing slow lorises from 18:00 to 06:00.

The survey effort for each area is reported in APPENDIX 2; Cipaganti is included twice, with the first two visits included as a survey and the later period included as the long-term study. For each animal sighting I recorded the GPS location, date, time and weather conditions (Sutherland 2006).

CHAPTER 3

Basic ethology and ecology of the Javan slow loris and potential sources for the sequestration of slow loris venom

1. Introduction

Although Sundaland is considered a biodiversity hotspot due to a high percentage of endemic species, much of its wildlife, such as the Javan slow loris, are threatened by habitat loss and hunting for traditional medicine or the luxury product market (Sodhi et al. 2010, CHAPTER 1, section 6.2). Many nocturnal, solitary and arboreal primates are difficult to study (Wiens & Zitzmann 2003) and lack long-term studies of their behaviour and ecology in the wild (Nekaris & Bearder 2011). Likewise, the Javan slow loris was listed as Data Deficient until 2006 (Nekaris et al. 2013b). Although we now have some information regarding wild greater slow lorises from Malaysia (Wiens et al. 2006), pygmy slow lorises from Cambodia (Starr et al. 2013), and Bengal slow loris from various parts of its range (Das et al. 2009, Pliosungnoen et al. 2010, Swapna et al. 2010, Rogers & Nekaris 2011), it is still not clear to what extent these species differ in social organization, diet and home range size, and we cannot plan effective conservation strategies for Javan slow lorises based on what is known about their congeners. Winarti (2011), Nekaris (2012) and Wirdateti (2012) all identified the agro-forest gardens around Cipaganti, Garut, as containing high numbers of Javan slow lorises, and urged that long-term studies of the species be undertaken.

While data on slow loris ethology and ecology are missing in general, the diet of wild slow lorises has been described in a handful of studies (Wiens & Zitzmann 2003, Swapna et al. 2010, Rogers & Nekaris 2011) but not for wild Javan slow lorises. As explained in CHAPTER 1, section 5.3, venom may be sequestered from food sources such as arthropod prey and gum (Nekaris et al. 2013a), which are two of the most important food sources for slow lorises (Streicher 2004, Wiens et. al 2006, Swapna et al. 2010, Starr & Nekaris 2013). Data on venom composition of Javan slow loris diet are not yet available for investigating sequestration. Direct observation of arthropod feeding and identification of taxa in the field is difficult (CHAPTER 2), so the assessment of availability of noxious arthropods as well as the analysis of faecal samples can be a first step towards examining the possibility of venom sequestration. Arthropod abundance can be affected by several environmental factors, such as ambient temperature (Lessart et al. 2010), humidity (Gao et al. 2011), rainfall (Tanaka & Tanaka 1982) and the phase of the lunar cycle (Tigar & Osborne 1999). Similarly, gum availability may change depending on environmental conditions (Nussinovitch 2009). Variation in venom composition may reflect seasonal changes in gum and arthropod availability.

Here, I present the first behavioural and ecological data recorded from wild Javan slow lorises. My aims were to provide an ethogram of wild Javan slow lorises and describe their activity budget, the diet, basic social behaviour and habitat use over the first three months of a fourteen months study. This analysis serves as a general foundation for this study. Furthermore, I aimed to explore whether secondary plant compounds such as gum and noxious arthropods that may be used for venom sequestration form a part of slow lorises' diet. While data on venom composition and variation in slow lorises are not yet available for a comparison, here I investigated the potential arthropod prey of Javan slow lorises in a rural agriculture system in Cipaganti in order to assess whether noxious arthropods may be available as a source of venom sequestration in slow lorises. I furthermore explored the effects of environmental and abiotic factors (ambient temperature: Lessart et al. 2010; humidity: Gao et al. 2011; rainfall: Tanaka & Tanaka 1982; lunar illumination: Tigar & Osborne 1999) on the abundance of potential arthropod prey. I did not examine the variation in gum availability.

2. Methods

Details of the study site are described in CHAPTER 2, section 3.1.

Data collection

Capturing, faecal sampling, morphometric measurements, radio-tracking and behaviour sampling are described in CHAPTER 2, section 4.1. I included all vegetation of more than 1 m high in the vegetation dataset, because I observed animals moving on bushes and other small plants. A tree was defined as having a minimum diameter at breast height (DBH) of 2.5 cm, and was at least 3 m high. This definition, especially the small DBH, was adopted to accommodate the structural requirements of slow lorises (Ganzhorn et al. 2011, Nekaris pers. comm.). In order to test whether slow lorises showed a preference for certain tree species, I recorded random tree species in the study site along nine, approximately 1 km long, parallel line transects through the home ranges of the radio-collared animals. I used point intercept transects with intercepts of 15 m (Hill et al. 2005, Rode et al. 2013a). At each point I recorded the nearest tree species, and classified the vegetation type as cultivated field, abandoned field, bush, bamboo patch, tree patch or path (Rode et al. 2013a). This method was deemed appropriate as I needed to minimize damage to the crops of the local farmers. I took samples of the tree species used by the animals, which were identified at LIPI.

When animals were feeding, I noted the food type and recorded qualitative observations of the feeding method. Additionally I collected faecal samples during the 3-monthly routine health checks of radio-collared animals during the whole 14 months study period from April 2012 to June 2013.

Research on arthropods was conducted from February to June 2013, covering the end of the wet weather period and the beginning of the dry period. I chose two adjacent trapping sites on 1425 m and 1460 m asl, and c. 200 m apart. Both were tea fields enclosed by bamboo (*Gigantochloa* spp.), green wattle and Cajeput trees. Slow lorises that were subject to the radio-tracking study inhabited both areas. I trapped arthropods at each area once every two weeks during three consecutive nights. As the effect of arthropod traps varies per order and forest strata (Basset et al. 2003), I used different trap types to cover different arthropod orders and multiple forest strata. I placed a Malaise trap in the centre of each area and used it to capture flying arthropods. Intercepted arthropods moved upwards inside the trap and subsequently fell into a collection pot filled with a 70 % alcohol solution (Campos 2000). At each site, I established two line transects of 50 m in length between the rows of tea bushes to the left and right of the Malaise trap. At each step I took a sweep on each side of the transect. After five steps (10 sweeps) I emptied the net and recorded the contents. I generated three random GPS locations in each area and placed in total six pitfall traps to target ground dwelling arthropods (Topping et al. 1992). I left the Malaise and pitfall traps for 12 hours (18:00 to 06:00) before collecting the contents. I walked each sweep net transect once every trapping night. All collected arthropods were included in the research. Orders were identified with the aid of McGavin & McGavin (2001). I used a weather station to collect data on environmental factors (CHAPTER 2, section 4.1.5).

Data analysis

I used descriptive statistics (means and standard deviations), and calculated differences in activity budgets between the sexes using a Pearson Chi-square test for association (Dytham 2001), only including radio-collared adult animals with more than 100 observation points. I grouped feeding and foraging, sleeping and resting, alert and freezing, and social activity (aggression, playing, other social activities) for the activity budget (for the ethogram see APPENDIX 3). For the general activity budget I merged auto- and allogrooming into a single category ("grooming") so that the latter was not considered in the category "social behaviour". I used an arcsine transformation before presenting the activity data in a graph. When I analysed details of social behaviour I included allogrooming into the analysis. Social activity and distance between animals were recorded for all animals. I used a Pearson Chi-square test to detect if there were differences between the frequency at which the lorises used certain tree species and the frequency at which these species occurred in a random sample at the site. The null hypothesis was that there was no difference between the frequencies at which the animals used the different tree species and a random sampling of tree species, meaning that the lorises used trees at the study site randomly. A positive deviation from the null hypothesis was interpreted as a preference for the more frequently used tree species. I included only the ten most frequently used tree species in my analysis. All other trees used were added as a single category "other" into the analysis.

To analyse faecal samples, I poured the sample that was stored in 70 % ethanol into a petri dish and diluted it with water. I examined the sample using a microscope with a total magnification of 100x and 400x. I report the prevalence of different food items gum, arthropods, arthropods with wings, caterpillar and seeds. I defined prevalence by the number of samples containing the food item divided by the total number of samples examined. Samples of the same individual but from different captures were treated as two different samples.

For each sampling method there was no significant difference in total arthropod abundance captured at the two areas (Mann Whitney U tests; Malaise trap: $U = 40.5$, $p = 0.345$; $n = 21$, sweep net: $U = 19$, $p = 0.114$; $n = 17$; pitfall trap: $U = 9$, $p = 1$; $n = 9$) data of both areas were merged. I focussed on the most abundant arthropod taxa that are also reported to be eaten by lorises (adult Lepidoptera, Hymenoptera, Orthoptera and Arachnida) for statistical tests. As environmental factors I used minimum temperature per night, average humidity in the last 24 hours (06:00 to 06:00), rainfall in the last 24 hours, wind in the last 24 hours and average lunar illumination during this night (percentage of the night with moon over the horizon multiplied by the moon phase). As abundance data were not normally distributed and sample size per trap type small, I used non-parametric statistics. I used Spearman rank correlations to test for correlations between environmental variables and trap type – order combinations (Lepidoptera adults – Malaise trap, Lepidoptera adults – sweep net, Orthoptera – sweep net, Arachnida – sweep net). I performed all tests using SPSS 20.0 with significance level set to 0.05.

3. Results

In April and May 2012 I captured 12 Javan slow lorises (Table 3.1). Three of these animals were not collared because they were juveniles. On various occasions uncollared animals were sighted. The female adult individuals RO and EL were lost on 11 June and 6 July, respectively. RO was later brought to the field station by local inhabitants and was suspected to have been in captivity. When she was released at the site where people claimed they had found her, she started to travel very long distances, and was finally lost in the nearby protected forest area. The collar of EL broke and, although there were a few sightings of her, I did not catch her again.

Table 3.1: Details and basic morphometrics of 14 Javan slow lorises, including 9 radio-collared individuals. Asterisks indicate animals that were not radio-tracked. Confidence intervals are given by standard deviations.

No.	ID	Sex	Age	Date captured	Weight (g)	Obs.	Days
1	GU	Male	Adult	17/04/2012	885	284	26
2	EN	Female	Adult	18/04/2012	740	339	22
3	YO *	Male	Sub-adult	19/04/2012	740	37	9
4	HE *	Female	Sub-adult	20/04/2012	676	4	4
5	AZ	Male	Adult	20/04/2012	855	121	16
6	ON	Female	Adult	20/04/2012	994	118	14
7	TE	Female	Adult	07/05/2012	765	247	22
8	MO	Male	Adult	08/05/2012	945	175	11
9	EL	Female	Adult	09/05/2012	935	165	8
10	RO	Female	Adult	11/05/2012	904	162	7
11	CH	Female	Adult	11/05/2012	915	205	15
12	MR *	Male	Adult	12/05/2012	904	27	7
13	TA *	Unknown	Juvenile	-	-	40	9
14	LU *	Unknown	Infant	-	-	1	1
	UN *	-	Adult	-	-	64	16
Average adult males (n = 4; 3)					897.25 ± 37.7	1989	
Average adult females (n = 6)					875.5 ± 100.5		

I followed the radio-collared animals for 327.75 hours on 70 days between 4th April and 1st August 2012. I collected 1989 5-minute observation points, totalling 165.75 hours of direct observation. Thus, the animals were out of sight 50 % of the time.

Figure 3.1 shows the activity budget for nine adult radio-collared and several unidentified Javan slow lorises. Animals spent almost half of their time on inactive behaviours e.g. sleeping and resting, and alert and freezing, and almost a third of their time feeding and foraging. Although individual variation was detected, preliminary results suggest that females spent more time foraging while males were more alert, travelled more and showed more social behaviour (^{2}= 70.971, df = 9, $p < 0.001$, n = 1590). This result may have been influenced by one prolonged bout of aggression between the adult male GU and an uncollared individual, and the intensive relationship between GU and the juvenile male YO (including social activities like playing, allogrooming and following each other). Removing GU from the analysis still resulted in a significant test outcome (^{2}= 73.010, df = 9, $p < 0.001$, n = 1396) but no significant difference between sexes in social behaviour.

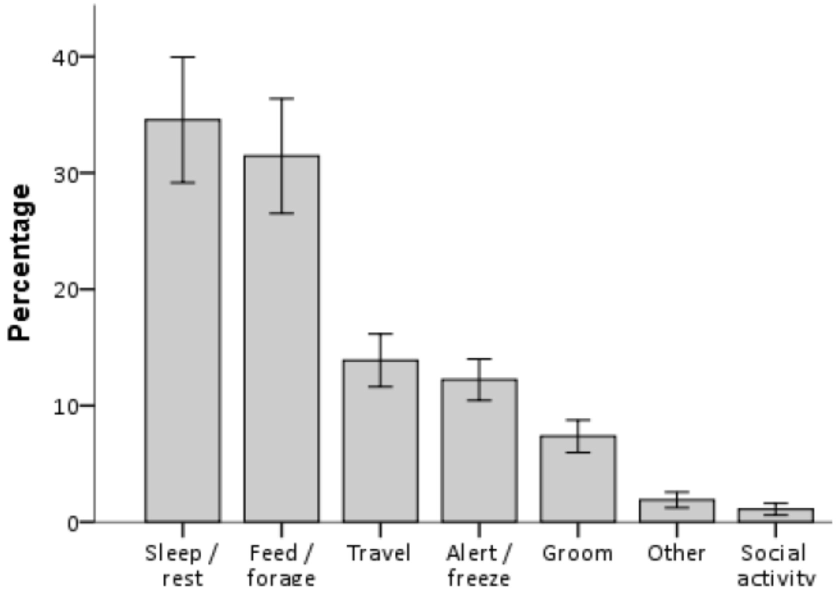


Figure 3.1: Proportion of instantaneous sample points of nine radio-collared and unidentified adult Javan slow lorises (n = 1590). Error bars denote ±1 standard error

In accordance with other studies (Table 3.2), the percentages of resting and sleeping, being alert and freezing were relatively high, in contrast to the findings of Wiens and Zitzmann (2003), who reported low frequencies of resting and sleeping in Malaysian greater slow loris.

Table 3.2 Activity budget of slow loris species: 1 = Swapna et al. 2010, 2 = Rogers & Nekaris 2011, 3 = Wiens & Zitzmann 2003, 4 = this study

	N. bengalensis[1]	***N. bengalensis***[2]	***N. coucang***[3]	***N. javanicus***[4]
Rest, sleep	40.5	41; 7	5.4	33
Travel	23.2	36 (incl. forage)	-	14
Forage, feed	5.1; 22.3	6 (only feed)	20.5 (only feed)	31
Groom	7.2	4	-	7
Alert	-	7	-	12
Social	0.4	0	3.5	1

Animals were seen within sighting distance of other lorises in 13 % of the observations (n = 258). In 57 % of these cases (n = 147), animals were closer than 5 m, while in 37 % of cases (n = 96), animals were in bodily contact or less than a body length away. Social behaviours recorded (n = 40) included allogrooming (38 %), playing (35 %), aggression (15 %; only one incident, between two adult males) and other social behaviours (13 %). I also observed following and sleeping in contact with another animal.

In total, 261 random trees and 1875 used trees of 38 species were recorded (Table 3.3). Comparing the numbers of the ten most commonly used tree species and the category "other tree species" with randomly sampled trees, I found that slow lorises prefer bamboo (string bamboo ***Gigantochloa apus***, and sweet bamboo ***G. atter***), green wattle, and red calliandra, but use other common species less than expected (cajeput tree ***Melaleuca leucadendra,*** Chinese mahogany, Japanese persimmon, other tree species) (^{2}= 205.926, df = 10, $p < 0.001$, n = 2136). On the transects I recorded 65% of the points to be in cultivated fields, 18 % in abandoned fields, 8 % in bush area, 5 % on paths, 3 % in tree patches and 2 % in bamboo patches (n = 354), adding up to only 5 % of dense and high vegetation (trees and bamboo).

Table 3.3: List of plant species that were used by Javan slow lorises during this three month study, their use by local people and the percentage of samples: used by slow lorises (n = 1875), and presence in transects (n=261). Bold numbers indicate that tree species were used significantly more often by lorises than expected by chance, while numbers underlined indicate that the trees were used significantly less often. 1 = Consumption (including smoking), 2 = construction material, 3 = house (including traditional roof), 4 = furniture, 5 = garden (flower, fence, stable), 6 = fire wood, 7 = natural prevention of erosion, 8 = mortar, 9 = packing material. *= ten most commonly used tree species

	Scientific name	Family	English	% used	% random	Count used	Count random	Trees used for
1	*Gigantochloa apus* (Schult.) Kurz, *Gigantochloa atter* (Hassk.) Kurz	POA	String bamboo, sweet bamboo	**37**	4	682*	11	2, 5
2	*Melaleuca leucadendra* (L.) L.	MRT	Cajeput tree	22	39	399*	102	3, 4, 5
3	*Acacia decurrens* (Willd.)	FAB	Green wattle	**9**	2	166*	6	6
4	*Persea Americana* (Mill.)	LAU	Avocado	9	9	160*	23	1, 3
5	*Calliandra calothyrsus* (Meisn.)	FAB	Red calliandra	**7**	4	120*	11	6, 7
6	*Toona sureni* (Blume) Merr.	MEL	Suren, Indonesian mahogany	5	10	87*	27	3, 4
7	*Grevillea robusta* (A.Cunn. ex R.Br.)	PRT	Silky oak	3	3	62*	7	3, 4
8	*Artocarpus heterophyllus* (Lam.)	MOR	Jackfruit	2	2	28*	4	1, 3, 8
9	*Diospyros kaki* (L.f.)	EBN	Japanese persimmon	1	3	19*	9	1, 3
10	*Coffea Arabica* (L.)	RUB	Arabica coffee	<1	<1	17*	1	1, 6
11	*Casuarina junghuhniana* (Miq.)	CAS	?	<1	4	15	11	3
12	*Musa acuminata* (Colla)	MUS	Banana	<1	7	10	18	1, 9
13	*Schima wallichii* (Choisy)	TEA	Needle wood	<1	<1	10	2	3
14	*Dendrocalamus asper* (Schult.) Backer	POA	Giant bamboo	<1	0	9	0	2, 5
15	*Maesopsis eminii* (Engl.)	RHM	Umbrella tree	<1	4	8	10	3, 4
16	*Chromolaena odorata* (L.) R.M.King & H.Rob.	CMP	Siam weed, Christmas bush	<1	0	7	0	6, 7
17	*Ageratina riparia* (Regel) R.M.King & H.Rob., *Lycianthes denticulata* (Blume) Bitter, *Gaultheria sp.*(L.)	CMP, SOL, ERI	Mistflower, ?, ?	<1	0	7	0	6
18	*Gigantochloa sp.* Kurz ex Munro	POA	Clumping bamboo (genus)	<1	<1	5	2	2, 5
19	*Cestrum aurantiacum* (Lindl.)	SOL	?	<1	0	4	0	7
20	*Citrus aurantiifolia* (Chrism.) Swingle	RUT	Key lime (?)	<1	<1	3	1	1
21	*Aleurites moluccanus* (L.) Willd.	EUP	Candlenut	<1	0	2	0	1, 3
22	*Arenga pinnata* (Wurmb)	PAL	Sugar palm	<1	0	1	0	1, 3, 9
23	*Calliandra tetragona* (Willd.) Benth.	FAB	White calliandra	<1	0	1	0	6, 7
24	*Brugmansia suaveolens* (Humb. & Bonpl. ex Willd.) Bercht. & J.Presl	SOL	Angel trumpet	<1	0	1	0	5, 7

	Scientific name	Family	English	% used	% random	Count used	Count random	Trees used for
25	*Eriobotrya japonica* (Thunb.) Lindl.	ROS	Loquat	<1	0	1	0	1, 6
26	*Camellia chinensis* (Sims) Kuntze	TEA	Tea	<1	0	1	0	1, 6
27	*Manglietia blumei* Prantl	MAG	?	0	3	0	9	3
28	*Cinnamomum burmanni* (Nees & T.Nees) Blume	LAU	Indonesian cinnamon	0	1	0	3	1, 3, 4
29	*Carica papaya* (L.)	CRC	Papaya	0	1	0	3	1
30	*Anthocephalus cadamba* (Roxb.) Miq.	RUB	Common bur flower, kadamb	0	<1	0	1	3, 4
				n = 1875	**n = 261**			

I recorded animals feeding 81 times (4.7 %). In 68 cases I could identify the food items. Animals fed mainly on the gum of green wattle ***Acacia decurrens*** (55.9 %), the nectar of flowers of red calliandra (32.2 %) and insects (7.4 %). In only two cases, animals fed on fruit (Japanese persimmon and jackfruit ***Artocarpus heterophyllus***). The consumed insects that could be identified were two caterpillars (Lepidoptera), two grasshoppers (Orthoptera) and one cockroach (Dictyoptera). When feeding on exudates, animals climbed up and down the trunks and branches and checked already existent, loris-made gouge holes, or created new holes. They then licked the leaking exudates or increased the holes by anchoring their teeth and gouging strongly or chiselling away the bark. The nectar of red calliandra was eaten as described by Moore (2012), by climbing among the terminal branches of the tree or bush, stabilizing themselves in a standing or hanging position, and grabbing and bending the flower towards them using one or both hands. They then licked the nectar accumulating in between the stamens without damaging the flower. I examined 43 different faecal samples and found gum in 70 %, arthopod remains in 95 %, wings in 72 %, caterpillars in 28 % and seeds in 40 % of the samples. Samples with arthopod remains contained a median on eleven countable arthopod pieces (range 1 to 52) and samples with seeds contained a median of one seed per sample (range 1 to 64). The taxa of arthopod remains and seeds could not be identified.

I conducted 21 trap nights for Malaise traps, 17 for sweep nets and 9 for pitfall traps. In total I caught 1185 arthropods many of which were from arthropod groups that include potentially noxious taxa (Table 3.4). Of all 118 Hymenoptera caught, 103 were ants.

Table 3.4: Abundance of all arthropods caught during 5 months in the agriculture *talun* fields of Cipaganti, West Java. "Potentially noxious" are taxa on Java known to produce toxic secretions, indicated by citations

Arthropods	Total caught	Potentially noxious	Source
Insect order	**N**		
Blattodea (cockroaches)	6	Blattidae	Hebard 1929, Wallbank & Waterhouse 1970
Coleoptera (beetles)	70	Tenebrionidae	Chen & Xia 2001, Seena & Thomas 2013
Dermaptera (earwigs)	14	Arixeniidae	Marshall 1977, Eisner et al. 2000
Hemiptera (true bugs)	71	Heteroptera: Reduviidae	Ryckman 1979, Ishikawa et al. 2007
Hymenoptera (bees, ants, wasps)	118	Formicidae, Formicinae: *Polyrhachis*	Maschwitz et al. 2000, Torres et al. 2013
Lepidoptera (butterflies, moths)	393	Arctiidae	Rothschild et al. 1970, Sutrisno 2010
Mantodae (mantids)	21	-	
Odonata (dragonflies)	3	-	
Orthoptera (grasshoppers, crickets, katydids)	266	Tettigoniidae	Nickle et al. 1996, Rentz 2001
Other arthropod classes			
Arachnida (arachnids)	220	Araneae	Murphy & Murphy 2012
Chilopoda (centipedes)	1	Geophilomorpha: *Mesoschendyla*	Attems 1907, Edgecomb & Giribet 2007
Diplopoda (millipedes)	2	Spirostreptidae	Hoffman 1975, Eisner et al. 1978

The median abundance per arthropod taxa and trap type are illustrated in Figure 3.2. When checking the correlations between the different arthropod taxa – trap type combinations and environmental factors using Spearman Rank correlations, only two correlations were significant. The abundance of adult Lepidoptera captured by Malaise trap correlated significantly negatively with wind strength ($R = -0.824$, $p = 0.006$, $n = 9$). The abundance of Orthoptera captured with sweep nets correlated significantly negatively with average humidity ($R = -0.790$, $p = 0.011$, $n = 9$). All other combinations showed no significant correlations with any of the abiotic factors collected.

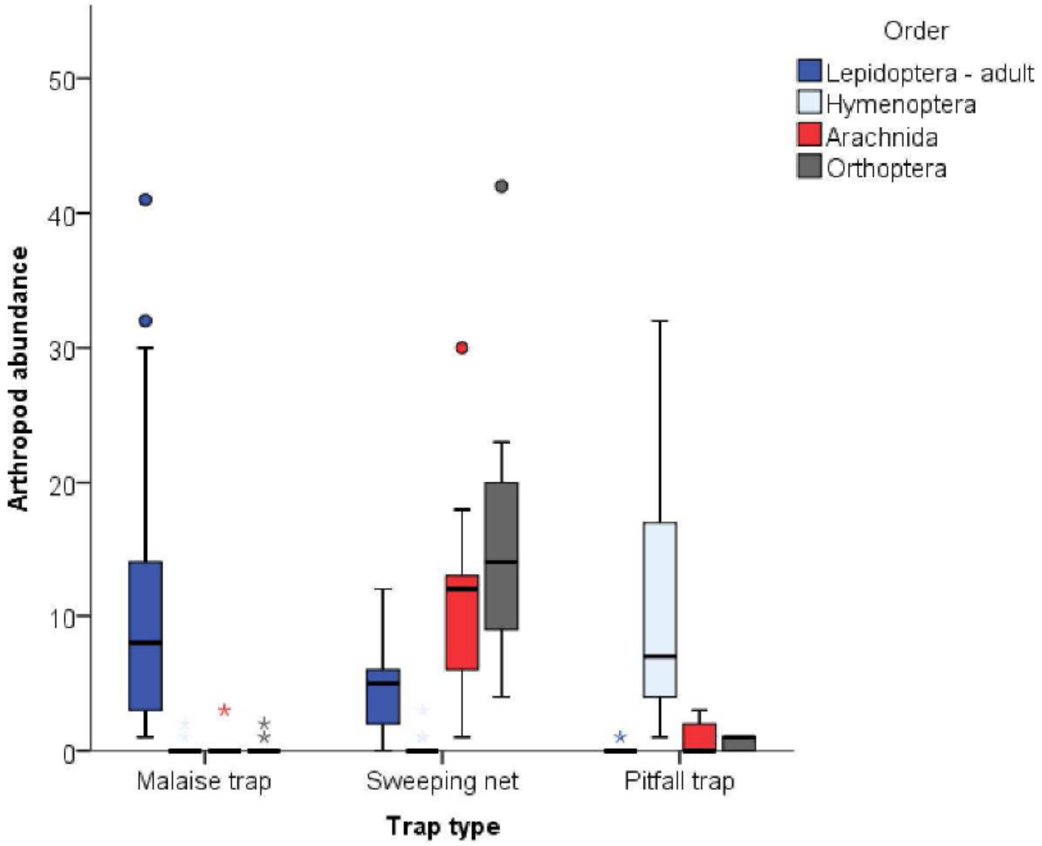


Figure 3.2: Median abundance of the most frequently captured arthropod taxa per trap type. Sample size: Malaise trap n = 21, sweep net n = 17, pitfall trap n = 9. Error bars: ± 1SE

4. Discussion

The study area is situated in an area of Java where most land has been modified by humans (Smiet 1990, Lavigne & Gunnell 2006). Natural habitat remains only in inaccessible places such as at high altitude and on steep slopes (Smiet 1992, Lavigne & Gunnell 2006). At the study site, slow lorises live in agricultural areas (*talun*) where humans live and work. They are confined to small habitat fragments surrounded by fields, threatened by habitat loss through the cutting of trees and bamboo, and exposed to human activities mainly during the day. Although lorises may come to the ground and low vegetation (Wiens 2002, APPENDIX 4, Section 6) to travel between fragments, according to my transect data, high and dense vegetation that can be used by slow lorises (e.g. trees and bamboo) make up a very small proportion of the available habitat. The area is not protected and thus lorises rely on the good will of people for their survival. This situation is similar for other threatened primates throughout Asia, such as purple-faced langurs ***Trachypithecus vetulus*** (Moore et al. 2010) and Hainan gibbons ***Nomascus hainanus*** (Zhou et al. 2005). Effects of degraded and human-altered habitat on primates may include reduced feeding resources, fewer sleeping or hiding places, higher susceptibility to invasive or aerial predators, increased hunting pressure, disturbance and higher exposure to parasites (Wright et al. 2009, Schwitzer et al. 2010a, Schwitzer et al. 2011). Slow lorises, however, apparently are able to adjust to human-modified habitats like this mosaic landscape of agricultural fields, bamboo stands and forest fragments.

The activity budgets of adult Javan slow lorises in my study conform to the published activity budgets of Bengal slow lorises (Swapna et al. 2010, Rogers & Nekaris 2011), however Wiens and Zitzmann (2003) report a very small proportion of time spent resting, although they did not provide an exhaustive ethogram. Furthermore, my study and that of Swapna et al. (2010) were conducted during the dry, cold season. The combination of season, temperature and light may have affected the level of activity and alertness.

Solitary mammal species usually forage alone during their active period, yet may still be in contact with conspecifics (e.g. via olfaction or vocalizations), sleep in groups or live in complex social networks (Waser & Jones 1983). Several studies in captivity concluded that slow lorises are very gregarious given the opportunity. Animals spent one third of their time in proximity and shared nest boxes (Ehrlich & Musicant 1977) and rarely engaged in agonistic behaviours (Daschbach 1983, Ehrlich & MacBride 1989). Although animals occasionally show aggressive behaviour in rescue centres, this might be a by-product of the trauma animals have experienced in the pet trade, and rescue centres may house up to eight animals in social groups (Moore 2012). In wild Javan slow lorises, I only observed one case of aggression in three months (but see CHAPTER 4). In Bengal, greater and pygmy slow lorises social activities clearly occur outside the sample points that make up activity budgets, as the frequency of social activities recorded was relatively low (Table 3.2). Individuals of Javan and greater slow lorises were often observed within sighting distance of one another (13 % for Javan slow lorises, this study; 8 % for greater slow lorises, Wiens 2002). I have shown that the social behaviours of wild Javan slow lorises are similar to those of other species of lorises studied in the wild, including allogrooming, playing, following, and sleeping in contact with another animal (Wiens & Zitzmann 2003). Therefore slow lorises do not qualify as gregarious, but they are definitely social.

Few studies have reported the tree species that slow lorises use during general activity. The amount of bamboo in a forest seems to have a positive effect on the encounter rates of Javan slow lorises (Voskamp et al. 2014). Bamboo species seem to be important as sleeping and resting sites (Winarti 2003, 2011, Dahrudin & Wirdateti 2008). Bengal slow lorises were found more often in plantations with high numbers of *Acacia* and *Leucaena* trees and *Bauhinia* lianas (all members of the legume family Fabaceae) as compared to primary forest (Pliosungnoen et al. 2010). Diet is also likely to influence tree species preferences. Fabaceae, for instance, are used by all slow loris species as sources of exudates (Nekaris et al. 2010a). In this study, green wattle and red calliandra were preferred for their gum and nectar. As for diet, the preferences of lorises for certain tree species may change with the season (APPENDIX 5, section 9). Non-preferred tree species may not play a special role in the animals' diet or sleeping site choice, but may be used during travel. Almost all tree species recorded in this study as used by Javan slow lorises are non-native. Nevertheless, I found a healthy population of lorises in this habitat and the animals seemed to be well adapted to the dietary options, habitat structures and the relatively confined space provided by this human-modified landscape. Adjustment to human-modified mosaic landscapes and exotic tree species bear important implications for the reintroduction of confiscated animals that might have been caught in those habitats. One of the possible reasons for failed reintroductions of Javan slow lorises to the wild is that animals that have grown accustomed to agricultural areas and their component plant species are released into dense rainforests; newly released Javan slow lorises often moved out of the old stage forests where they were released into agricultural areas up to a few kilometres away (Moore 2012). One of my hypotheses is that gum is sequestered from secondary plant metabolites. Although most tree species used by animals in my field site are non-native, Javan slow lorises use similar native plant genera (Moore pers. comm.). Das et al. (2014) report as much as 43 native plant species (trees, climbers and lianas) used for exudativory by Bengal slow lorises. As bites of slow loris conspecifics in rescue centres are still venomous, a part of the venom may be produced *de novo*, while a sequestered part may vary according to the plant species available. Thus, even though slow lorises used non-native tree species here, feeding on gum is not a recent innovation as their morphology is highly adapted to exudate feeding (Nekaris et al. 2010a, Starr & Nekaris 2013, Nekaris 2014). The sequestration of venom subsequently is likely to have developed a long time ago as well (the split of *Loris* and *Nycticebus* occurred approximately 25 million years ago, Pozzi et al. 2014).

Slow lorises feed on gum, invertebrates, nectar of flowers, fruit, small vertebrates, molluscs, bird eggs, leaves, bark, bamboo and fungi (Table 3.5) (Tan & Drake 2001, Wiens 2002, Wiens & Zitzmann 2003, Winarti 2003, Pliosungnoen & Savini 2008, Streicher et al. 2009, Nekaris et al. 2010a, Swapna et al. 2010, Rogers & Nekaris 2011, Winarti 2011, Starr & Nekaris 2013, Streicher et al. 2013). Nash and Burrows (2010) reviewed several primate species that form part of a gum-feeding guild. Some species use gum opportunistically while searching for insects on tree surfaces or as a staple or fallback food in times of food shortage (Porter et al. 2009, Streicher 2009). For other species gum is an obligatory dietary component. Only a few species are able to stimulate exudate flow actively by gouging. This behaviour is shown by the callitrichine genera ***Callithrix***, ***Callibella, Mico*** and ***Cebuella***, the Masoala fork-marked lemur ***Phaner furcifer*** and the Southern needle-clawed galago ***Euoticus elegantulus*** (Vinyard et al. 2003, Schwitzer et al. 2010b). Sixty-five per cent of the diet of fork-marked lemurs is gum, which is available all year round. Needle-clawed galagos include 75 % gum in their diet; the rest consists of insects and fruit (Charles-Dominique 1977). African lesser bushbaby ***Galago moholi*** fed primarily on gum and insects, with higher gum intake during winter when gum showed a higher energy content (Nowack et al. 2013). All slow loris species gouge, and spend a considerable amount of their feeding time consuming exudates (pygmy slow loris: Tan & Drake 2001, Nekaris et al. 2010a, Starr & Nekaris 2013, Streicher et al. 2013; greater slow loris: Barrett 1984, Wiens et al. 2006, Nekaris & Munds 2010; Bengal slow loris: Pliosungnoen & Savini 2008, Nekaris et al. 2010a, Swapna et al. 2010, Das et al. 2014; Javan slow loris: Winarti 2003, Nekaris et al. 2010a, Winarti 2011, Bornean slow loris: Nekaris et al. 2010a) (Table 3.5). Nekaris et al. (2010a) reviewed exudate feeding in Asian lorises, and listed 12 plant families exploited by slow lorises for exudates. Javan slow lorises were seen feeding on exudates of Fabaceae, Arecaceae and Moraceae (Nekaris et al. 2010a, Winarti 2011). In this study we can confirm by direct observations and faecal samples that Javan slow lorises are feeding extensively on gum.

Nectar is another important component of the diet (Table 3.5). Re-introduced Javan slow lorises spent 90 % of their feeding time consuming nectar (Moore 2012). Javan slow lorises feed on the nectar of red calliandra (Moore 2012, this study) and banana ***Musa x paradisiaca***, family Musaceae (Winarti 2011). Pliosungnoen and Savini (2008) saw Bengal slow lorises feeding on ***Parkia*** flowers, family Fabaceae. Porter at al. (2009) observed the Goeldi's monkey ***Callimico goeldii*** in Bolivia using pod exudates of ***Parkia*** flowers as a fallback food during the dry season. Nectar could not been identified in the faecal samples.

Table 3.5: Feeding budgets of slow loris species: 1 = Swapna et al. 2010, 2 = Das et al. 2014, 3 = Wiens et al. 2006, 4 = this study (in brackets: prevalence in faecal samples), 5 = Streicher et al. 2013, 6 = Starr & Nekaris 2013

	N. bengalensis[1]*	***N. bengalensis***[2]	***N. coucang***[3]	***N. javanicus***[4]	***N. pygmaeus***[5]	***N. pygmaeus***[6]*
Exudates	86.5	80.9	43.3	55.9 (70)	60	50
Insects	2.9	2.3	2.5 (Arthropods)	7.4 (95)	40	20
Nectar	6.4	3.2	31.7	32.2 (-)		10
Fruit	0.3	4.5	22.5	2.9 (40)		18
Fungi						3
Bamboo						5
Vertebrates						1
Bark	1.9	7.3				
Bird eggs	1.2					
Tender leaves		1.8				
Bouts (samples)	329	629	139	68 (43)	27	168

*= averaged between seasons

My study was conducted during the onset of the dry season and dietary component proportions may differ between seasons (Charles-Dominique 1977, Hladik et al. 1980). Considerable seasonal differences in feeding budgets were observed for greater and pygmy slow lorises (Swapna et al. 2010, Starr & Nekaris 2013). The proportion of gum in the diet was higher in the winter, while more nectar and insects were consumed in the summer by Bengal slow lorises (Swapna et al. 2010). Pygmy slow lorises did not feed on nectar or fruits in the cold season at all, and more than doubled the proportion of insects they consumed (Starr & Nekaris 2013).

Gum and nectar are potential sources for secondary plant metabolites, that may serve in the sequestration of venom is slow lorises (CHAPTER 1, section 5.3). The high frequency of these diet components shown for all slow loris species may serve as a basis for further research, e.g. on the dietary composition of gum and nectar in this area.

The arthropod prey of slow lorises includes the insect orders Lepidoptera (larvae and imagines), Hemiptera, Coleoptera, Hymenoptera and the class Arachnida (Hladik 1979, Wiens et al. 2006, Streicher et al. 2009); orders that include a variety of noxious taxa (Table 3.4) and may be used for venom sequestration. For instance Wiens et al. (2006) report that 40 % of greater slow loris faecal samples contained ants and 12.8 % contained caterpillar remains. In this study almost all samples contained arthropod remains, and 28 % contained caterpillar remains. Although ant remains were present in the samples I examined, I could not determine the number of individual ants. I furthermore saw Javan slow lorises consuming moths and cockroaches during the study period. Caterpillars, ants and cockroaches may contain toxins that may be used for defensive purposes (Table 3.4). It is possible that these taxa belong to the arthropods that serve as sources for venom sequestration in slow lorises. Many other animals are known to sequester toxins from a noxious diet and accumulate them in their tissue (CHAPTER 1, section 5.3). Comparing the rare direct observation of arthropod feeding with the high prevalence of insect remains in the faeces found in this study, this diet component was likely to be underestimated. Feeding on arthropods often involved very fast movements between sampling intervals, and could easily be missed, especially when animals were in very dense habitat like bamboo or bushes.

I examined the available arthropods in the field site to understand the availability of noxious arthropods in the diet of slow lorises and the environmental determinants of abundance of different arthropod taxa. When venom becomes available for analysis, variation of venom composition in relation to environmental conditions may be detected and related to variations in the arthropod community. I found only some significant correlations between trap type – taxa combinations and environmental factors. Fewer Lepidoptera were captured in the Malaise trap in strong wind, while air humidity had a suppressing effect on the abundance of Orthoptera caught with the sweep net. Wind has been shown to have a negative effect on the activity of flying insects in several studies (e. g. Williams 1940, Wolda 1977). Humidity was found to usually have a positive effect on insect activity; however it may also be suppressed by high humidity (Gilbert 1985). No relation between arthropod abundance and rainfall in the last 24 hours was found in my study. This conforms to previous research indicating a three-week lag between rainfall and a numerical response in arthropod communities (Tanaka & Tanaka 1982) and seasonality, rather than short term rainfall, as major drivers of arthropod abundance in the tropics (Fogden 1972, Robinson et al. 1974, Frith 1975, Bigger 1976, Wolda 1978). Studies on the effect of temperature on insect activity found a lower temperature threshold below which flight is inhibited (Taylor 1963) and an increase in wing-beat frequency and activity in Lepidoptera and Diptera with increasing temperature (Sotavalta 1947). Most studies on the effect of lunar illumination found that flying insects are more active in dark nights (reviewed in Nowinszky 2004, Lang et al. 2005). However both Nowinsky (2005) and Lang et al. (2005) warn against jumping to conclusions, as the effectiveness of light trapping (although Malaise traps are regarded as passive traps, most traps include a white-coloured tent that may enhance attraction to insects) may be higher in dark nights due to a stronger light contrast. As with trap type, effects of environmental factors were not consistent between different arthropod taxa, emphasising how essential careful study design is. I encourage continuing to sampling arthropods and collect slow loris faeces to see if the diet of slow lorises tracks predictable changes in the arthropod community, or whether they search for preferred prey irrespective of environmental conditions.

Even though I saw animals feeding on two different fruits (Japanese persimmon and jackfruit) also consumed by humans, this occurred rarely and did not qualify slow lorises as a pest species. I never observed animals feeding on vegetables planted in the fields. Although seeds may have been avoided or spat out, the amount of seeds in faecal samples seem to confirm the low contribution of fruits to the diet.

Considering that slow lorises consume a high amount of secondary plant metabolites and (noxious) arthropods, one role of venom could be as a pre-digestive aid; this is the primary function of venom suggested for monitor lizards (*Varanus* spp.) (Arbuckle 2009). In combination of BGE salivary amylases may work more efficiently on carbohydrates in the exoskeleton of arthropods, and may assist in the detoxification process of secondary plant metabolites or toxins in arthropods. This hypothesis may be the subject of future research.

In summary, although slow loris species differ in aspects of their ecology, they seem to have similar needs in terms of fundamental feeding and social activities to other slow loris species. This has implications for the husbandry of animals in zoos, rescue centres or when preparing rescued animals for release. This means that animals should be fed a diet that is close in its composition to the natural diet of wild slow lorises, for example including gum as a large proportion of this. In respect to the importance of secondary metabolites and noxious arthropods for the venom ecology of slow lorises future studies should explore relations of slow loris venom composition with the actual diet of slow lorises. This can be measured by direct observations and in faecal samples, the abundance and availability of noxious arthropods and gum at the field site, and environmental factors.

CHAPTER 4

Take up your arms!

Intraspecific competition, territoriality and social system in Javan slow lorises

1. Introduction

Weaponry in animals has evolved in response to natural selection for predator defence, or social or sexual competition for resources (Stankowich 2011). The use of venom can be seen as a weapon and is documented for many species (Ligabue-Braun et al. 2012, Casewell et al. 2013). While the ecological function of venom is predominantly prey acquisition and predator defence (Casewell et al. 2013), venom use in the context of social and sexual competition has rarely been discussed. There are only some species that are known to use venom for intraspecific competition. The platypus possesses a crural system that consists of crutinised spurs on their hind legs that are associated with venom producing crural glands (Grant & Temple-Smith 1989, Krause 2009, Whittington & Belov 2007). The venom has been explained by sexual competition as only male platypus produce venom during the mating season (Temple-Smith 1973). The second gnathopods of ghost or skeleton shrimps (*Caprella* spp., order Amphipoda, family Caprellidae) are armed with a so-called poison tooth that is connected to a venom-producing gland (Takeshita & Wada 2012). The second gnathopods are bigger in males and are used in often fatal combats with sexual competitors (Takeshita & Wada 2012). Cone snails (superfamily Conidea) use their extendible proboscis and a needle-like radular tooth that are connected to an esophageal venom gland to prey on worms, molluscs or fish (Olivera et al. 2014). Olivera et al. (2014) report that cone snails not only catch prey with the help of venom, but also use it against potential predators and in intra- and interspecific competitive interactions.

Slow lorises may be one of the animal groups that use venom for social and sexual competition (Nekaris et al. 2013a, CHAPTER 1, section 5.4). Slow lorises seem to be territorial, with male lorises licking their venom gland during territorial fights (Nekaris et al. 2013a) and bites caused by conspecifics are frequent in captivity, rescue centres and illegal wildlife markets. Bitten individuals show extreme physical reactions which have been attributed to the toxicity of the venom combined with saliva (Sutherland-Smith & Stalis 2001, Streicher 2004, Wiens & Zitzmann 2003, Fuller et al. 2014, Nekaris et al. 2013a).

In this chapter I examined whether venomous Javan slow lorises showed high levels of social and sexual competition that can explain the use of venom. I did this by looking at the degree of competition in their social system. The social system of a species can be described by three components: social organisation, mating system and social structure (Kappeler & Schaik 2002). The social organization is a demographic concept incorporating patterns of age and sex structure of societies and how they vary in space and time. Species can exhibit social monogamy, multi-male systems, harems or social polyandry (Mueller & Thalman 2000). While many diurnal mammals live in cohesive groups, most nocturnal mammals show a dispersed social organisation (forage solitary but live in social networks) or spatial social organization (no social relations outside the mating season) (Mueller & Thalman 2000). The mating system specifically describes the reproductive interactions between individuals and is usually described in terms of the strategies. Strategies can be monogamous, polygynous, polyandrous, or promiscuous (Kappeler & van Schaik 2002). These terms partly overlap with terms used in regard to social organisation, and should be read in context or specified clearly. Finally, the social structure includes all relationships between individuals in a group, such as the nature, frequency, and intensity of affiliative and agonistic interactions (Kappeler & Schaik 2002). All components of the social system are associated with different degrees of intra- and intersexual social competition, between and within groups (Koenig et al. 2013).

As the greater slow loris lives in a dispersed monogamous social organisation with territories shared only with a member of the opposite sex and one or two offspring (Wiens & Zitzmann 2003, Nekaris & Bearder 2011), I hypothesise that Javan slow lorises have the same social organisation with high home range overlap and affiliations between partners and their offspring, but low home range overlap and affiliations between neighbours. In border areas of territories there should be higher numbers of agonistic encounters, patrolling and grooming, that possibly includes the uptake of venom to prepare for fights.

A monogamous social organisation is usually associated with a monogamous mating system where males defend their female partners directly or indirectly by protecting their home range (Emlen & Oring 1977, Mueller & Thalman 2000, Hilgartner et al. 2012). Monogamy in primates is characterised by contest competition, indicated by high sexual dimorphism, small testicles, frequent injuries and male use of weapons (such as teeth), as well as slightly larger home ranges in males (Kappeler 1997a). I adapted this basic framework because in addition to sexual competition, both sexes in slow lorises should demonstrate high social competition for resources. Tree exudates are the main component in the diet of slow lorises (Wiens et al. 2006, Swapna et al. 2010, Starr & Nekaris 2013, Streicher et al. 2013, Das et al. 2014, CHAPTER 3) and occur in a small number of non-randomly distributed trees (Schuelke & Kappeler 2003). Defendable good quality territories with a certain number of this important resource can be monopolised and lead to inter-group contest competition (Sterck et al. 1997, Schuelke & Kappeler 2003). Thus, as social competition acts on both sexes I tested the hypotheses that Javan slow lorises show no sexual dimorphism, high frequency of injuries and the secretion of venom in both sexes, but still small testicles and same-sized home ranges in males due to the monogamous mating system. Slightly larger home ranges may occur due to male excursions.

Finally, regarding the social structure, dispersed socially monogamous species have often been reported to avoid each other or even show increased agonistic behaviour due to resource competition (Schuelke & Kappeler 2003, Koenig et al. 2013), especially if feeding resources are non-randomly distributed as is the case with exudate-feeding fork-marked lemurs (Schuelke & Kappeler 2003). As some lorisid species such as Mysore Slender Loris (***Loris lydekkerianus lydekkerianus***) in the wild (Nekaris 2003) or greater slow lorises in captivity (Ehrlich & Musicant 1977) have been described as relatively social, and because the potentially dangerous effect of venomous bites by conspecifics has to be avoided, I hypothesised a low rate of agonistic encounters and possibly rather high frequencies of affiliative encounters.

2. Methods

Details about the study site can be found in CHAPTER 2, section 3.1.

Data collection

I captured and took morphometric measurements of 28 Javan slow lorises according to the methods indicated in CHAPTER 2, sections 4.1.1 and 4.1.2. From measurements of the length and width of each testicle, I calculated testis volume with the formula for a regular ellipsoid $V = 1/6 * (\pi W^2 L)$ where W was the average width of both testes and L was the length of the longest testis (Kappeler 1997b). To receive the relative testis size I divided mean testis volume by mean body mass (Schwab 2000). I thoroughly examined the body of each loris, especially the extremities, digits and ears for wounds, injuries and scars. I scored the venom secretion at the beginning of the examination right after the capture, using the categories “no secretion”, “little”, “medium”, and “a lot”. Radio-collaring and data collection of behaviour and ranging are described in CHAPTER 2, sections 4.1.2 and 4.1.3. During behavioural observations I noted the presence of, distance to and identity of other slow lorises if the lorises were less than 10 m apart, including bodily contact.

Data analysis

A home range is defined as the area traversed by the individual in its normal activities of food gathering, mating, and caring for young (Burt 1943). I used RANGES 8 (Anatrack Ltd., UK) to calculate home ranges and home range overlap. To ensure compatibility, I used two different methods of estimating home range sizes that are often used in ecological studies (Harris et al. 1990). A Minimum Convex Polygon (MCP) draws a line around the outmost locations of an area to build a polygon (Kenward 2001). This method is known to include areas which might have never been visited by the animal and thus might overestimate the home range (Kenward 2001, Pimley et al. 2005). In addition, I used fixed kernel density estimation (Kernel home range = KHR), with a reference bandwidth (href) and smoothing multiplier = 1 as the smoothing parameter (Rodgers & Kie 2011). Kernel methods are statistical techniques that estimate density of the distribution at any point by looking at the proximity of observations to each evaluation point, e. g. observation (Seaman et al. 1998). They then model contours on the density estimates. Thus, these estimators acknowledge the intensity of use, show different centres of activity, and exclude areas that are not used by the animals (Kenward 2001, Pimley et al. 2005). For both methods, I used several core areas by choosing a certain percentage of fixes: 100 % MCP, 95 % MCP, 75 % MCP, 50 % MCP, 95 % KHR, 75 % KHR and 50 % KHR. I excluded four of the radio-collared animals as two were dispersing and two were immature (Table 4.1). I calculated home range sizes for two different “seasons” (e.g. weather period): a drier period with low minimum temperatures between May and October 2012 and a wetter period with warmer nights between November 2012 and April 2013. Several animals were radio-collared in November so that for these animals home ranges are only available for the wet period. Home ranges for several animals did not asymptote and were not used in the analyses (Table 4.1). This can be the case if animals shift their home ranges, disperse, or simply when not enough locations have been sampled (Harris et al. 1990). Home range overlap was also calculated with RANGES 8 and is defined by the percentage overlap of the polygons derived from the chosen home range estimator, such as 95 % KHR. I defined fixes located outside an individual’s 95 % KHR as the “border area” and as excursions.

For the following tests, only adult animals were included. I compared the frequency of behaviours in border areas against those within the annual 95 % KHR using Pearson Chi-Square tests. I applied the same tests to investigate whether focal animals met more pair partners or more neighbour animals in the border area of their home range. I tested for sexual dimorphism by examining the effect of sex on body mass and head body length using independent t-tests. Using the data set of 18 strepsirhines compiled by Kappeler (1997b) I calculated a regression line $y = 1.7x + 80.5$, where y is testis volume (mm^3) and x is body mass (g). I used this equation to calculate the expected testis volume for Javan slow lorises. I calculated a venom index per individual as an indication of the intensity of venom secretion of that animal. To derive this index I scored the venom categories from no secretion to a lot of secretion with the numbers 1 to 4, added the scores for each capture (up to 5) and divided them by the number of captures. I calculated an injury index by scoring different types of injuries: scars on the body and stiff digits = 1, head scars = 2, missing digits or ears = 3. I did not score minor fresh wounds as I noticed during consecutive captures that these would heal to the extent that they were not noticeable anymore in later captures. Due to the good healing power possessed by slow lorises (Nekaris et al. 2013a) permanent scars could potentially indicate a quite serious injury in the past. As the injury and venom index were not normally distributed, I used a Mann Whitney U test to assess whether there are differences between sexes. For the analysis of home range sizes I only used the home ranges of adults. Home range sizes that did not asymptote were excluded from the analysis. I examined the effect of sex and season and their interaction on home range size using a 2-way independent factorial ANOVA. I compared the testis volume of adult male slow lorises with the expected volume for strepsirhines with a one-sample t-test. All analyses were done with SPSS 20.0, with significance level set to 0.05. If not indicated differently, all confidence limits are standard deviations of the means.

I constructed a sociogram with UCINET 6 (Borgatti et al. 2002) for 11 radio-collared adults including immature animals to show the affiliative associations based on frequencies of animals closer than 5 m proximity. I also reported the frequencies of associations within proximities of less than 10 m. In the sociogram I excluded dispersing animals and one animal (ST) that was not seen in close proximity of any other known slow loris. I only used observations where the animals were clearly seen, e.g. where behavioural observations could be made. The higher frequency was chosen for each dyad. I report minimum frequencies for pair partners, as not all animals were radio-collared from the beginning. To avoid biases, I excluded all encounters between focal animals and uncollared, unidentifiable individuals.

3. Results

In total, I collected 7169 5-minute observation points of Javan slow lorises, resulting in 600 hours of direct observation. The combined data of animals in the sociogram included 4740 observation points, and I collected 3350 fixes of the 12 radio-collared animals (2978 fixes if immature were excluded).

3.1 Morphology, injuries and venom secretion

I could not detect sexual dimorphism in adult Javan slow lorises (Body mass: t(19) = 0.704, p = 0.49; head body length: t(17) = 0.597, p = 0.558). Adult males had an average testis volume of 1439 ± 336 mm^3 (Table 4.1). Compared to the expected 1539 mm^3, Javan slow lorises have smaller but not significantly different testis sizes (one-sample t-test -0.890, p = 0.399, n = 9). The average relative testis volume was 1.61 ± 0.43 mm^3/g. Over 14 months of study 60 % of the captured adult slow lorises (n = 20) showed injuries and scars. Most injuries were head scars (n = 7) and missing digits or ears (n = 6), three of the animals had more than one digit missing. Four animals had scars on other body parts, two animals showed stiff, broken or swollen digits and one animal had an eye cataract. In three cases observed scars were not visible during the next capture. The healing process was exemplified by the adult male, AZ, who was caught in a devastating health condition that suggested a low probability of survival. He showed severe damage of one eye (including loss of reflection by the ***tapetum lucidum***) and the nose, scars on the head and extremities, open wounds on knees and feet, and a stiff digit. During the next capture, three months later, everything except a small scar on the nose had healed, including the eye damage (Nekaris et al. 2013a). My data did not show a significant effect of sex on injury intensity or amount of venom secretion (venom index: U = 65.5, p = 0.422, n = 21; injury intensity index: U = 42.5, p = 0.678, n = 20).

Table 4.1: Details about morphometrics, venom secretion, injuries, and radio-tracking of 28 Javan slow lorises. F = female, M = male, A = adult, I = immature, S = sub-adult. Fixes in brackets indicate that animals were not radio-collared

ID	Sex	Age	N	Head body length (cm)	Weight ± sd (g)	Testis volume ± sd (mm^3)	Rel. testis volume ± sd (mm^3/g)	Wounds presence	Wounds intensity index	Venom index	First capture	Total fixes	Comment
AP	F	A	1	31.4	840			no	0	3	13/01/2014	N/A	
CH	F	A	4	32.4	920 ± 50			yes	4	1.60	11/05/2012	373	
EL	F	A	1	31.2	935			no	0	2.00	09/05/2012	120	Dispersed
EN	F	A	4	33.6	765 ± 48			yes	13	2.00	18/04/2012	461	
LU	F	A	1	29.8	845			no	0	1	10/01/2014	N/A	Daughter of CH
OE	F	A	5	31.5	951 ± 29			yes	3	1.40	20/04/2012	304	Mother of HE
RO	F	A	1	31.6	904			no	0	2.00	11/05/2012	69	Dispersed
SH	F	A	2	32.3	920 ± 75			yes	2	1.33	12/11/2012	148	Mother of UT
SI	F	A	1	30.1	974			no	0	2.00	12/11/2012	175	Mother of GA
TE	F	A	4	31.4	831 ± 46			yes	1	2.25	07/05/2012	349	Mother of TA
102	F	A	1	31.7	839			yes	4	2.00	23/06/2012	N/A	
106	F	A	1	31.5	886			no	0	3.00	08/08/2012	N/A	
CO	F	I	2	27.1	788 ± 77			yes	1	0.00	13/08/2012	(24)	Blind, brought to rescue centre
DE	F	J	1	28.3	390			no	0	3	15/01/2014	N/A	
GA	F	S	1	31.3	805			no	0	2	09/01/2014	N/A	Daughter of SI
HE	F	I	2	30.4	763 ± 123			no	0	4.00	20/04/2012	(11)	Daughter of OE
TA	F	I	2	28.5	645 ± 35			no	0	1.00	07/11/2012	253	Daughter of TE, died during dispersal Nov. 2013
104	F	S	1	30.3	805			no	0	2.00	25/06/2012		
107		S	1	30.6	967			no	0	2.00	08/08/2012	N/A	
Mean adult F				**31.5**	**884.2**								
SD adult F				**1.0**	**60.8**								
N adult F				**12**	**12**								
AZ	M	A	5		870 ± 23	2050 ± 620	2.35 ± 0.67	yes	10	1.60	20/04/2012	311	
DR	M	A	1	33.1	1025	1360	1.33	yes	0	2.00	05/07/2012	N/A	
GU	M	A	3	36.9	868 ± 53	1737 ± 895	1.98 ± 0.97	yes	3	1.00	17/04/2012	382	
KA	M	A	1	30.5	820	1727	2.11	yes	0	2.00	06/07/2012	N/A	

ID	Sex	Age	N	Head body length (cm)	Weight ± sd (g)	Testis volume ± sd (mm^3)	Rel. testis volume ± sd (mm^3/g)	Wounds presence	Wounds intensity index	Venom index	First capture	Total fixes	Comment
MO	M	A	5	31.3	899 ± 61	1247 ± 485	1.43 ± 0.60	yes	6	1.33	08/05/2012	332	
MR	M	A	1	33.0	904	1294	1.43	-	-	0.00	12/05/2012	N/A	
PB	M	A	1		990	1346	1.36	no	0	2	13/01/2014	N/A	
TO	M	A	2	31.3	861 ± 4	935 ± 403	1.08 ± 0.46	no	0	3.00	10/11/2012	143	
101	M	A	1	29.9	895	1257	1.40	yes	9	2.00	23/06/2012	N/A	
UT	M	I	1	26	583			no	0	2.00	02/12/2013	(7)	Son of SH
WI	M	J	1	28.6	640			yes	2	3	15/01/2014	N/A	Son of EN
YO	M	I	5	28.6	800 ± 55	608 ± 409	0.74 ± 0.5	yes	1	2.00	19/04/2012	119	Collared on 11/11/2012
103	M	S	1	29.9	845	1634	1.93	yes	2	2.00	23/06/2012	N/A	
105	M	S	1	28.9	735	323	0.44	no	0	2.00	25/06/2012	N/A	
108	M	S	1	29.9	822			no	0	3.00	09/08/2012	N/A	
Mean adult M				**32.3**	**904.6**	**1439.2**	**1.61**						
SD adult M				**2.4**	**64.7**	**336.3**	**0.43**						
N adult M				**9**	**9**	**9**	**9**						

3.2 Home range size

Average home range sizes of slow lorises for different sexes and seasons using different home range parameters are listed in Table 4.2. In most cases males had larger home ranges than females. However, none of the models showed a significant effect of sex, season, or their combination on home range size (Table 4.2). I also could not find a significant effect of sex on home range size if I combined the seasons to an annual home range ($t(8)_{100\%MCP} = 1.191$, $p = 0.268$, $t(8)_{95\%MCP} = -0.038$, $p = 0.971$, $t(8)_{75\%MCP} = 1.355$, $p = 0.213$, $t(8)_{50\%MCP} = 0.697$, $p = 0.506$, $t(8)_{95\%KHR} = 0.970$, $p = 0.361$, $t(8)_{75\%KHR} = 1.232$, $p = 0.253$, $t(8)_{50\%KHR} = 0.854$, $p = 0.418$).

Table 4.2: Home range sizes in hectare of 10 adult Javan slow lorises (4 females and 3 males in the dry season, 6 females and 4 males in the wet season), using Minimum Convex Polygons and Kernel, and results of the two-way independent factorial ANOVA models with home range size as dependent variable and sex and season and their interaction as independent variables

			MCP (ha)				Kernel (ha)		
	Season	**Fixes**	**100**	**95**	**75**	**50**	**95**	**75**	**50**
Dry period									
Mean	females	209.25	3.25	2.37	1.46	0.64	2.47	1.45	0.78
SD		45.40	1.06	0.95	0.67	0.23	1.20	0.77	0.39
Mean	males	205.33	5.24	3.03	1.68	0.71	3.19	2.02	1.13
SD		67.53	2.50	0.75	0.32	0.40	0.20	0.12	0.18
Mean	both	207.57	4.10	2.66	1.55	0.67	2.78	1.69	0.93
SD		50.55	1.94	0.87	0.52	0.29	0.94	0.63	0.35
Wet period									
Mean	females	85.33	4.08	3.26	1.33	0.53	3.57	2.03	1.15
SD		12.48	2.52	2.64	0.64	0.35	2.41	1.17	0.65
Mean	males	77.00	4.04	2.87	1.57	0.70	4.43	2.49	1.34
SD		16.10	1.49	0.68	0.39	0.41	0.99	0.77	0.55
Mean	both	82.00	4.06	3.10	1.42	0.60	3.91	2.21	1.23
SD		13.84	2.07	2.02	0.54	0.36	1.94	1.01	0.58
Both periods									
Mean	females	227.83	4.82	3.53	1.48	0.71	3.35	2.01	1.15
SD		114.43	2.26	2.56	0.56	0.35	1.95	1.04	0.55
Mean	males	233.75	6.47	3.48	1.90	0.86	4.33	2.67	1.42
SD		115.90	1.96	0.52	0.29	0.27	0.38	0.22	0.39
Mean	both	230.20	5.48	3.51	1.65	0.77	3.74	2.27	1.26
SD		108.45	2.20	1.93	0.50	0.31	1.56	0.85	0.49
Two-way independent factorial ANOVA									
		F(3,13)	0.539	0.207	0.307	0.271	0.941	0.905	0.808
		P-value	0.664	0.890	0.820	0.845	0.449	0.465	0.512

3.3 Home range overlap

The members of four opposite sex dyads overlapped extensively with their partners using all home range estimators (Figure 4.1 for annual 95% KHR; Table 4.3 for 95 % KHR dry and wet period). 95 % KHR annual home ranges overlapped on average 87.6 ± 9.1 % for females and 49.4 ± 27.3 % for males. Even home range cores (50 %) overlapped intensively, indicating strong bonds between the individuals (60.0 ± 9.9 % for females, 43.6 ± 27.0 % for males). In contrast, home ranges of neighbouring individuals that did not belong to the same pair only slightly overlapped (an average of 15.1 ± 20.3 % for all 38 possible dyads; 27.4 ± 27.7 % for male-male dyads, 6.9 ± 5.0 % for female-female dyads and 15.2 ± 20.2 % for mixed-sex dyads), while home range cores did not overlap between any neighbouring animals. Differences in neighbour overlap between the dyad types approached significance with dyads involving two females having lower overlap (H = 5.974, df = 2, p = 0.05, n = 38). High variations of neighbouring home range overlap are caused by the individuals of the dyads MO and CH, and TO and SH where animals were probably related (see below). Excluding the neighbour dyads involving these likely related animals, the average overlap decreases to 8.3 ± 6.3 % (12.6 ± 6.0 % for male-male dyads, 7.5 ± 5.4 % for female-female dyads and 7.1 ± 6.5 % for mixed-sex dyads). All individuals that were offspring of adult females (GA, HE, LU, TA, UT, WI, YO, Table 4.1) had their home ranges or recorded single fixes within the home range of the mother. The associations between several dyads and small groups are supported by the sociogram for frequency of being in close proximity (up to 5m distance; Figure 4.2). The small family group of TE, GU, TA and YO consisted of one male, one female and two offspring of different age. YO showed dispersal tendencies in early 2013, and TA died during dispersal in November 2013. Although home range overlap suggested the social associations MO and CH, as well as TO and SH, it also indicates overlap between MO and SH. As MO showed dispersal frequencies in early 2014, I assume a certain relatedness between the individuals in this group, such as MO being a son of TO and SH. However, this has yet to be confirmed by genetic analysis.

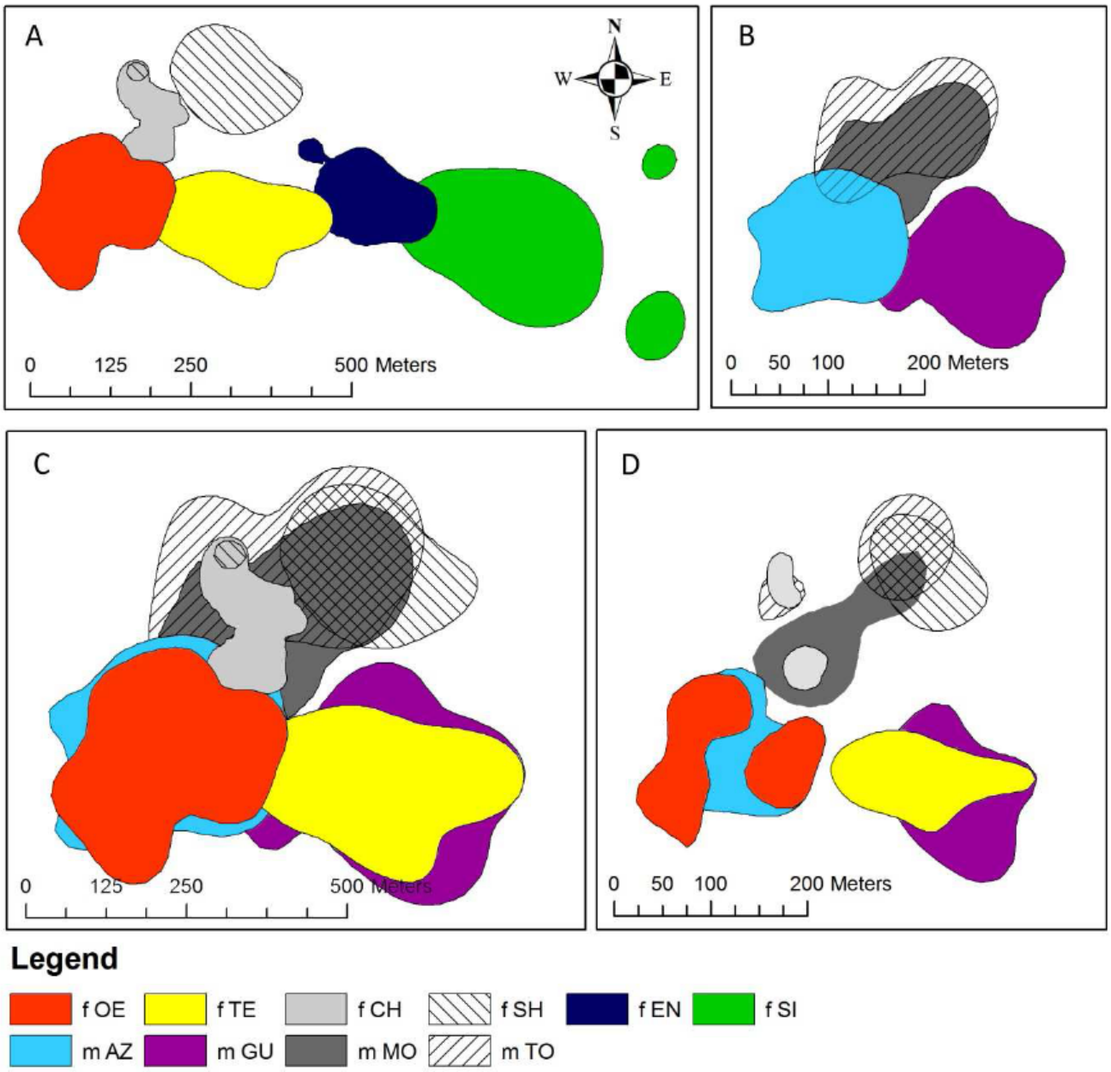


Figure 4.1: Annual 95% KHR for ten adult Javan slow lorises. A: only females. B: only males. C: only couples. D: 50 % KHR only couples. In the legend, individuals on top of each other indicate pair partners.

Table 4.3: Home range overlap (50 % and 95 % Kernel) for both seasons. The individuals EN and SI had no overlap with other radio-tracked individuals using 50 % Kernel home ranges. The home ranges of the individuals listed in the columns are the reference home ranges, e.g. 80% of AZ's home range overlaps with OE's home range. Dark grey boxes denote overlap of 70 % and higher, light grey boxes overlap between 20 % and 70 %.

95 % Kernel	Sex	Age	AZ	OE	MO	CH	GU	TE	TA	YO	TO	SH	EN	SI
AZ	M	A		80	19	7	10	11			9			
OE	F	A	91		13	1	8	10			5			
MO	M	A	21	13		27					77	38		
CH	F	A	24	5	91						74	6		
GU	M	A	9	7				72	27	30			3	
TE	F	A	12	10			94		35	38			3	
TA	F	S					100	100		61				
YA	M	S					100	95	54					
TO	M	A	8	4	66	19						41		
SH	F	A			60	3					74			
EN	F	A					6	5						19
SI	F	A											6	

50 % Kernel	Sex	Age	AZ	OE	MO	CH	GU	TE	TA	YO	TO	SH
AZ	M	A		62								
OE	F	A	56									
MO	M	A				13					18	18
CH	F	A			53						32	
GU	M	A						52	16	24		
TE	F	A					75		22	11		
TA	F	S					100	99		14		
YO	M	S					100	34	9			
TO	M	A			23	10						56
SH	F	A			23						56	

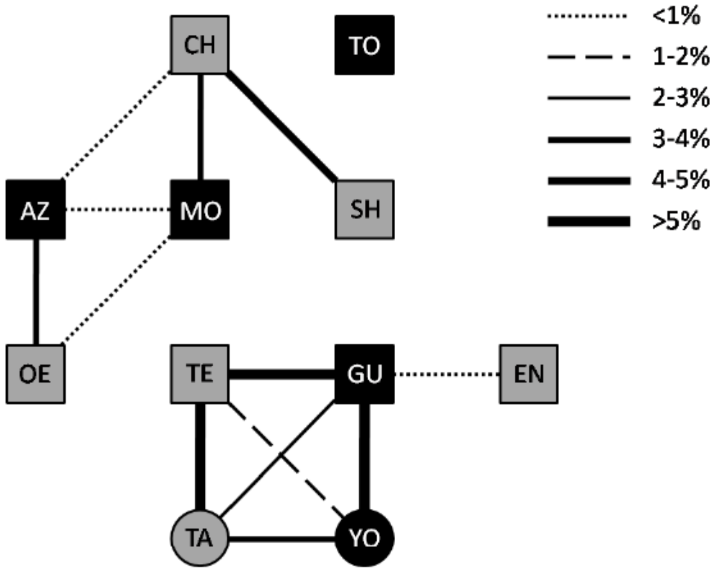


Figure 4.2: Sociogram for eleven radio-collared Javan slow lorises, based on frequencies of encounters within 5m distance including body contact. Squares denote adults, circles denote sub-adults, black denotes males, gray denotes females

3.4 Behaviour in border areas

My hypothesis was that observations of animals travelling and grooming in border areas would be more frequent when compared to within 95 % KHR, as an indication of patrolling and applying gland exudates for possible antagonistic intraspecific encounters. However, I could not find any difference between the border area and within home range observations (^{2} = 2.555, df = 5, p = 0.768, n = 1871). Testing the sexes separately, I could not find any difference in males (^{2} = 3.113, df = 5, p = 0.683, n = 779). Although not significant females tended to feed and forage more and sleep and rest less in border areas (^{2} = 9.552, df = 5, p = 0.089, n = 1092). Only looking at the behaviour in border areas, there was a significant difference in sexes (^{2} = 15.216, df = 5, p = 0.009, n = 108), with females feeding and foraging more, and males feeding and foraging less, but showing more social activities.

3.5 Affiliative and agonistic behaviour

Minimum encounter rates for partner and neighbouring animals are listed in Table 4.4. Neighbouring animals were observed in proximity to each other much less frequently than pair partners. Female-

female dyads were never seen in close proximity. I have excluded uncollared, unidentifiable animals from the analysis, but encounters with those animals can increase the encounter frequency of individuals by up to 3.7 % for less than 5 m distance, and 4.7 % for less than 10 m. I observed aggression extremely rarely, only twice in 600 hours of observation. During one incidence, two males were fighting almost continuously over approximately two hours but where interrupted by periods where one animal escaped and hid and the other searched for it. This fight included chasing each other in close distance, bite attempts, the chased animal falling several meters, and loud vocalizations. The second time a male chased another male individual. Both cases were fights between two males, with females less than 20 m away. In the first, rather long fight, the males alternately joined the female in the bamboo, but were then disturbed and chased away by the other male, and subsequently continued fighting.

Table 4.4: Frequencies of slow lorises in proximity of less than 5 m and less than 10 m from another slow loris (both including body contact) during instantaneous behavioural observations. Proximities to unidentified slow lorises are excluded, and thus real frequencies to any other slow loris may be higher.

		Mean ± sd	Minimum	Maximum	Count
		Partner			
	<5 m	2.47 ± 2.05	0.00	5.43	8
	<10 m	3.28 ± 2.78	0.00	7.87	8
		Neighbour			
male-male	<5 m	0.05 ± 0.14	0.00	0.43	9
female-female		0.00 ± 0.00	0.00	0.00	13
mixed-sex		0.30 ± 0.95	0.00	4.26	20
Mean		0.15 ± 0.67	0.00	4.26	42
male-male	<10 m	0.09 ± 0.22	0.00	0.65	9
female-female		0.00 ± 0.00	0.00	0.00	13
mixed-sex		0.33 ± 0.95	0.00	4.26	20
Mean		0.18 ± 0.67	0.00	4.26	42

4. Discussion

4.1 Home range size

Average annual home range sizes (95 % KHR) of Javan slow lorises were relatively uniform with an average of 3.74 ha, and with no significant differences between sexes or weather periods. Wiens and Zitzmann (2003) also did not detect a sex or seasonal effect in greater slow lorises, although there was a high variation in individual home range sizes from 0.4 ha to 25 ha, depending on the habitat

(Wiens & Zitzmann 2003). Other non-folivorous nocturnal primates with similar body masses have similar home range sizes: for example, in grey slender lorises (***Loris lydekkerianus***), which exhibit a semi-dispersed multi-male system, adult male home ranges average 3.9 ha, and adult female home ranges average 1.66 ha (Nekaris 2003). The home ranges of fork-marked lemurs, which are also socially monogamous, display home range sizes very similar to Javan slow lorises, around 3.8 – 4 ha (Charles-Dominique & Petter 1980, Schuelke & Kappeler 2003). Other species such as the potto (***Perodicticus potto edwardsi***) or species of Galagines have larger home ranges of up to 28 ha and 50 ha, respectively (Harcourt & Nash 1986, Pullen et al. 2000, Pimley 2002, Pimley et al. 2005, Nekaris & Bearder 2011). Pimley et al. (2005) caution that large differences in home range sizes can stem from the use of different home range estimators. Home range sizes also depend on the habitat of different populations. Wiens and Zitzmann (2003) found average home range of 2, 6 and 18 ha for greater slow lorises, depending on whether lorises lived in primary forest, logged forest or savannah. The study site Cipaganti consists of an agricultural area with a mixture of agricultural fields, forest patches, bamboo patches, and bush patches (CHAPTER 2). This rather open habitat could lead to a larger home range size than in primary or secondary forest (Wiens & Zitzmann 2003). On the other hand, although the main food plants of lorises in this area - nectar-producing red calliandra and gum-producing green wattle - are not preferably used by humans (CHAPTER 2), some of them may occur in a higher density than in continuous forest and facilitate smaller home range sizes.

4.2 Home range overlap

Although nocturnal mammal species have traditionally been described as solitary, many nocturnal primate species were found to exhibit complex social organization (Mueller & Thalman 2000, Bearder et al. 2003, Nekaris & Jayewardene 2003, Gould & Sauther 2011, Nekaris & Bearder 2011). Studies of social organization in nocturnal primates are often based on ranging patterns, vocalisations or olfaction (Sterling et al. 2000, Mueller & Thalman 2000, Nekaris 2003, Pimley et al. 2005, Bearder & Nekaris 2011). Spatial overlap of home ranges in my study indicated that Javan slow lorises live in socially monogamous pairs. A typical home range group consisted of one female, one male, and one or two associated offspring. The 95 % KHRs of pairs in Javan slow lorises had a high overlap of 49.4 % for males and 87.6 % for females. Although not statistically significant, male home ranges were larger and often included most of the females' home range. This is similar to greater slow lorises where female home ranges almost entirely lie within the male home range with overlaps of 38 % and 81 % for one pair in primary forest and 84 % and 98 % in logged forest (Wiens & Zitzmann 2003). Socially monogamous sportive lemurs ***Lepilemur*** spp. showed comparable overlap patterns: 43 %, 50 % and 61 % for males, and 81 %, 80 % and 89 % for females for white-footed sportive lemurs *L. leucopus* and two studies of red-tailed sportive lemurs *L. Ruficaudatus*, respectively (Zinner et al. 2003, Hilgartner et al. 2012, Droescher & Kappeler 2013). The fork-marked lemur also showed almost perfect overlap between pairs (Schuelke & Kappeler 2003).

Not many mammalian species have a monogamous social organisation (Reichard & Boesch 2003). In a dataset of 2545 mammalian species, Lukas and Clutton-Brock (2013) identified only 9 % of mammals as monogamous, while social monogamy was more common in the orders primates (29 %) and carnivores (16 %). Social monogamy has been described for many different nocturnal primate species: greater slow loris (Wiens & Zitzmann 2003), potto (Pimley 2002, Pimley et al. 2005), most individuals of Lariang tarsier *Tarsius lariang* and spectral tarsier *T. spectrum* (Gursky 1998, Driller et al. 2009, Gursky-Doyen et al. 2010), eastern woolly lemur *Avahi laniger* and western woolly lemur *A. occidentalis* (Ganzhorn et al. 1985, Harcourt 1991, Warren & Crompton 1994, Ramanankirahina et al. 2011), fat-tailed dwarf lemur *Cheirogaleus medius* (Mueller 1998, 1999, Fietz 1999a, Fietz et al. 2000), fork-marked lemur (Charles-Dominique & Petter 1980, Schuelke & Kappeler 2003), Milne-Edwards's sportive lemur *Lepilemur edwardsi*, red-tailed sportive lemur and most individuals of white-footed sportive lemur (Warren & Crompton 1994, Zinner et al. 2003, Rasoloharijaona et al. 2006, Méndez-Cárdenas & Zimmermann 2009, Hilgartner et al. 2012, Droescher & Kappeler 2013).

4.3 Territoriality

A territory is defined as a stable and exclusive area that is defended by fights or "keep-out" signals (Brown & Orians 1970, Davies 1978, Powell 2000). Exclusiveness of home ranges is a criterion of territorial use that is investigated most easily in the field. While nocturnal primate species living in multi-male multi-female social organization have highly overlapping ranges between all individuals irrespective of sex (e.g. aye aye *Daubentonia madagascariensis*: Sterling 1993, Ancrenaz et al 1994, Sterling 1994; grey mouse lemur *Microcebus murinus*: Fietz 1999b, Schwab 2000; golden-brown mouse lemur *M. ravelobensis*: Weidt et al. 2004; brown mouse lemur *M. rufus*: Atsalis 2000), in most socially monogamous pairs there is minimal overlap between neighbouring home ranges. Neighbouring home ranges in Javan slow lorises showed a small overlap (on average 15.1 %), and further decreases to 8.3 % if the almost certainly related animal dyads MO and CH, and TO and SH are removed from the average. Other socially monogamous nocturnal primate species had similar minimal home range overlap between neighbours (e.g. eastern woolly monkey: Ganzhorn et al. 1985; Milne-Edwards's sportive lemur: Méndez-Cárdenas & Zimmermann 2009, Rasoloharijaona et al. 2006; fork-marked lemur: Charles-Dominique & Petter 1980). Droescher and Kappeler (2013) report just 2 % overlap for nine neighbouring dyads for the white-footed sportive lemur. Similar overlap patterns are known for other socially monogamous mammals, e. g. the rock-haunting possums ***Petropseudes dahlia*** (Runcie 2000).

Regarding territorial fights, Javan slow lorises showed surprisingly low frequencies of aggressive encounters. Possibly they rather use indirect methods of defending territories, such as scent-marking, to avoid potentially dangerous bites by conspecifics. However, both observations of aggression in Javan slow lorises were made in border areas. Although there were no significant differences in behaviours in border areas, males had the tendency to groom more frequently in border areas than females, which might indicate that they were preparing for the potential use of venom. Olfactory and vocal "keep-out" signals must be confirmed in further studies. Other territorial species showed clearer signs of patrolling and vocalizations in border areas. In partly monogamous Zanzibar bushbaby ***Galago zanzibaricus*** both sexes defended territories, indicated by chasing and fights during excursions (Harcourt & Nash 1986). Sportive lemurs seem to demark their territories with extensive vocalisations and duetting (Méndez-Cárdenas & Zimmermann 2009, Rasoloharijaona et al. 2006). In the venomous, polygynous platypus the home ranges of males may overlap in the non-breeding season, but in the breeding season home ranges are either exclusive, or when overlapping are temporally separated and animals avoid each other (Serena 1994, Gardner & Serena 1995), possibly to prevent dangerous fights.

Stability of home ranges as a criterion of territories can only be measured in long-term studies. While home ranges of males in multi-male social organisations usually increase in size during the mating season, home range sizes in monogamous species usually do not significantly change between seasons or years (e. g. red-tailed sportive lemurs: Zinner et al. 2003, fork-marked lemurs: Schuelke & Kappeler 2003). An absence of a seasonal change of home range size is confirmed for Javan slow lorises, but stability over years must be assessed in further studies. A factor influencing stability is also change of habitat; in this study area, habitat is frequently altered by human deforestation activities and natural landslides which might affect home range position (CHAPTER 3).

4.4 Mating system

Although we witnessed extremely low rates of aggression, it is notable that both observations of aggression were of two males fighting in proximity to a female. Females are only receptive for a few days during one reproduction period (Izard et al. 1988) and during this time they are an important resource. Throughout receptive nights in slender lorises, several males including those who were not resident in the area visited the female (Nekaris 2003), and similar behaviour was observed for several species of slow lorises (Nekaris pers. comm.). It is thus likely that sexual competition at least during these times is high.

The results suggest high contest competition in Javan slow lorises as is typical for a monogamous mating system. Testis size was relatively small compared to other strepsirhine species (Kappeler et al. 1997b), but not significantly so. Monogamous species or species with sexual competition that is characterised by contest rather than scramble competition should exhibit small testes (Harcourt et al. 1981, 1995, Kappeler et al. 1997a). Socio-ecological theory predicts that the type of mating system depends on ecological factors, such as the abundance, distribution and quality of resources (Koenig et al. 2013). Male mating tactics follow the spatial and temporal distribution of receptive females (Emlen & Oring 1977, Eberle & Kappeler et al. 2004, Koenig et al. 2013). If solitary females are too widely distributed to be monopolised in a group, the defence of one single female or her territory may be more advantageous, and monogamy is favoured (Emlen & Oring 1977, Lukas & Clutton-Brock 2013). As strictly monogamous species mate with only one partner, large testicles are not needed (but see Fietz et al. 1999a, Schuelke et al. 2004). In contrast, male tactics in promiscuous species such as mouse lemurs *Microcebus* spp. (Fietz 1999b, Ancrenaz et al. 1994, Atsalis 2000, Schwab 2000, Weidt et al. 2004), the aye-aye (Sterling 1993, 1994) or *Mirza* spp. (Kappeler et al. 1997a, Kappeler et al. 2005, Rode et al. 2013b) are indicated by scramble competition which includes wide roaming in search of females and other traits related to maximising mating success (Harcourt et al. 1981, 1995, Kappeler et al. 1997a, Eberle & Kappeler 2002, 2004). High mating frequencies and sperm competition in these species may select for large testes (Gomendio et al. 1998, Birkhead 2000, Vahed & Parker 2012).

I did not find sexual dimorphism in body mass or head body length. Although the frequency of injuries was generally high there was no sexual difference in injuries or venom secretion between sexes. Usually, monogamy as well as polygyny are characterised by male contest competition for females (Schwab 2000, Lukas & Clutton-Brock 2013). Contest competition in general is related to traits of male competitive ability, such as size, strength, weapons and aggressive potential that help in fighting and guarding (Darwin 1871, Plavcan & van Schaik 1992, Kappeler et al. 1997a). In the solitary promiscuous Coquerel's giant mouse lemur *Mirza coquereli*, or polygynous group-living Mexican mantled howler monkeys *Alouatta palliata mexicana*, males were more likely to have injuries than females, particularly in the mating season (Kappeler et al. 1997a, Cristóbal-Azkarate 2004). Males of many species that live in polygynous mating systems (harems) with contest competition have high rates of wounds (e. g. walrus: Sjare & Stirling 1996) and dominant males die a few years after their reproductive peak (e. g. elephant seal *Mirounga angustirostris*: Le Boeuf 1997). In most mammal species, weapons such as antlers and horns are only present or more prominent in males (Berglund 2013). The fact that I did not find any such sexual difference indicates high social competition in both sexes. Accordingly, another branch of socio-ecological theory focuses on grouping patterns of females and predicts female solitary grouping patterns if there is intense competition about feeding resources (van Schaik 1989, Koenig et al. 2013). The main diet of slow lorises consists of tree exudates (Wiens et al. 2006, Swapna et al. 2010, Starr & Nekaris 2013, Streicher et al. 2013, Das et al. 2014, CHAPTER 3) which are low in productivity and availability, and patchily distributed and thus promote high contest competition and territoriality in females (Charles-Dominique & Petter 1980, Hladik et al. 1980, Powell 2000, Schuelke & Kappeler 2003, Koenig et al. 2013). The diet of fork-marked lemurs also heavily relies on gum, animals show high competition for feeding resources, with single individuals having access to an average of nine gum-producing trees in pair home ranges (Charles-Dominique & Petter 1980, Hladik et al. 1980). Gummivory pygmy marmosets *Cebuella pygmaea* live in small family groups and the location of their home ranges depends on the location of gum-producing trees (Yepez et al. 2005). Although folivorous, males of fat-tailed dwarf lemurs patrol their territory's boarder after emerging from hibernation in order to secure food supply for the family (Mueller 1998, 1999). In my study site Cipaganti, this competitive situation may even be exacerbated by the human-modified and open habitat with even lower availability of more patchily distributed resources.

Finally, I found overall larger home range sizes in males, but no significant sexual difference. This supports my hypothesis and is in contrast with scramble competition where males' home ranges are much larger (Kappeler et al. 1997a). Spatial characteristics of aggression and male aggregations during mating in slow lorises (Elliot & Elliot 1967, Wiens & Zitzmann 2003, this study) suggest polygynous tendencies which explain larger territories in males (Schuelke et al. 2004, Droescher & Kappeler 2013). Despite social monogamy animals may still monitor receptivity of females and presence of males by roaming slightly wider than females (Droescher & Kappeler 2013). Many pair-living species have flexible or mixed mating strategies and temporarily may adopt a promiscuous or polygynous mating system (Wiens 2002, Driller et al. 2009, Gursky-Doyen 2010, Droescher & Kappeler 2013). Indeed, behavioural evidence for social monogamy cannot be used as an indication of a monogamous mating system. Instead, genetic monogamy can only be examined by testing genetic paternity, e. g. using microsatellite genotyping or multilocus minisatellite fingerprints (Isvaran & Clutton-Brock 2007). Extra-pair or extra-group paternity exists in all forms of social organisation and holds true for stable social pairs (Isvaran & Clutton-Brock 2007, Huck et al. 2014). While a few socially monogamous mammal species may show almost exclusive monogamy (e.g. California mouse ***Peromyscus californicus***: Ribble et al. 1991; Malagasy giant jumping rat ***Hypogeomys antimena***: Sommer 2003; Azara's night monkey ***Aotus azarae***: Huck et al. 2014) many other species have relatively high rates of extra-pair paternity, such as the fat-tailed dwarf lemurs with 40 % (Fietz et al. 2000), fork-marked lemurs with 30 % (Schuelke et al. 2004), the Lariang tarsier with 20 % (Driller et al. 2009), the large tree shrew (***Tupaia tana***) with 50 % (Munshi-South 2007) or the Alpine marmot (***Marmota marmota***) with 31 % (Goossens et al. 1998) (reviewed in Isvaran & Clutton-Brock 2007, Huck et al. 2014). Although the resulting promiscuous mating system and sperm competition theory would predict higher testis volumes in these species, the large tree shrew, the fork-marked lemur and the fat-tailed dwarf lemur have relatively small testis volumes (Fietz et al. 1999a, Schuelke et al. 2004, Munshi-South 2007). Possibly the females take a more active role in the promiscuity of this species by actively seeking out extra-pair partners (Fietz et al. 2000).

4.5 Social structure: affiliative and agonistic interactions

Social monogamy in Javan slow lorises is supported by the pattern of affiliative behaviour, e. g. frequency of time spent in proximity or body contact. Cohesion of monogamous pairs measured in affiliative behaviours differs between species. For pair partners in Javan slow lorises I report that animals spent 2.5 % of observations in proximities less than 5 m and 3.3 % less than 10 m, while Wiens and Zitzmann (2003) observed affiliative behaviour for only five of eight pairs of greater slow lorises, but overall social interactions were seen for 3 % of the active time. Social behaviours in slow lorises include playing, allogrooming, following each other and sleeping in body contact (Wiens 2002, CHAPTER 3). While some species are described as relatively cohesive and peaceful (e. g. western woolly lemur: Ramanankirahina et al. 2011), many other nocturnal primates living in social monogamy have similar low rates of direct affiliation as slow lorises. However, in contrast to slow lorises they show low levels of affiliation and rather avoid each other. For instance, pairs of Zanzibar bush babies are rarely seen together (Harcourt & Nash 1986), and fork-marked lemurs also avoid each other (Schuelke & Kappeler 2003). Although Droescher and Kappeler (2013) counted 72 social encounters in 516 hours (= 14 %) for white-footed sportive lemurs, 78% were neutral in 1-5 m distance, 21 % agonistic, and only 1 % affiliative. Red-tailed sportive lemurs spent 26 % in proximities of less than 10 m in pre- and mating season, and 9 % in non-mating season (Hilgartner et al. 2012), but no affiliative behaviour was observed. Nekaris and Bearder (2011) argue that when rates of affiliative behaviours are reported they may often include social behaviour between females and offspring, which should be accounted for in the interpretation of data. Close proximity and affiliations between neighbours in Javan slow loris are low but occur regularly. It is interesting to note that adult female slow lorises in this study have never been observed in close proximity (less than 5m) to other females. This emphasizes the aspect of high social competition for ecological resources like food in females.

Although I witnessed agonistic encounters between Javan slow lorises only twice in 600 hours of observation over 14 months, 60 % of the adults had long-lasting injuries and scars that point to a high potential for social and sexual competition. The same discrepancy was reported for greater slow lorises, where around half of captured animals had similar types of fresh or old wounds to Javan slow lorises, such as scars on the head and missing digits or ears, which can be related to intraspecific aggression (Wiens 2002, Wiens & Zitzmann 2003, Nekaris et al. 2013a). Slow lorises possess very high healing powers, possibly aided by the effects of anointment with brachial gland secretion such as disinfection (Nekaris et al. 2013a), and thus fresh injuries and wounds might occur even more frequently. It is not yet clear what causes the aggression that leads to these wounds. So far we have only observed aggression between males in competition regarding mating opportunities (section 4.4). I never observed direct conflicts between pair partners, in contrast to the dispersed monogamous fork-marked lemurs that exhibit high rates of aggression between pairs (Schuelke & Kappeler 2003). Although red-tailed sportive lemurs live in relatively cohesive monogamous pairs, 47.3 % of social encounters between pair partners were agonistic (Hilgartner et al. 2012). Western woolly lemurs are described as very peaceful, with 15 agonistic encounters between pairs in 874 hours of observation (Ramanankirahina et al. 2011). While Ehrlich and Musicant (1977) describe greater slow lorises as peaceful with low frequencies of non-severe aggression in captivity, animals in rescue centres seem to be more aggressive causing extreme damage when biting conspecifics (Streicher 2004, Nekaris et al. 2013a). Data collected over 13 and 30 years respectively (Sutherland-Smith & Stalis 2001, Fuller et al. 2014) indicate, that if agonistic encounters occur in zoos, often through introduction of new group members or by accident, wounds inflicted by other slow lorises can be severe. In the wild we have never seen adult females together, and they seem effectively to avoid each other. In the illegal pet trade animals are likely to be put together in cages regardless of their sex. Zoos may prefer to keep two females together than two males (or bachelor groups of two males). Conflicts between animals in captive situations cannot be solved by avoidance or escape and may often result in fights. Apart from restricted opportunities to escape and the trauma caused by the illegal pet trade, another reason for the severity of injuries in captivity may be restricted healing powers of BGE due to missing natural dietary items such as gum or noxious insects (Nekaris et al. 2013a). I found a discrepancy of a high frequency of injuries and scars but low frequencies of agonistic encounters in wild Javan slow lorises. This suggests that, additional to other costs of aggression such as energy loss and less time for other substantial behaviours such as feeding and foraging, bites by conspecifics are potentially very risky and dangerous and thus need to be avoided. Traumatic wound healing increases metabolic rates considerably (Demling 2009), which should especially affect animals with low metabolic rates, such as slow lorises (Whittow et al. 1977, Mueller 1979, Rasmussen & Izard 1988, Wiens et al. 2006).

The maintenance of affiliative relationships and prevention of aggression is possible by intensive use of indirect ways of communication, such as vocalizations and olfactory or chemical communication aided by the sense of smell, specialized scent glands and urine (Colquhoun 2011, Nekaris & Bearder 2011). Vocalization is the better-studied means of communication in nocturnal primates (Zimmermann 1995a,b, Zimmermann 2013). Calls may be used for territorial spacing, aggression, affiliation, infant contact and other social contexts (Nekaris 2000, Coultas 2002, Rasoloharijaona et al. 2006, Zimmermann 2009, Bernede et al. 2013, Fichtel & Hilgartner 2013, Zimmermann 2013). Some sportive lemur species even maintain cohesion by duetting (Rasoloharijaona et al. 2006, Méndez-Cárdenas & Zimmermann 2009). While more agile species such as galagos, mouse lemurs, sportive lemurs or fork-marked lemurs are highly vocal (Charles-Dominique & Petter 1980, Zimmermann 1988, 2009, 2013, Rasoloharijaona et al. 2006, Méndez-Cárdenas & Zimmermann 2009), less agile species such as the potto and lorises vocalize to a lesser extent (but see Zimmermann 1985, Bernede et al. 2013), although calls can be ultrasonic and thus less conspicuous to researchers (Zimmermann 1985). Slow lorises have up to eight different affiliative and agonistic call types, including a specific whistle when in estrous and snarls, screams and grunts for medium to close distance aggression (Daschbach et al. 1981, Zimmermann 1985). Another form of communication is olfactory or chemical communication ("perfuming"). Although not well studied, especially in field situations (Colquhoun 2011, Nekaris & Bearder 2011), it has been shown that scent markings can serve as intraspecific signalling and transfer information about sexual receptiveness, age, sex, identity, and even sexual attractiveness and avoidance (Charles-Dominique 1977, Clark 1982a,b, Fisher et al. 2003a,b, Heymann 2006, Scordato et al. 2007, Colquhoun 2011). Slow lorises use urine marking, including competitive countermarking in males (Fisher et al. 2003a,b). In order to be effective in intraspecific communication, the odours must bear an individual signature (Knapp et al 2006). Hagey et al. (2007) found that slow loris venom contains a high number of volatile and semi-volatile compounds and thus may be a medium to communicate information about the sender. The exudates of the specialised scent glands of ring-tailed lemurs contain volatile compounds whose concentrations relate to genes of the individual's MHC. The identification of volatile compounds of slow loris BGE in relation to information about the sender and its genes may support the hypothesis that venom serves as a form of olfactory communication. These forms of indirect communication, especially in nocturnal species, on the one hand make it possible for the animals to stay in social contact despite not being in close spatial proximity, while on the other hand also facilitate the avoidance of direct aggressive and potentially harmful encounters if not absolutely necessary.

4.6 Why are slow lorises venomous?

Especially intense sexual competition has led to the evolution of weapons in many species (Emlen 2008, Tobias et al. 2012). Although weapons in females are less common (Berglund 2013), they are present in several species where females compete for non-sexual resources such as feeding grounds or territories (e.g. reindeer ***Rangifer tarandus***: Espmark 1964; duikers Cephalophinae: Stankowitch & Caro 2009). Venom can be viewed as a weapon, although examples for their function in intraspecific competition are documented less often than their usual function in predator defence or prey capture (Casewell et al. 2013). In order to assess whether slow lorises may use their venom for intraspecific competition, I examined the social system of Javan slow lorises.

My results suggest that social and sexual competition in Javan slow lorises is high. Javan slow lorises are socially monogamous and have highly overlapping pair home ranges, but show small overlap between neighbouring animals. Animals compete intensively through social competition for resources; especially adult females that were never seen in close proximity to each other in 600 hours of observation and show minimal overlap between home ranges. Social monogamy points to a monogamous mating system that is usually characterised by high sexual competition between males defending their female partners or the pair's territory. The only aggression I could observe was in relation to mating opportunities. Monogamy is compatible with the relatively small testes in Javan slow lorises, and supported by the absence of harems or leks. However, similar to other social monogamous species slow lorises also seem to show tendencies towards polygamy and promiscuity by monitoring neighbouring home ranges for relatively rare mating opportunities. Slightly larger male home ranges back up this finding. Other socially monogamous species have comparable small testes despite extra-pair paternities and mixed mating strategies (Fietz et al. 2000, Wiens 2002, Schuelke et al. 2004, Driller et al. 2009, Gursky-Doyen 2010, Droescher & Kappeler 2013). In summary, venom may be used as a weapon for intraspecific competition in Javan slow lorises. Injuries that presumably were inflicted by conspecifics were common in male and female Javan slow lorises and venom secretion during capture events occurred in amounts irrespective of sex. This indicates that the weapon venom may be used in both, sexual and social competition.

Many weapons have initially or primarily evolved for a certain purpose, but gained usefulness for a secondary function (Stankowich 2011). In nocturnal mammal species, including slow lorises, animals use chemical and vocal communication to maintain dispersed social systems during their active period (Colquhoun 2011, Nekaris & Bearder 2011). Thus, it is possible that slow loris venom has evolved as a scent secretion (Hagey et al. 2007), but has developed into a chemical weapon for intraspecific competition. The platypus has been shown to possess venom glands used in sexual competition (Grant & Temple-Smith 1998, Whittington & Belov 2007). The related long-beaked echidna (*Zaglossus* sp.) also has spurs like the platypus, but its spurs cannot be erected (Wong et al. 2013). Still, a milky substance is secreted in the breeding season, which may act as communication (Wong et al. 2013). Similarly, noxious anal gland secretions in some carnivores may have evolved because robust anal glands were already present and already bristled hair has modified into robust spines in hedgehogs and tenrecs (Stankowich 2011).

Another primary function of venomcould be for the defence against predators. Compared to diurnal mammal species, nocturnal species are more exposed to macrocarnivores than aerial predators and thus are more likely to develop chemical defence mechanisms such as foul odours or sprays than other types of weapons (Caro 2005, Stankowich 2011). Possibly slow loris venom has evolved as a chemical defence directed at tigers and other partly arboreal olfactory-oriented predator species, but developed into the secondary function of social competition.

The question remains why venom has not evolved more often into a weapon for intraspecific competition. The strength and power of small, inconspicuous weapons are not easy to assess by competitors and can cause more damage (Emlen 2008). Many weapons and ornaments have evolved into large and exaggerated signals which potential competitors can easily evaluate before an actual fight. This may be less easy for small weapons, including venom that cannot be visually assessed. Although often underestimated olfactory communication is very important for nocturnal mammals and as such the smell of venom may perfectly fulfil the requirement to be assessable before direct fights.

CHAPTER 5

Distribution and ecology of potential predators of Javan slow lorises and other small carnivores and medium-sized nocturnal mammals on Java

1. Introduction

Sundaland, which encompasses the Sunda shelf, is considered a top biodiversity hotspot based on its large number of endemic species and high habitat loss (Myers et al. 2000, Brooks et al. 2002, CHAPTER 2, section 2.1). The accelerating loss of habitat is causing many wildlife populations and biodiversity to plummet and has triggered the extinction of some larger mammals or caused highly fragmented distribution (Javan rhino, Javan tiger, leopard) (Santiapillai & Ramono 1992, Whitten et al. 1996, Fernando et al. 2006). Much of the remaining natural primary or secondary forest coincides with areas that are difficult to access, such as mountains (Smiet 1992, Lavigne & Gunnell 2006). Apart from habitat loss, threats include trade in wild animals for pets, traditional medicine or other economic uses. The lack of law enforcement means that trade is mostly unregulated and the actual quantities of traded wildlife remain unknown. Previous studies (Shepherd 2012a, b, Nekaris et al. 2013b) indicate that the volume of wildlife being traded is high and is considered unsustainable. Sometimes new trends in demand cause a sudden increase in numbers of wild animals for sale in markets. Examples include the soaring trade in slow lorises and owls (Strigiformes) as a result of social or international media presence (Shepherd 2012b, Nekaris et al. 2013c) as well as the rise in popularity of civet coffee (*kopi luwak*) afflicting common palm civet (Shepherd 2012a). This may cause rapid population declines, in both protected and unprotected species.

Small to medium-sized forest-dwelling mammals are often nocturnal and solitary, and therefore difficult to study (Bekoff et al. 1984, Kappeler 1997c, Eberle & Kappeler 2004, Lim & Ng 2010). With respect to the island of Java, few distribution surveys exist for small- and medium-sized carnivores (many of which are nocturnal) and in general for nocturnal mammals less popular amongst the general public. Many of the published distribution data stem from chance sightings (Duckworth et al. 2008, Robson 2008, Eaton et al. 2010, Moore 2011), with formal surveys such as camera trapping extremely rarely written up in easily accessible reports (e.g. Marliana & Ruehe 2012). Because many populations of nocturnal forest-dwelling animals in Southeast Asia are declining (Ceballos & Ehrlich 2002, Sodhi et al. 2004), more frequent studies are required. Many medium-sized nocturnal mammals on Java are listed as Least Concern on the IUCN Red List (IUCN 2014), despite almost no data being available on their exact populations and distributions in the forests of Java (Shepherd 2012a).

The lack of distribution data and the rapid population declines on Java make regular surveys essential for assessing the impact of threats on wildlife populations. For regular surveys to be feasible, they must be well designed and efficient. Apart from survey effort, not much information is available about intrinsic and extrinsic factors influencing the detectability of certain species. Most studies on Java focus on threatened species in protected and forested areas, on the western parts of the island. The exclusion of study species and sites due to naïve assumptions can lead to bias; or - in the worst case - can have serious consequences, such as an undetected plummet of population numbers in Least Concern species.

In the case of Indonesia, many medium-sized carnivores and nocturnal mammals, including some that are endemic, are considered as Least Concern on The IUCN Red List of Threatened Species (IUCN 2014), despite the scarcity of field data that are needed to support this (Shepherd 2012a). Javan ferret badger ***Melogale orientalis*** (Data Deficient - DD), Javan chevrotain ***Tragulus javanicus*** sensu stricto (DD) Javan colugo ***Galeopterus variegatus*** (Not Recognised - NR) and Javan warty pig ***Sus verrucosus*** (Endangered – EN) are endemic to Java or to Java and Bali, but there are few data on their occurrence, levels of tolerance to human disturbance and overall conservation status. To aid in updating IUCN Red List status and as a baseline for designing conservation schemes, field data for nocturnal mammals on Java are urgently required.

The general faunal community may include species that prey on Javan slow lorises. However, apart from orangutans, that do not occur on Java, hawk eagles, snakes and monitor lizards (CHAPTER 1, section 5.4) not much is known about potential predators of Javan slow lorises. Direct observations of predation or near predation events are very rare and have not been observed in the 14 month radio-tracking of Javan slow lorises. The knowledge about the potential predator community of Javan slow lorises could serve as a foundation for the hypothesis that slow lorises use venom for predator defence. This data could also reveal sites where this hypothesis can be studied most effectively due to a high density of slow lorises and potential predators.

In this chapter I present data on various small to medium carnivores and similarly-sized nocturnal mammals of Java collected over a period of two years and two months (I partly added camera trap and survey data collected by the project staff after I left from the field), at most sites by nocturnal spotlight transects, supplemented by camera trapping and collection of incidental observations at one site and replaced by nocturnal fixed-point surveys at another. I detail the distribution and encounter rate of the survey species in different parts of Java and highlight coexistence between slow lorises and potential predator species. The species considered comprise (Table 5.1): all carnivores except big cats ***Panthera*** spp. and Dhole ***Cuon alpinus***, all giant flying squirrels ***Petaurista*** spp., Sunda porcupine ***Hystrix javanica***, Javan chevrotain ***Tragulus javanicus***, Javan colugo ***Galeopterus variegatus***, Sunda pangolin ***Manis javanica,*** Javan slow loris and Javan warty pig ***Sus verrucosus***. The Eurasian wild pig ***S. scrofa***, also present on Java, was not included as it is non-native.

Furthermore, I aimed to provide a basis for effective survey planning for finding good locations for future studies on slow lorises, their potential predators and the general medium-sized mammal community. I tested whether the conservation status and Indonesian protection status of the species, the protected status of the study area, the geographical location and the survey effort affect the probability of detecting the focus species in my study sites. Although per definition threatened and protected species would be expected to be rare, due to the infrequent direct observations or detection of their traces this is not always the case. The IUCN Red List status could be out-dated or not appropriate, and the Indonesian protection status does not always match the IUCN Red List status (Table 5.1). Indonesia has many protected areas where protection is not well enforced (CHAPTER 2, section 2.1.3). Furthermore, most studies on Java focus on West Java, assuming that biodiversity and populations densities are greater in the west, however, this has never been shown. Such an assumption may lead to the fact that reported population densities for Javan species reflect only the densities in the west of the island, and to overlooking important biodiversity sites. Survey effort should increase the detection rate of all focus species.

In order to facilitate the detection of two potential predators of the Javan slow loris, the common palm civet (*Paradoxurus hermaphroditus*) and the leopard cat (*Prionailurus bengalensis*), that were present at the long-term field site, I test the hypothesis that adverse weather conditions such as wind, rain and low temperature will affect detection negatively. Avoiding bright nights might give predators an advantage when hunting (Packer et al. 2011). As stated above, the survey effort should lead to a higher detection rate.

Finally, as not much is known about many small and medium-sized mammals, I report on various observations on behaviour, ecology and threats.

2. Methods

Survey sites

The general survey area, Java, is described in CHAPTER 2, section 2.1. Survey sites, with their protection status, are listed in APPENDIX 2, and described in CHAPTER 2, section 3.1 and 3.2. Survey sites were selected because of (i) the known presence of this species; (ii) species distribution models (Thorn et al. 2009); (iii) suitable habitat; and (iv) information that it might occur.

Data collection

Similar to the selection of the survey sites, survey methods and equipment were optimised for detecting lorises. Even the camera traps were set specifically to examine presence of ground-dwelling potential loris predators. This bias has to be taken into account when interpreting other species' records.

For the general survey results I used data from three expeditions: one (April to June 2012) focusing on 14 sites distributed across Java (Voskamp et al. 2014), one (May to July 2013) in East Java, and one (February to May 2014) in West Java. The three other main observers were all trained by AN, VN or me to ensure accuracy of identification. On each expedition the main survey method was direct sighting of animals from walked nocturnal transects, replaced at one site by nocturnal static observations. Incidental sightings are included from the period April 2012 to May 2014 in the Javan slow loris project of this thesis and around the village of Cipaganti, on the eastern slopes of Mount Papandayan in West Java (CHAPTER 2, Figure 2.2).

The setting of camera traps, collection of weather data and general methods used during forest surveys are described in CHAPTER 2, section 4.1.4 to 4.1.6. Data from Cipaganti result from observations incidental to routine study of Javan slow loris and from camera traps (Cuddeback Attack IR; Bushnell Trophy cam night vision; one to six units set on 283 nights, totalling 705 individual camera trap-nights). Again, for the statistical models, I used only data from my own data collection, using one to four units set on 185 nights, totalling 304 camera trap-nights.

For the data presented here, I also performed fixed-point surveys between 18:00 and 04:00. At each point, three spots 10m from each other were selected. At each spot the observer stood silently and systematically scanned all levels of the vegetation for 5 minutes, adding up to individual points surveyed for 15 minutes. Surveys were repeated after a minimum of four hours. The individual points were placed randomly along a 1,700 m transect. During fixed-point surveys, red light was used whenever possible, aided with white light if terrain was difficult.

Survey effort for each area is reported in APPENDIX 2; Cipaganti is included twice, with the first two visits included as a transect survey comparable to the others, and the later period included as the long-term study.

Table 5.1 lists the 22 small carnivores and similarly-sized mammals included in the surveys. For each animal sighting I recorded the location using a Garmin GPS 60 and 62st with an average precision of about 5 m, in addition to date, time and weather conditions (Sutherland 2006). I recorded the animal species, number of individuals and - if observed in a tree - the height of animal and height of tree (Nekaris et al. 2008). I recorded *ad libitum* observations about the sex, age class, behaviour, and reaction towards and distance from the observers. Camera trap photographs were excluded when reporting heights of the animals in trees, because of the bias of camera placement. For sightings with a GPS data point I measured the distance to the nearest human settlement of five or more houses using Google Earth V (7.1.1.1888).

Table 5.1: Small carnivores and similarly-sized species considered in this survey of various sites in Java, Indonesia, 2012 to 2014 (excluding Javan slow loris)

Family	**English name**	***IUCN Red List***[1]	**Nat'n'l law**[2]
Order Carnivora			
FELIDAE	Fishing cat *Prionailurus viverrinus*	EN A2cd+4cd	P
FELIDAE	Leopard cat *Prionailurus bengalensis*	LC	P
HERPESTIDAE	Javan mongoose *Herpestes javanicus*	LC	NP
MEPHITIDAE	Sunda stink-badger *Mydaus javanensis*	LC	P
MUSTELIDAE	Indonesian mountain weasel *Mustela lutreolina*	DD	NP
MUSTELIDAE	Javan ferret badger *Melogale orientalis*	DD	NP
MUSTELIDAE	Asian small-clawed otter *Aonyx cinereus*	VU A2acd	NP
MUSTELIDAE	Smooth-coated otter *Lutrogale perspicillata*	VU A2acd	NP
MUSTELIDAE	Yellow-throated marten *Martes flavigula*	LC	NP
PRIONODONTIDAE	Banded linsang *Prionodon linsang*	LC	NP
VIVERRIDAE	Binturong *Arctictis binturong*	VU A2cd	P
VIVERRIDAE	Common palm civet *Paradoxurus hermaphroditus*	LC	NP
VIVERRIDAE	Small Indian civet *Viverricula indica*	LC	NP
VIVERRIDAE	Small-toothed palm civet *Arctogalidia trivirgata*	LC	NP
Order Cetartiodactyla			
SUIDAE	Javan warty pig *Sus verrucosus*	EN A2cd	NP
TRAGULIDAE	Javan chevrotain *Tragulus javanicus*	DD	P
Order Dermoptera			
CYNOCEPHALIDAE	Javan colugo *Galeopterus variegatus*	LC	P
Order Pholidota			
MANIDAE	Sunda pangolin *Manis javanica*	EN A2d+3d+4d	P
Order Primates			
LORISIDAE	Javan slow loris *Nycticebus javanicus*	CR A2cd+4cd	P
Order Rodentia			
HYSTRICIDAE	Sunda porcupine *Hystrix javanica*	LC	P
SCIURIDAE	Red giant flying squirrel *Petaurista petaurista*	LC	NP
SCIURIDAE	Spotted giant flying squirrel *Petaurista elegans*	LC	P

[1] Global status on The IUCN Red List of Threatened Species (IUCN 2014)

[2] Protection status in Indonesia, according to *Lampiran Peraturan Pemerintah Nomor 7 Tahun 1999 & Undang-Undang No. 5 Tahun 1990*. P = protected, NP = not protected.

Data analysis

I tested the effects of different factors on the detection probability of the focus species by using three different logistic regression models. For the first model, I used presence or absence of the respective species at each site as the binary dependent variable and included the predictor variables as shown in Table 5.2. The IUCN protection status of the survey site correlated highly with the influence of humans on the habitat type (secondary forest and agricultural area) (Spearman's rho = 0.843, $p < 0.001$, $n = 195$). In this model, I only considered the eleven species that were detected in at least one study site.

I used two further logistic regression models to investigate the influence of "season" (e.g. weather period), weather, moon and effort (Table 5.2) on the probability of common palm civets and leopard cat sightings, respectively. I used the direct observations and camera trap photos from Cipaganti. I included the presence or absence of the respective species on a certain night as the binary dependent variable. I created the index of effort by multiplying the number of teams observing per night by two and adding the number of camera traps working that night. Based on rainfall in Cipaganti, I defined the wet season from November to April (> 150 mm precipitation per month) and dry season from May to October (< 150 mm precipitation per month). Days without observations or camera traps were excluded from the analysis. None of the predictor variables correlated significantly above $r^2 = 0.60$. I used the forced entry method as I had specific model predictions (Hill & Lewicki 2006, Field 2009). If the odds ratio of a factor is above 1 there is a positive relationship between the dependent and independent variable when controlling for other factors in the model. I appreciate that species absence is difficult to determine as animals could be missed (Hirzel et al. 2002, Rode et al. 2013a), but I use it as an indication of sighting likelihood.

Table 5.2: Predictor variables and their categories included in a logistic regression to test their effect of species presence

Model	Predictor variable	Categories
Model 1	IUCN Red List status (IUCN 2014)	Least Concern Threatened Data Deficient
	Protection status of the species according to Indonesian law (*Lampiran Peraturan Pemerintah Nomor 7 tahun 1999 & Undang-Undang No. 5 Tahun 1990*	Protected Not protected
	Protection status of the survey site (as retrieved from www.protectedplanet.net)	Protected Not protected
	Part of Java	West East
	Survey effort (km)	(continuous)
Model 2 and 3	Season	Wet Dry
	Minimum temperature (°C)	(continuous)
	Average humidity (g/m^3)	(continuous)
	Rain (mm/24h)	(continuous)
	Wind (m/s)	(continuous)
	Lunar illumination (%)	(continuous)
	Survey effort (km)	(continuous)

3. Results

Combined transect survey efforts were 82.1 km for protected areas and 44.8 km for unprotected areas. All methods combined recorded 13 of the 22 target species (Table 5.3). Combined encounter rates in protected areas, excluding slow lorises, were almost double the encounter rates in unprotected areas. The encounter rate of slow lorises, however, was eight times higher in unprotected areas and combined encounter rates were affected by this difference accordingly. The yellow-throated marten, the Javan ferret badger and the small Indian civet were only encountered during the long-term study site in Cipaganti. These species, plus the spotted giant flying squirrel, were only encountered in unprotected areas, while the Javan chevrotain was only observed in protected areas. The only other wild mammal larger than rats (Muridae) and treeshrews ***Tupaia*** spp. camera-trapped was the Eurasian wild pig, with 17 camera trap records showing groups of up to seven animals between August 2012 and March 2013. Pigs were often encountered directly in Cipaganti, especially during the dry season (farmers report that this is because they come down from the higher forest area to search for food), but mostly in undergrowth so that species identification was not possible. The potential predators of Javan slow lorises, the leopard cat and the common palm civet were detected in two and ten of thirteen survey sites respectively. Both sites that had leopard cat encounters (Cipaganti and Tasikmalaya) were unprotected sites and also contained slow loris populations. Common palm civets coexist with Javan slow lorises in all unprotected areas and three of the seven protected areas where at least one of the species was detected.

Table 5.3: Number of encounters and distribution of nocturnal mammals and carnivores at various sites on Java, Indonesia, 2012 to 2014. The Javan slow loris and two potential predator species, the leopard cat and the common palm civet are highlighted in red.

Location	LC	JM	JFB	YtM	BL	B	CPC	SIC	JCh	JCo	SFGS	RGFS	Total (excl. JSL)	JSL	Total (incl. JSL)
Ujung Kulon							5		1	2			8	1	9
Carita										12			12		12
Mount Gede					1	1	4						6	1	7
Dieng Plateau							4						4		4
Mount Bromo							1						1		1
Ijen Plateau										1		1	2		2
Meru Betiri		2					9		2	2		5	20	5	25
Alas Purwo							5						5		5
Limbangan, Mount Masgit Kareumbi														3	3
Cipaganti*	1						3						4	16	20
Sumedang							3						3	12	15
Tasikmalaya	1						2			7			10	17	27
Pangalengan (fixed-point survey)							1				2	7	10	n.a.	n.a.
Cipaganti: direct observation	106		3		1	2	71	7					190	n.a.	n.a.
Cipaganti: camera trap	13	2	34	1			37	1					88	n.a.	n.a.

Grand Total	**121**	**4**	**37**	**1**	**2**	**3**	**145**	**8**	**3**	**24**	**2**	**13**	**363**	**55**	**418**
Encounter rate per km protected area	**0**	0.02	n.a.	n.a.	0.01	0.01	**0.34**	n.a.	0.04	0.20	n.a.	0.06	0.55	**0.12**	0.83
Encounter rate per km unprotected area	**0.02**	0	n.a.	n.a.	0	0	**0.18**	n.a.	0	0.18	n.a.	0.02	0.29	**1.00**	1.38
Total encounter rates per km	**0.01**	**0.01**			**0.01**	**0.01**	**0.28**		**0.02**	**0.19**		**0.05**	**0.46**	**0.43**	**1.02**

Grey shadings = Protected locations. Sightings in Cipaganti (non-survey) are not used in encounter rates.

Species: LC = leopard cat, SIC = small Indian civet, JFB = Javan ferret badger, YtM = yellow-throated marten, JM = Javan mongoose, BL = banded linsang, B = binturong, CPC = common palm civet, JCh = Javan chevrotain, JCo = Javan colugo, RGFS = red giant flying squirrel, SGFS = spotted giant flying squirrel, JSL = Javan slow loris (Table 5.1 gives scientific names). ‘n.a.’ signifies that the species was found only by methods other than nocturnal walked transects. Two survey sites, Limbangan and Cimungkat (APPENDIX 2), are omitted because no animals were seen.

Table 5.4 shows frequencies of presence and absence of the focus species per categories of the predictor variables used in the logistic regression model 1. The model with species presence in a study site as the binary outcome variable was highly significant (^{2}= 17.669, df = 6, p = 0.007, n = 143), with protection under Indonesian law and survey effort having significant effects on whether a species was detected or not (Table 5.5). The IUCN Red List status approached significance. While the protection under Indonesian law had a negative effect on presence of the species at a site (protected species less likely to be present), survey effort had a positive effect.

Table 5.4: Frequencies of presence and absence for 11 species and 13 survey sites (n = 143) shown for each category of the predictor variables used in model 1.

		Presence (%)	Absence (%)
IUCN Red List status	Least Concern	28	72
	Threatened	23	77
	Data Deficient	8	92
Protection status of species	Protected	19	81
	Unprotected	33	67
East vs. west	West	24	76
	East	21	80
Protection of site	Protected	21	79
	Unprotected	27	73
Survey effort (mean)		12 km	9 km

Table 5.5: Results of the logistic regression model with detectability (presence/absence) of 11 species in 13 survey sites as the binary outcome variable

			95 % C.I. for EXP(B)		
	B	Sig.	Lower	Odds Ratio	Upper
Constant	-3.347 (1.099)	0.002		0.035	
IUCN Red List Status		0.057			
IUCN Red List Status (1)	1.904 (0.818)	0.02	1.351	6.714	33.377
IUCN Red List Status (2)	2.083 (0.932)	0.025	1.292	8.032	49.923
Protection status of species	-1.216 (0.519)	0.019	0.107	0.296	0.819
West vs. east	0.895 (0.574)	0.119	0.795	2.448	7.533
Protection status of site	-0.215 (0.454)	0.635	0.331	0.806	1.962
Survey effort	0.076 (0.031)	0.015	1.015	1.079	1.148

Note: R^2 = 0.116 (Cox and Snell), 0.176 (Nagelkerke), Model ^{2}= 17.669, df = 6, p = 0.007, n = 143

The logistic regression model 2 on the detectability of leopard cats was significant (^{2}= 14.834, df = 7, p = 0.038, n = 314; Table 5.6). Only survey effort index had a significant influence on the detection of leopard cats, with greater effort leading to more sightings of leopard cats. The logistic regression model 3 for common palm civets was significant as well (^{2} = 23.967, df = 7, p = 0.001, n = 314; Table 5.7), with three significant variables. When effort increased, the probability of detecting common palm civets increased as well, but detectability decreased on brighter nights. Finally, it was shown to be more likely to detect common palm civets in the wet season.

Table 5.6: Results of the logistic regression model with detectability (presence/absence in a night) of leopard cats in the long-term study site Cipaganti as the binary outcome variable

			95 % C.I.for EXP(B)		
	B (SE)	**Sig.**	**Lower**	**Odds ratio**	**Upper**
Constant	-7.285 (4.321)	0.092		0.001	
Season	1.166 (0.769)	0.129	0.711	3.209	14.489
Effort index	0.504 (0.158)	0.001	1.215	1.656	2.257
Rain	0.002 (0.027)	0.916	0.951	1.003	1.057
Minimum temperature	-0.042 (0.227)	0.851	0.614	0.958	1.496
Humidity	0.045 (0.057)	0.428	0.935	1.047	1.171
Wind	-0.802 (0.799)	0.315	0.094	0.448	2.148
Lunar illumination	-0.479 (1.891)	0.800	0.015	0.619	25.245

Note: R^2 = 0.076 (Cox& Snell), 0.167 (Nagelkerke), Model ^{2}= 14.834, df = 7, p = 0.038, n = 314

Table 5.7: Results of the logistic regression model with detectability (presence/absence in a night) of common palm civets in the long-term study site Cipaganti as the binary outcome variable

			95% C.I.for EXP(B)		
	B (SE)	**Sig.**	**Lower**	**Odds ratio**	**Upper**
Constant	3.836 (2.881)	0.183		46.337	
Season	1.861 (0.611)	0.002	1.942	6.435	21.320
Effort index	0.325 (0.135)	0.016	1.063	1.384	1.802
Rain	-0.011 (0.026)	0.658	0.940	0.989	1.040
Minimum temperature	-0.282 (0.181)	0.120	0.529	0.754	1.076
Humidity	-0.027 (0.037)	0.467	0.905	0.973	1.047
Wind	0.231 (0.371)	0.533	0.609	1.260	2.606
Lunar illumination	-4.597 (1.700)	0.007	<0.001	0.010	0.282

Note: R2 = 0.12 (Cox & Snell), 0.2 (Nagelkerke), 2 = 23.967, df = 7, p = 0.001, n = 314

All three models showed a significant effect of survey effort in km or the effort index on the probability of detection. When plotting the number of detected animals against the survey effort during forest surveys for only the Javan slow loris, leopard cat and common palm civet, the same effect is visible but could not be tested due to small sample size (Figure 5.1). The total number of animals encountered and species richness also increase with increasing survey effort (Figure 5.1). Cumulative survey effort, according to the order the survey sites were visited, shows that the maximum number of animals detected was reached after 85.7 km (Figure 5.2). This depended on the order that sites were visited in, e.g. if the survey sites Mount Gede (survey effort 18.7 km), Meru Betiri (survey effort 29.2 km)and Cipaganti (survey effort 8.9 km) had been visited first, the maximum species richness would have been reached after 56.8 km.

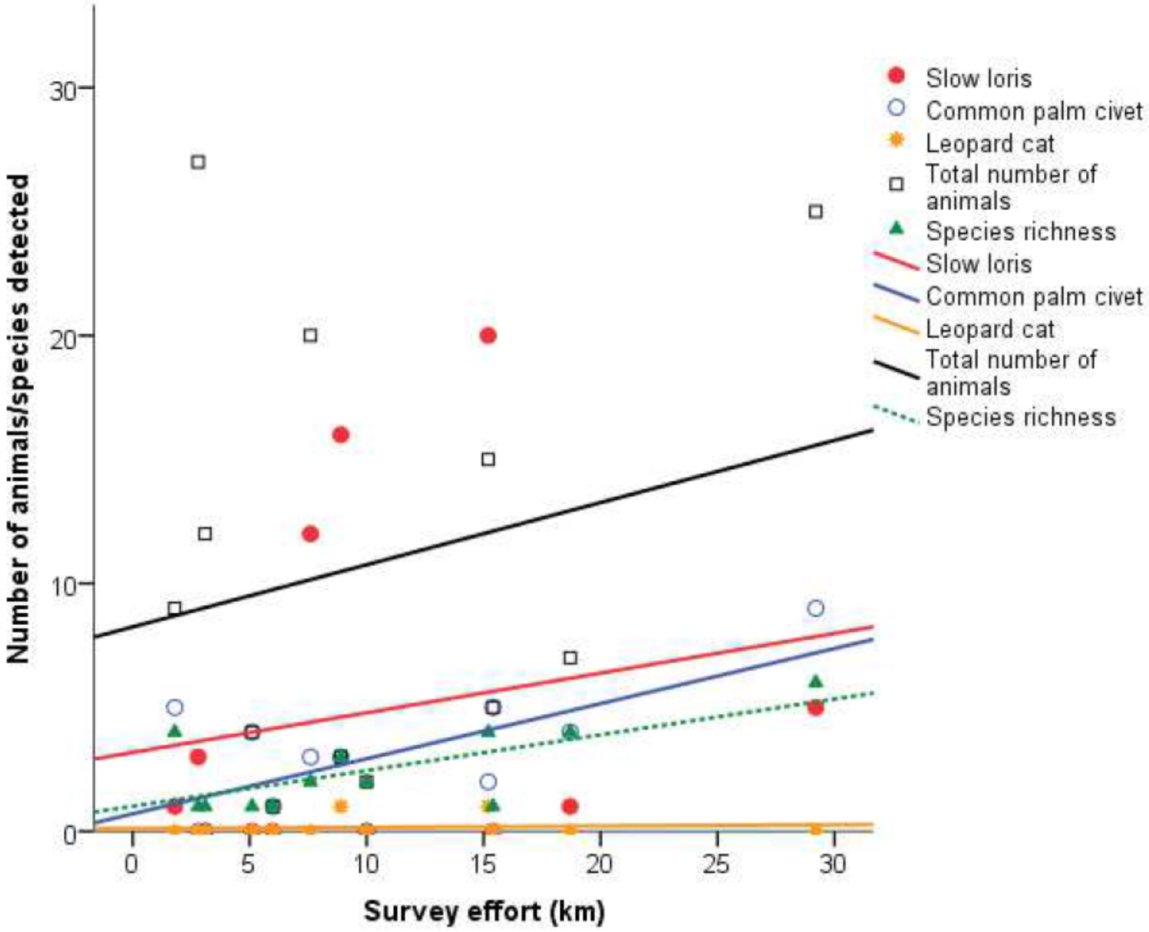


Figure 5.1: Number of animals and species detected during surveys with different survey effort

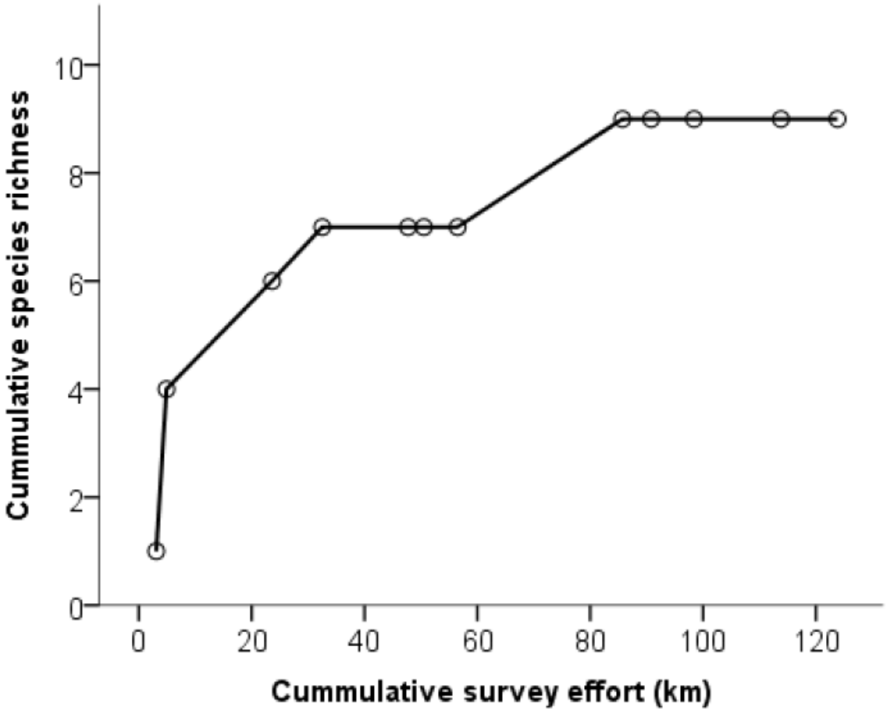


Figure 5.2: Number of species (= species richness) detected at the 12 survey sites visited in this study (excluding the fixed-point survey), in relation to cumulative survey effort.

Several species were frequently recorded close to human settlements (Figure 5.3). Leopard cats and common palm civets came to the perimeter of villages and Javan colugos were seen within villages, including twice at sport fields surrounded by trees. Cipaganti yielded numerous lengthy sightings of small carnivores at distances of 5 to 20 m. Leopard cat and common palm civet in Cipaganti seemed relaxed and disinterested in the observers when encountered. I observed them several times for 10 to 30 minutes while they were generally resting. One leopard cat was observed grooming for 20 minutes (Figure 5.4). On another occasion, one crossed a stream, where it caught and consumed a large whitish rodent on the bank. Common palm civets frequently walked along or sat on rubber-coated water hoses (used for irrigation) suspended aerially between trees. The camera traps recorded both leopard cat and common palm civet faecal and scent marking a single large stone. In one case a leopard cat scent-marked the stone, then two days later a common palm civet faecal-marked the same stone after sniffing at the exact spot of the leopard cat mark. Whether this was responsive marking remains speculative. Only one Javan colugo was seen gliding. The others were stationary on trees or poles. If disturbed, they remained where they were or ‘hopped’ up the tree.

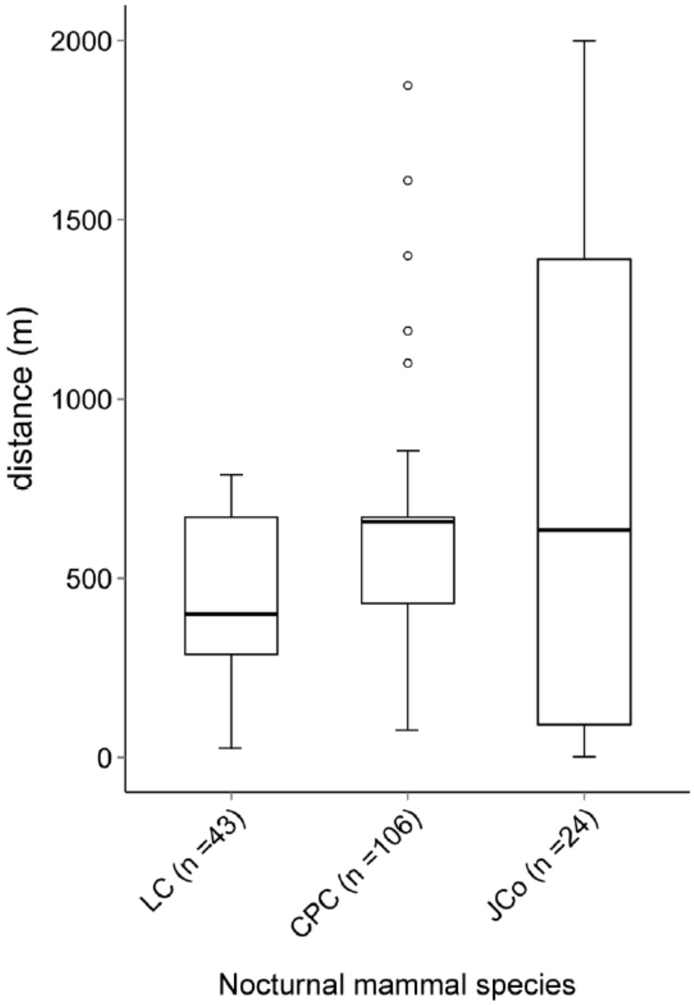


Figure 5.3: Median distances (in metres) from individual sightings of three species of nocturnal mammal to human settlements (of at least five houses). The box indicates the 75th and 25th percentiles, the whiskers show the maximum values of the data, circles indicate outliers. All surveys and the long-term study in Cipaganti were included. LC = leopard cat *Prionailurus bengalensis*, CPC = common palm civet *Paradoxurus hermaphroditus*, JCo = Javan colugo *Galeopterus variegatus*

Figure 5.4: Leopard cat *Prionailurus bengalensis* at Cipaganti, West Java, Indonesia on 4 March 2013 at 20:30 (photo: E. J. Rode-Margono). This animal was approached to 6m and observed for 20 minutes.

In terms of habitat use, leopard cat and Javan chevrotain were found exclusively on the ground, whereas banded linsang and binturong were observed on the ground and in trees. In Cipaganti, one binturong that was seen on the path turned immediately upon illumination and disappeared. In the second sighting there, the binturong sat resting in the 12 m high bamboo, apparently comfortably despite its size, at 4 m height. The binturong in Mount Gede Pangrango was spotted on the path and moved under an observer platform. While in Cipaganti canopy cover is very open; in Mount Gede Pangrango it was closed. The banded linsang in Cipaganti crossed an asphalt road in an agricultural area with farms, fields and interspersed trees, then disappeared in tall grass and undergrowth. A stream about 3 m wide was less than 500 m away, the nearest larger continuous forest about 1,500 m. The linsang in Mount Gede Pangrango was sighted about 6m up in an 8m high tree in closed-canopy habitat. I typically sighted common palm civet in trees, at a median height of 5 m (range 0–33 m; 54 records), and colugo at 8.5 m (range 2–18 m; 24 records). Height of the trees used by common palm civet was 11 m median (range 6–35 m; 38 records) and by colugo, 14 m (2–30 m; 23 records).

The only two records of feeding were both of common palm civet, once each on jackfruit and fig *Ficus* sp. In Cipaganti, I also found civet faeces with coffee beans *Coffea arabica*, birds, small mammals and invertebrates. Camera traps recorded Javan ferret badgers digging, sniffing and extracting items from the ground, once in a duo.

Concerning sociality, I had six direct observations of immature solitary leopard cats in Cipaganti, and two where a small individual was together with a large one (duos in December 2012 and April 2014). Camera trap video revealed an adult and juvenile leopard cat playing (April 2014). On four occasions I observed common palm civet kittens: in Tamanjaya one adult with four kittens (roughly one to two months old) in a tree trunk fork at the height of 14 m on a 20 m tree (March 2012), and in Cipaganti one adult with three kittens on the ground (January 2012, kittens about a third of the mother's body length), one mother–infant duo (June 2012), and one single young (July 2012). Also in Cipaganti, for three consecutive days, I located one civet nest (species unknown) in the base of a banana trunk lined with dead banana leaves, containing at least two kittens (April 2012). The yellow-throated marten record was a camera-trapped duo of the same size (September 2013; Figure 5.5). In two cases, colugos carried their relatively small but active baby in the patagium (March 2012 in Ujung Kulon; April 2012 in Tasikmalaya); both times the mother carried the baby while suspending from horizontal branches. A single juvenile colugo (about 50 % the linear size of an adult) was parked in relatively dense terminal branches (March 2012 in Ujung Kulon). Red giant flying squirrels were observed in duos or in small groups of up to four individuals at Pangalengan (April 2014), the Ijen plateau and Meru Betiri (both June 2013); the spotted giant flying squirrels in Pangalengan were a duo (April 2014). I also observed a duo of Javan chevrotain, comprising animals of similar size (June 2013).

Figure 5.5: Yellow-throated marten *Martes flavigula* at Cipaganti, West Java, Indonesia on 12 September 2013 at 05:40 (photo: Little Fireface Project)

Despite reports of hunting from neighbouring communities, in Cipaganti I have only one report on the hunting of nocturnal mammals. In November 2013 I found a civet trap set possibly to catch animals for civet coffee farms (Figure 5.6). I dismantled the trap for four nights. On the fifth night it was gone. Local people reported that outsiders set the trap; the land owner reported that he had chased the poacher from his land. The species is not protected, but the trapping was illegal because it was on private land. In Carita, I encountered two hunters with rifles in the protected forest hunting for colugos. They reported that local people use colugos for food and medicine.

Figure 5.6: First civet traps sighted during the field work in Cipaganti, in November 2013 (photo: W. Tarniwan)

4. Discussion

Predator community of the Javan slow loris

Two medium-sized potential predators of the Javan slow loris have been encountered in the surveys presented here, the leopard cat and the common palm civet. The leopard cat has only been detected in two unprotected sites, at the long-term field site Cipaganti and at the survey site Tasikmalaya. Both sites are also inhabited by slow lorises. The main prey types of leopard cats are small rodents (Rajaratnam et al. 2007, Corlett 2011); they have not yet been reported to prey upon slow lorises. Although they were only observed on the ground, in human-modified habitats like the agriculture fields in my long-term study site Cipaganti, leopard cats may occasionally encounter slow lorises crossing between natural vegetation patches (CHAPTER 3). In all unprotected and three protected areas we encountered both, slow lorises and common palm civets. Common palm civets are amongst the more frugivorous viverrids, feeding on all kind of fruits, but also prey upon rodents, birds, vertebrates and occasionally raid chicken (Su Su & Sale 2007, Jothish 2011). Although they also have not been reported to prey on slow lorises, they are mainly arboreal (Joshi et al. 1995, Su Su & Sale 2007) and should frequently encounter slow lorises and their parked infants during nocturnal foraging. Another big carnivore species that might be a predator of the slow loris is the Javan leopard. It occurs in several survey sites that we visited such as Mount Gede, Ujung Kulon or Meru Betiri (Ario et al. 2008); however, we have not included the Javan leopard in our focus species list as it occurs in very low densities and was very unlikely to be encountered. As direct observations of predation events are rare, the potential predators mentioned here may be candidates for behavioural experiments in captive facilities such as rescue centres, e.g. presenting the smell of slow lorises and their BGE to the animals.

General faunal community and biogeography

Many nocturnal mammal species remain poorly studied, leading to gaps in knowledge not only of their behavioural ecology and taxonomy but also their current distribution, abundance and conservation status. Nine species in the survey's remit were not encountered: fishing cat, Sunda stink-badger, two otter species, small-toothed palm civet, Indonesian mountain weasel, Javan warty pig, Sunda pangolin and Sunda porcupine. This might reflect rarity of these species on Java or coverage of sites and/or use of methods unlikely to find them.

Fishing cats seem to be associated with coastal areas on Java (Melisch et al. 1996), so their absence from my survey sites, all inland, is not surprising. Indonesian mountain weasels are so poorly known that their activity patterns have not been reported. Other tropical Asian weasels seem to be diurnal (e.g. Abramov et al. 2008, Ross et al. 2013) and if this species is similar, then the lack of records from spotlighting is uninformative about its status. Moreover, it is a montane species; the lowest-altitude record traced by Meiri et al. (2007) was from 1,400 m. Few sites were surveyed above this altitude (APPENDIX 2). Otters depend on water and are rarely camera-trapped unless those traps are specifically set for this purpose. Although a stream was present at Cipaganti, it was dry during the sampling periods, thus the absence of records at Cipaganti is not of concern. At the few sites with seemingly suitable habitat (e.g. Bodogol, Mount Gede Pangrango), survey effort was probably too low to experience sightings. Javan warty pigs were still present in several locations in West Java in 2003 (Semiadi & Meijaard 2006). Although difficult to record on spotlight surveys, being difficult to distinguish from Wild Pigs when encountered briefly, they should be relatively easy to camera trap when present. None of the many camera-trapped pigs in Cipaganti were warty pigs. Although possible to camera trap, Sunda pangolins are difficult to spotlight, as they are elusive, tend to freeze when disturbed and have non-reflective eyes. They may well inhabit at least some survey sites, although are perhaps unlikely to occur at the camera-trapped site of Cipaganti.

The absence of records the three species small-toothed palm civet, Sunda porcupine and Sunda stink-badger raises concern. Based on surveys in other countries, they should have been recorded, probably frequently, by these surveys if at all common and widespread in the surveyed areas. I surveyed in many of Java's protected and most natural areas (such as unprotected forest plantations). Although survey effort at some sites was low, the total spotlighting effort should have revealed at least some sightings if the species are at all common. However, inspection of the patterns of records of those nocturnal species that were recorded shows that it is just possible that the lack of records of small-toothed palm civet, Sunda porcupine and Sunda stink-badger is a chance effect rather than an indication of genuine rarity in Java. Discounting Javan mongoose and yellow-throated marten, which are predominantly diurnal and so stood little chance of being found on the spotlight transects or static counts, all other species in Table 5.2 are largely or entirely nocturnal. Five of these ten species were found only zero to two times in all spotlight transects and static counts combined. This suggests the further species not dissimilar to them in status in the spotlit survey sites may have been overlooked simply by chance. This possibility is supported by the difference in species recorded at Cipaganti between spotlight transects (two species) and the incidental sightings and camera trapping (eight species). Thus, it is quite plausible that the other surveyed areas have faunas as rich as, or even richer than, Cipaganti's.

The difference in species composition between the methods used at Cipaganti has a major implication for interpreting the findings at the other survey sites. Any species that does not occur at Cipaganti, and which stood a similar chance of being spotlit at any of the other sites as did half the nocturnal species in Table 5.2, could have been overlooked entirely. Without the long-term slow loris study (comprising camera trapping and volumes of incidental direct observations) at Cipaganti, the yellow-throated marten, small Indian civet and Javan ferret badger would have had no records either. It is thus possible that the three 'surprising absences' from all survey sites, Sunda porcupine, small-toothed palm civet and Sunda stink-badger, simply do not occur at Cipaganti (which is, after all, a non-protected area of highly disturbed habitat) and were overlooked in other areas. Although their island-wide status in Java is thus not necessarily that dissimilar to that of small Indian civet, Javan ferret badger and yellow-throated marten, this cannot be assumed.

Sunda stink-badger is readily camera-trapped and is spotlit with some regularity, although apparently not commonly (e. g. Wilting et al. 2010, Rustam & Giordano 2014). It remains numerous in at least northern Borneo (Samejima et al. in prep.) and the Javan populations have not been proposed to be taxonomically distinct. Java constitutes a large proportion of its entire range (otherwise, Sumatra, Borneo and the North Natunas). The other two 'surprising absences' raise higher global concerns because the species or sub-species are endemic to Java (small-toothed palm civet) or to Java and a few smaller islands to the east (Sunda porcupine). Allied (sub) species of the civet and the porcupine are readily spot-lit (e. g. Duckworth 1992, Willcox et al. 2012). Whilst ground-level camera trapping is unlikely to detect the civet (Willcox et al. 2012), Sunda porcupine should be easily camera-trapped (e.g. Datta et al. 2008). Although the porcupine is protected by Indonesian law, I have traced nothing on the species' field status within the last 30 years or more. The IUCN Red List only describes the Javan form of small-toothed palm civet as a representative for the whole genus' range. Although the other forms are very distinctive there has been no taxonomic revision since Van Bemmel (1952), made when taxonomic thinking was very different from today's. The failure to find it at any site in over 250 hours of spotlighting suggests the possibility, considered by Eaton et al. (2010), that the paucity of recent records might relate to limited appropriate survey effort rather than true rarity, is unlikely. Targeted searches for this civet should not be delayed until the genus receives a modern taxonomic review irrespective of when this might happen.

Until now, the Javan colugo had been believed to occur only in western Java east to Pangandaran, close to the border with Central Java (IUCN 2014). I found it in western Java as far east as Tasikmalaya, close to Pangandaran, within this known range. Records at the Ijen plateau and Meru Betiri National Park in the island's far east (Figure 5.7) represent an extension of known range by some 600 km. All observations were made below 900 m ASL. I surveyed no lowland sites between Tasikmalaya and Meru Betiri, so more focused research might find the species in Central Java as well.

Almost all species encountered during the surveys and the long-term observations share their habitat with Javan slow lorises. This and the fact that several species have only been detected during the long-term observations at the study site Cipaganti emphasises the important role that a slow loris conservation research project such as LFP can play. Slow lorises can be used as a flagship species (Barua 2011, Caro 2010), as it is charismatic, draws financial support, can stimulate conservation awareness and action (Nekaris et al. 2014b). The conservation work that is being done on slow lorises helps to protect other species and their habitat. Reporting on these other species in the scope of slow loris research may also draw the attention of researchers to these often under-studied species.

Figure 5.7: Javan colugo *Galeopterus variegatus* at Meru Betiri National Park, East Java on 1 June 2013 (photo: Guiaumme Douai). This represents an eastward extension of known range of some 600 km.

Unresolved taxonomic issues may lead to (regional) extinctions

Regional extinctions are especially likely to equate to global extinctions of cryptic species where the taxonomy of many species has not been reviewed recently, as is the case for Java. Some recent taxonomic studies that included Javan taxa found them distinct, including Javan slow loris (Wirdateti et al. 2006, Nekaris & Jaffe 2007), Javan colugo (Janečka et al. 2008), Javan chevrotain (Meijaard & Groves 2004), adding to animals long considered species endemic to Java (and in some cases Bali) such as Javan ferret badger or Javan warty pig. The chevrotain, ferret badger and Javan warty pig on Java may each even comprise two clearly defined subspecies distributed allopatrically in the west and the east of the island (Long 1992, Meijaard & Groves 2004) or with a second species on Bawean island in the case of the Javan warty pig (Groves & Grubb 2011). Yellow-throated marten and small-toothed palm civet on Java are both particularly distinct from the respective species' populations elsewhere (Schreiber et al. 1989). It is possible that among species with no comprehensive recent taxonomic review that they are species, currently unrecognised, endemic to Java or nearly so. Where these are also in decline, extinction may be facilitated by a lack of conservation interest in what is currently perceived as only an indistinct taxon at best.

Factors affecting the detection of species

The exact distribution and abundance of many nocturnal mammal species remains poorly-studied (Eberle & Kappeler 2004), leading to difficulties assessing their current conservation status. Camera traps are frequently used to confirm the presence or abundance of species (O'Connell et al. 2011), especially in long-term field sites. Distribution maps are often made by combining data from camera traps, various single sightings of wild animals, and museum specimen localities. Data from single sightings and museum specimens may be accumulated over long periods of time presenting a biased species distribution or abundance record. As many populations of nocturnal forest-dwelling animals are facing rapid population declines, more focused studies within a shorter time period are required. To combat the high costs associated with frequent surveys, their design must be as effective as possible.

The selection of study sites is of high importance for comprehensive distribution surveys. Study sites can be selected based on previous reports, museum specimens, ethnobiological surveys, and ecological niche modelling. On the other hand, the selection of survey sites should not be based on common assumptions, as the exclusion of sites may lead to overlooking important populations and flaws in the conservation status assessment. Several taxa in my study have traditionally been classed as rainforest taxa (Heydon & Bulloh 1996, Colón 2002, but see Bali et al. 2007). However, my model did not find a higher presence of species in protected and forested landscapes, or areas that are very far from human settlements. Unprotected and human-modified areas must not be neglected in distribution surveys. Regardless of their conservation status, many nocturnal medium-sized species show certain degrees of behavioural flexibility and are able to live in or near to human-altered habitats (leopard cats: Rajaratnam et al. 2007, Mohamed et al. 2009; common palm civets: Corlett 1998; Javan ferret badger: Brickle 2007, Duckworth & Brickle 2008, Duckworth et al. 2008; binturong: Payne et al. 1985, Grassman et al. 2005; Javan slow loris: CHAPTER 3). During my surveys, Javan slow lorises, Javan colugos, common palm civets, leopard cats, and Javan ferret badgers were all found in substantial numbers in agricultural fields (*talun*) and forest plantations. Equally, geographic regions said to be less biodiverse should not be ignored. Many nocturnal small mammals have only been recorded in the western and central parts of Java (e.g. up to Dieng Plateau; Nijman & van Balen 1998, Marliana & Ruehe 2012), but surveys in eastern parts of Java are rarely conducted. However, I did not find any evidence in my model to support the assumption, that the species recorded in West and Central Java would only exist there and not on the eastern part of the island. In fact, the distribution of Javan colugos and Javan slow lorises has just recently been extended to East Java based on short-term surveys (Lehtinen 2013, Voskamp et al. 2014, see above).

The majority of species studied here are listed as Least Concern on the IUCN Red List and are thus regarded as common. My model suggests that species protected by Indonesian law and with a higher or Data Deficient conservation status on the IUCN Red List are less likely to be detected during surveys. Although I did not find a strong correlation, I can assume that the protection and conservation status implies that these species may be less likely to be detected due to their restricted distribution and lower abundance. However, my analysis only included species that were at least once detected during my forest surveys. Assumedly common species such as the Sunda porcupine or the small-toothed palm civet were absent from all surveyed sites despite almost 120km covered. Both legal and illegal wildlife trade in Indonesia is mostly unregulated and/or unsustainable. This may lead to rapid and sudden undetected population declines in some common species. Examples include the soaring trade in slow lorises and owls as a result of media presence in YouTube videos or movies (Shepherd 2012b, Nekaris et al. 2013c) as well as the civet coffee (*kopi luwak*) trade afflicting the common palm civet (Shepherd 2012a).

Knowledge of a species' biology and ecology is very important when designing effective surveys, and may be helpful in finding further study sites where the predator-prey relation between slow lorises and their potential predators can be studied. Inter-specific differences in biology and ecology may explain the different detection rates of animals. Although none of the predictor variables of the leopard cat model (apart from survey effort) were significant, the second model indicates that it is more likely to encounter common palm civets in the study site when lunar illumination is low and during the wet season. Even though I have had no accounts of big predators in the area, this lunarphobic behaviour is typically associated with a predator avoidance strategy (Beier 2006, Upham & Hafner 2013), possibly in relation to nocturnal predators such as pythons or big cats (Corlett 2011). Fruiting is higher in the wet season, which may explain the higher activity of common palm civets during this time of the year. Accordingly, surveys on common palm civets may lead to more sightings if conducted in the wet season and during high lunar illumination. Other species-specific characteristics, such as ecological requirements and habitat preferences may influence the presence of a species.

Finally, the results of all three models that I tested stress the importance of survey effort. Even though time and money can be saved with effective methodology that recognises factors influencing detection, the study effort as measured in kilometres covered is still the most important predictor of whether species are detected or not (Buckland et al. 2001). Specifically, we reached the maximum combined number of nine species after about 85 km survey. This however depends on the order that sites were visited in. If researchers want to study species communities they should allocate relatively high survey efforts (e.g. >100 km) to the survey sites of interest from the beginning. If they want to cover a whole geographic range they should assign medium survey effort (i.e. 20 to 30 km) for each of the selected study sites.

Surprising habitat flexibility in some species

Due to their ability to exploit food sources and find shelter available in human-altered habitat, and to adapt their temporal and spatial behaviour to avoid direct encounters with humans, several species evidently can live in close proximity to humans or in (sub-) urban environments (McKinney 2002, 2008). Examples of mammal species include insectivores (e.g. hedgehogs *Erinaceus europaeus*, Rondinini & Doncaster 2002), European pigs (Podgórski et al. 2013), or primates such as vervet monkeys *Cercopithecus aethiops* (Brennan et al. 1985), rhesus monkeys *Macaca mulatta* and hanuman langurs *Semnopithecus entellus* (Chauhan & Pirta 2010). Small- to medium-sized carnivores such as foxes *Vulpes vulpes* and mustelids (Dickman 1987, Herr et al. 2002) may profit from urban exploiters such as rats and mice (McKinney 20020). In my study, although the all-species spotlighting encounter rate was higher in protected areas (total 0.55 sightings/km) than in unprotected areas (total 0.29 sightings/km) (Table 5.3), many species were found in human-modified landscapes. Many common palm civets were recorded in agricultural fields (*talun*) and plantations, where they were not fearful of human presence. All but one of the 120 leopard cat records were at Cipaganti. The leopard cat is the most common cat species in Southeast Asia (Nowell & Jackson 1996, Sunquist & Sunquist 2002): my observations are consistent with previous studies showing its occurrence in both natural habitats and human-modified areas such as agricultural landscapes (e.g. Rajaratnam et al. 2007, Mohamed et al. 2009). All 37 ferret badger records were in the *talun* fields of Cipaganti. Javan ferret badger lives in both primary forest (e.g. Mount Gede, Mount Halimun and Meru Betiri) and near human settlements and tourist trails (Seidensticker & Syuono 1980, Yossa et al. 1991, Brickle

2007, Duckworth et al. 2008). Nearly all records (34 of 37) were from camera traps. There was also much observation in the camera trap area, so the small number of direct sightings of ferret badgers suggests a general elusiveness of this species. It might well have been overlooked by the spotlight surveys at the other sites. Seven of 24 Javan colugo sightings were in agroforest, or even in villages. This shows remarkable flexibility; Sunda colugo *G. volans* sensu lato has been said to depend on forests with relatively high trees (Lim 2007). This apparent dependence may be biased by the choice of study sites with high trees (CHAPTER 3). Average, minimum and maximum distances of sightings from human settlements were influenced by the choice of survey sites, but individual records of animals were close to human settlement, confirming the flexibility of these species.

Following the recent extensive forest loss on Java, many disturbance-sensitive species or species that depend on lowland habitat occur in only small, isolated populations with few recorded sightings (Schreiber et al. 1989, Melisch et al. 1994). Although I encountered Javan chevrotain only a few times overall and always inside protected areas, it was the fourth-most frequently spotlit species (Table 5.3) and the most frequently spotlit ground-dwelling species. This potentially indicates sensitivity to human disturbance. I also recorded banded linsang only rarely, but low encounter rates in this study might reflect that survey methods are unsuitable for this species (Cheyne et al. 2010). It is reputedly tolerant of disturbed forests and edge habitat (Lim 1973, van Rompaey 1993).

Ecology and behaviour of recorded species

Three of 21 species targeted in this study (Table 5.1) are listed as Data Deficient on the IUCN Red List, yet by no means are the other species well known on Java, or even globally. To my knowledge Java has hosted no long-term study on any of these species. The two species found that are listed as Data Deficient, Javan chevrotain and Javan ferret badger, are both endemic to Java and Bali (where occurrence of the chevrotain is not confirmed) (IUCN 2014). Javan chevrotain is presumed to be mostly found in forest (IUCN 2014) and may need dense understory vegetation (Hoogerwerf 1970). My three Javan chevrotain sightings were in dense undergrowth in relatively little-disturbed habitat; one involved a duo.

Leopard cats were always on the ground. I saw mostly singles, but also duos with a larger and a smaller individual, possibly female and young. Leopard cat feeds mainly on small rodents (Rajaratnam et al. 2007, Corlett 2011), which might contribute to its tolerance of human-modified habitat and close proximity to human settlements. Leopard cats let the observers watch them for many minutes. Local farmers start in the fields before dawn so leopard cats are perhaps habituated to human presence. In forests elsewhere, common palm civets chose the highest and tallest trees especially for resting, but the canopy is also their foraging habitat (Joshi et al. 1995, Su Su & Sale 2007). My sightings overall were somewhat lower (median 5 m), probably because most sightings were in agricultural areas, where trees are lower and animals are mostly on the ground to forage or pass between vegetation fragments.

I had only a few sightings of banded linsang and binturong. Linsang sightings are discussed above. Binturongs are usually arboreal (e.g. Nettelbeck 1997). Two of my three sightings were of binturongs on the ground. Just as with slow lorises in areas of discontinuous canopy (CHAPTER 2 and 3), binturongs may be forced to use the ground to cross between natural habitat patches. That they do so perhaps indicates adaptability to this kind of habitat.

Colugos are strictly arboreal and cannot walk on the ground (Lim 2007). I detected all individuals at heights between 2 m and 18 m. Colugos seem to rely on camouflage rather than escape (Lim 2007). Here they were never seen gliding when disturbed: they either froze or moved up the tree. Colugos have cryptic coloration and rarely vocalise (Lim & Ng 2010). The single juvenile that I saw was parked in dense terminal branches, similar to behaviour shown by slow lorises (Starr et al. 2011). All sites with Javan colugo records also contained Javan slow loris. The two species may occupy different feeding niches, with colugos feeding mainly on leaves and possibly tree sap (Lim 2007), and lorises on gum, nectar and insects (Wiens et al. 2006).

Social systems of giant flying squirrels are poorly studied. For each species, I observed multiple individuals in groups of two to four animals in close vicinity at all locations where they were observed.

Threats to study species

Although only four of the 12 species detected in this study are categorised by the IUCN Red List as globally threatened, many face potential threats, such as habitat loss, disturbance and hunting for wildlife trade (Ceballos & Ehrlich 2002, Shepherd et al. 2004, Sodhi et al. 2004, Corlett 2007). The extent to which these actually pose severe threats may be species-specific. Wildlife trade is one of the biggest threats to many Southeast Asian medium-sized mammals and to some bird species such as birds of prey; off-takes from wild populations are high (Shepherd et al. 2004, Nijman 2010, Shepherd 2012a,b). In Indonesia, numbers of wild civets and leopard cat in trade are increasing dramatically. Leopard cats are commonly offered for sale in markets either as pets (often young animals with removed teeth) or skins, even though legally protected (Shepherd et al. 2004, Shepherd 2012a). Some civets, especially common palm civet, are in demand for civet coffee (*kopi luwak*) and as a new trend in pets (Shepherd 2012a). Pangolins are heavily traded for traditional medicine (Lim & Ng 2007). Colugos are hunted for consumption in West Java and populations are declining in Southeast Asia (IUCN 2014). Species such as the Javan porcupine, Sunda colugo, Javan chevrotain, Sunda pangolin and binturong are hardly ever seen at main wildlife markets (Shepherd 2012a), but this does not mean that they are not traded. The Sunda pangolin is numerous in illegal international trade (e.g. Pantel & Chin 2009, Nijman 2010). Porcupines are heavily traded in Sumatra, Kalimantan and everywhere in mainland Southeast Asia; thus trade is highly likely also in Java (C. R. Shepherd in litt. 2014). Javan ferret badgers have recently started to appear on wildlife markets (Shepherd 2012a, EJR-M unpubl. data). A sudden rocketing of wildlife trade for particular animals can arise through new trends like civet coffee and the pet trade in lorises or owls following their media appearance in Web 2.0 platforms and movies (Shepherd 2012a,b, Nekaris et al. 2013c). It is not possible to predict which other species may be similarly affected in the future.

The causal relations between numbers of animals in trade, consumer demand, population trends in the wild and law enforcement or protection of the species are not clear. Whether a drop in animals in trade is caused by a decreasing wild populations or by other reasons, and whether an increase in numbers in trade may be followed by a decrease of wild populations can be assessed only if wild populations are reasonably monitored, but this is not the case in Java. Sudden declines of common species by human exploitation can drive Least Concern species to Critically Endangered status or even (local) extinction quickly (Casey & Myers 1998, Gaston & Fuller 2007).

On-going deforestation and modification of natural habitat (Lavigne & Gunnell 2006) affect species that are less flexible and more dependent on dense forest, particularly those needing lowland habitat with only low levels of human disturbance. Most species detected in this study were encountered in unprotected areas, except for Javan chevrotain, which was seen so few times in total that the lack of records from unprotected areas may simply have been a chance effect. Most species' encounter rates were higher in protected areas, although this could be a spurious result from relatively low survey effort. The clear difference in all-species encounter rates between protected and non-protected areas (excluding the Javan slow loris) was mainly, perhaps entirely, driven by common palm civet. The lack of a clear difference raises concerns about the effectiveness of protected areas on Java. Many PAs in Indonesia are not well managed and show high levels of ongoing resource exploitation and forest clearing (e.g. Curran et al. 2004, Sulistyawati et al. 2006, 2008, Bickford et al. 2007, Zuhri & Sulistyawati 2007). This may be severely inhibiting their role in species conservation: effectively managed PAs should hold wildlife communities radically different from those in anthropogenically impacted areas.

CHAPTER 6

Impact of climate and moonlight on the behaviour of Javan slow loris

1. Introduction

To secure maintenance, survival and reproduction, animals adapt their behaviour to various factors, such as climate, availability of resources, competition, predation, luminosity, habitat fragmentation, and anthropogenic disturbance (Kappeler & Erkert 2003, Beier et al. 2006, Donati & Borgognini-Tarli 2006). Animal behaviour can be seen as a trade-off between the risk of being preyed upon and the fitness gained from foraging (Charnov 1976). Perceived predation risk assessed through indirect cues that correlate with the probability of encountering a predator may shape an animal's behaviour (Vasquez 1994, Thorson et al. 1998, Orrock et al. 2004).

One of the indirect cues that animals use to assess predation risk is moonlight (Beier et al. 2006, Upham & Hafner 2013). Most mammals decrease activity or change habitat choice with increasing lunar illumination (lunarphobia) (Price et al. 1984, Hecker & Brigham 1999, Horning & Trillmich 1999, Nash et al. 2007, Penteriani et al. 2011, Saldana-Vásquez & Munguía-Rosas 2013, Prugh & Golden 2014) to be more concealed from predators. Some species increase their activity in brighter nights (lunarphilia) due to prey availability, higher foraging efficiency, or better visual detection of predators (Table 6.1) (Horning & Trillmich 1999, Packer et al. 2011, Prugh & Golden 2014). Whether a species is lunarphobic or lunarphilic depends on the primary sensory system (e.g. visual acuity), phylogenetic relatedness, and habitat cover (Hecker & Brigham 1999, Michalski & Norris 2011, Saldana-Vásquez & Munguía-Rosas 2013, Prugh & Golden 2014). Primates, for instance, are highly visually oriented (Gursky 2003, Bearder et al. 2006) and are mainly lunarphilic, as opposed to rodents, lagomorphs carnivores and bats, which are largely lunarphobic (Prugh & Golden 2014). Some species may be lunarneutral, although the chosen methods of study may have a certain influence on whether a certain reaction to moonlight is found (Nash 2007, Penteriani et al. 2011). Trade-offs regarding the reaction towards moonlight may vary between species, and even local populations (Lang et al. 2005, Saldana-Vásquez & Munguía-Rosas 2013).

Table 6.1: Reactions of some animal species towards moonlight, and adaptive explanations. PA = predator avoidance, FA = food availability, FE = foraging efficiency, PD = predator detection

Species	Scientific name	Response to lunar illumination	Adaptive explanation	Reference
Kangaroo rat	*Dipodomys* sp.	Lunarphobic	PA	Upham & Hafner 2013
Lesser bushbaby	*Galago moholi*	Lunarphilic	PA	Bearder et al. 2006, Bearder et al. 2001
Galapagos fur seal	*Arctocephalus galapagoensis*	Lunarphobic	FA, PA	Trillmich & Mohren 1981, Horning & Trillmich 1999
Spectral tarsier	*Tarsius spectrum*	Lunarphilic	FA, FE, PD	Gursky 2007
Freckled nightjar	*Caprimulgus tristigma*	Lunarphilic	FE	Ashdown & McKechnie 2008
African lion	*Panthera leo*	Lunarphobic	FE	Packer et al. 2011
Common poorwill	*Phalaenoptilus nuttallii*	Lunarphilic	PD	Woods & Brigham 2008
Male tree frogs	*Smilisca sila*	Lunarphilic	PD	Tuttle & Ryan 1982

Weather condition is a second cue that may affect animal activity, causing variation in the detection of prey and predators, and influencing thermoregulation (Hanya 2004). In general, low temperature causes animals – prey and predator species - to decrease activity to conserve energy. Low temperature especially affects the activity of poikilotherm species like amphibians or arthropods (Fitzgerald & Bider 1974, Fadamiro & Wyatt 1995) but also homeotherm species that may decrease activity, employ social and postural thermoregulation (Donati et al. 2011), or go into torpor or hibernation (Schmid 2000, Smit et al. 2001, Dausmann et al. 2005, Schuelke & Ostner 2007). Humidity and precipitation may affect animal activity. Strong rain or wind generally decrease insect availability and can impede the ability of predators to detect prey (Vickery & Bider 1981, Thies et al. 2006). Some animals are more active in high humidity and precipitation due to food availability or physiological needs (amphibians: Fitzgerald & Bider 1974; rodents: Orrock et al. 2004, insects: Fadamiro & Wyatt 1995; arthropods: Skutelsky 1996), some decrease activity due to energetic constraints (primates: Donati & Borgognini-Tarli 2006; bats: Voigt et al. 2011).

Asian lorises (Lorisinae) are characterized by a suite of morphological traits that makes them well adapted to predation avoidance, foraging and temperature. Both slow and slender lorises are arboreal slow climbers (Crompton et al. 1993), and rely on crypsis to avoid predators. Slow lorises are venomous, a trait that has been attributed to predator defence (Alterman 1995, Nekaris et al.

2013a), which might also affect its activity. High susceptibility to predators suggests that lorises would more likely be lunarphobic. Wild data, however, do not follow a consistent pattern. Wild red slender lorises ***Loris tardigradus*** tended to lower activity on bright nights, although this was not significantly different from dark night behaviour; they rested, groomed more and whistled more frequently during bright nights, but not significantly, so lunarneutrality cannot be ruled out (Bernede 2009). Although in general gray slender lorises were lunarneutral they were in some aspects lunarphilic (Bearder et al. 2001, 2006), whistling more in bright nights, and foraging more for energy-rich insects (Bearder et al. 2001). Infants of gray slender lorises however, sought more habitat cover in bright nights, possibly as predator avoidance strategy, indicating lunarphobia for this age class (Bearder et al. 2001). The majority of slow lorises are lunarphobic. In Cambodia, the pygmy loris was lunarphobic, especially on cold nights (Starr et al. 2012). Rogers and Nekaris (2011) report that Bengal slow lorises in Cambodia become more active during the dark moon phase. During surveys of the Javan slow loris lunar neutrality was suggested in that moonlight had no impact on detectability of the species (Nekaris et al. 2014a). Captive greater slow lorises reduced activity with higher illumination (Trent 1977).

It is notable that in the single wild study with clear evidence of lunarphobia, Starr et al. (2012) found that decrease in activity was heightened during low temperatures. Lorisines have low metabolic rates, good fur insulation, and possess extensive vascular ***retia mirabilia*** that help them to stay inactive for prolonged periods (Whittow et al. 1977, Mueller 1979). Most notably, slow lorises enter torpor for hours or days in cold temperatures (Nekaris & Bearder 2011). Starr et al. (2012) proposed that the combined risk of both predation and heat loss outweigh the benefits of being active, and that temperature should be considered in further discussions of loris activity.

The Javan slow loris, endemic to Java, Indonesia (Nekaris & Bearder 2011), weighs around 1 kg, is known to go into torpor, and occurs at least up to 1700m asl (Nekaris et al. 2014a, Nekaris & Rode-Margono unpub. data). Indeed, much of the forest left on Java where slow lorises are found is at altitudes above 1000 m (Nekaris et al. 2014a, Voskamp et al. 2014). I thus examined the effect of lunar illumination, temperature and other environmental factors on activity of the Javan slow loris at a high altitude site with at least two potential predators. I also examined microhabitat use in respect to predator perception.

2. Methods

The field site is described in CHAPTER 2, section 3.1, and details about capturing, radio-collaring and behaviour observation methods are given in section 4.1.1 to 4.1.3. I followed the ethogram in APPENDIX 3 and grouped resting and sleeping into the category “not active” and all other behaviours except other into “active”. Assuming that a higher position in the tree provides more concealment by the canopy, I used the relative height (height of the animal divided by height of the tree) of the animal’s tree as an indication of safety. I recorded any direct sightings of potential nocturnal predators, including common palm civets and leopard cats. Additionally, I had one to four camera traps (Cuddeback Attack IR; Bushnell Trophy cam night vision) installed for 185 nights (304 individual camera trap nights). Camera trap setting and collection of weather data are described in CHAPTER 2, section 4.1.4 and 4.1.5.

Statistical analysis

Due to the risk of measuring behavioural sequences such as sleeping for a prolonged time, I only used only every 6th data point of my dataset to increase independence of the data, yielding single observations of the same individuals that were at least one hour apart. I excluded the first and last hour of the night (18:00 to 19:00 and 05:00 to 06:00) to ensure that astronomical twilight is excluded from the data. Astronomical twilight is defined as the moon being 18° below the horizon (Erkert 2003). Twilight effects on activity may result in peaks at dawn and dusk and an overrepresentation of certain behaviours usually performed in these periods (Bearder et al. 2001, 2006, Erkert & Cramer 2006). I applied a logistic regression model due to the non-normal distribution of my data (Starr et al. 2012). I used the binary dependent variable “active” and “not active” (Field 2009). The predictor variables were sex, number of observers, luminosity, minimum nightly temperature, average humidity per night, wind, cloud cover, rain per hour and relative height of slow loris. Humans can be seen as predators (Charles-Dominique 1977), and although I did not witness hunting of slow lorises for the pet trade in my study area it was reported for neighbouring villages and is generally common in West Java (Nekaris et al. 2009). I then applied a similar model to the presence of potential predators with one night where a camera trap was operated or direct observations were conducted as sample unit. For camera trap data I used illumination of the night (number of hours the moon was visible multiplied by moon phase), and I excluded cloud cover. Days without observations or camera traps were excluded. I included an index of effort into the model, consisting of the number of teams observing per night weighted by two to account for a higher viewing angle, plus the number of camera traps working that night. For both models, none of the predictor variables correlated significantly above $r^2 = 0.6$. I used the forced entry method as I had specific predictions about the model (Hill 2006, Field 2009). If the odds ratio of a factor is above 1 there is a positive relation between dependent and independent variable.

3. Results

I collected 7169 5-minute observation points of 12 radio-collared adult individuals, resulting in approximately 600 hours of direct observation and 1036 used data points. The activity budget of all animals per hour of the night can be seen in Figure 6.1. There was a significant relationship between activity and the different hours of the night (^{2} = 22.708, df = 9, p<0.007), with animals being more active than expected between 19:00 and 20:00.

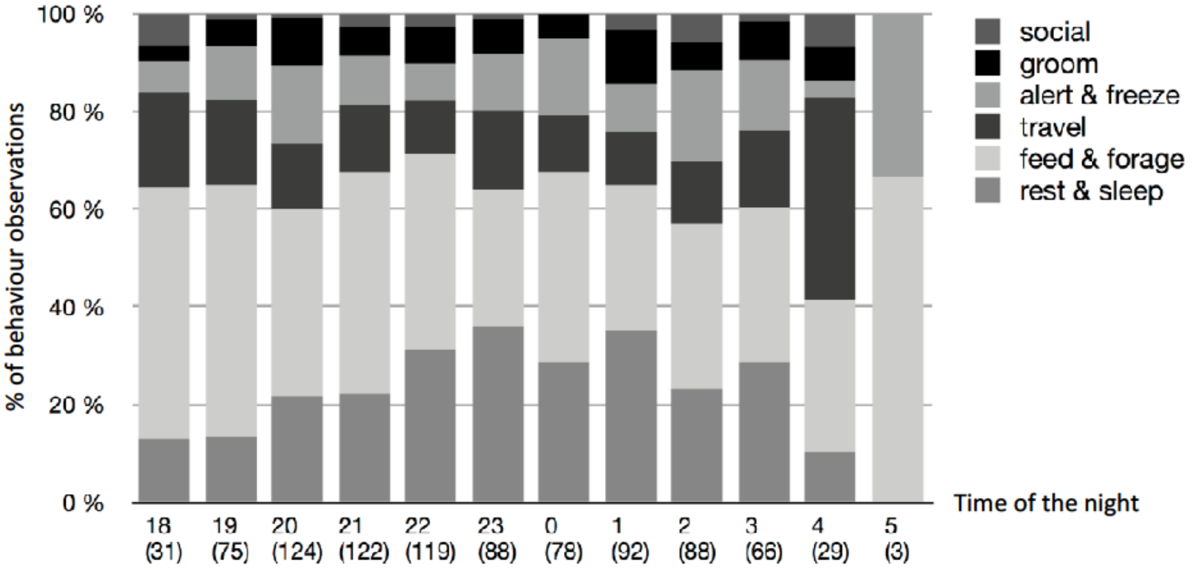


Figure 6.1: Activity budget per hour for 12 adult Javan slow lorises. N = 915. Data points were at least one hour apart. Sample sizes for the respective hours are given in brackets. Inactive behaviour is indicated by the category “rest and sleep”

The logistic regression model with slow loris activity as the outcome variable was highly significant (^{2} (1) = 116.158, df = 11, p < 0.001), with lunar luminosity, humidity, cloud, relative height and the interaction of minimum temperature and moon having a significant effect on whether slow lorises are active or inactive (Table 6.2). While luminosity and relative height have negative effects on activity, humidity and cloud cover have positive effects. The interaction of minimum temperature and moonlight showed that temperature affected activity during bright nights, but not dark nights. Slow lorises are more active when it is warmer. In dark nights they are equally active in warm and cold nights.

Table 6.2: Results of the logistic regression model with activity of Javan slow lorises as a binary outcome variable

			95 % C.I. for EXP(B)		
	B (SE)	**Sig.**	**Lower**	**Odds ratio**	**Upper**
Constant	1.520 (1.402)	0.278		4.572	
Sex	0.009 (0.184)	0.961	0.704	1.009	1.446
Number of people (#)	0.026 (0.125)	0.837	0.803	1.026	1.311
Moon (%)	-3.926 (1.863)	0.035	0.001	0.02	0.76
Minimum temperature (°C)	-0.053 (0.077)	0.491	0.815	0.948	1.103
Humidity (%)	0.039 (0.018)	0.029	1.004	1.04	1.078
Wind speed (m/s)	0.736 (0.417)	0.078	0.922	2.087	4.727
Cloud cover (%)	0.727 (0.308)	0.018	1.132	2.069	3.784
Rain (mm/h)	0.103 (0.452)	0.82	0.457	1.109	2.689
Relative height	-3.957 (0.492)	<0.001	0.007	0.019	0.05
Minimum temperature * moon	0.234 (0.113)	0.038	1.013	1.264	1.576
Cloud * moon	-0.615 (0.518)	0.235	0.196	0.541	1.493

Note: R^2 = 0.148 (Cox and Snell), 0.213 (Nagelkerke), Model ^{2} (1) = 116.161, df = 11, $p<0.001$

Camera trapping revealed six independent photos of the leopard cat, ten of the Javan ferret badger, and 14 of the common palm civet. The logistic regression model with predator presence as the outcome variable was not significant (^{2} (1) = 12.523, df = 7, $p < 0.085$) (Table 6.3).

Table 6.3: Results of the logistic regression model with presence of predators as a binary outcome variable

			95 % C.I. for EXP(B)		
	B (SE)	**Sig.**	**Lower**	**Odds Ratio**	**Upper**
Constant	-8.576 (4.127)	0.038		0	
Effort index	0.237 (0.119)	0.047	1.004	1.267	1.6
Moon (% illuminated per night)	22.827 (12.552)	0.069	0.169	8.20E+09	3.97E+20
Minimum temperature (˚C)	0.075 (0.221)	0.735	0.698	1.078	1.663
Average humidity (%)	0.067 (0.042)	0.107	0.986	1.069	1.16
Wind speed (m/s)	0.116 (0.358)	0.745	0.557	1.123	2.266
Rain last 24h (mm/24h)	-0.025 (0.028)	0.375	0.924	0.976	1.03
Moon * minimum temperature	-1.298 (0.738)	0.079	0.064	0.273	1.16

Note: R^2 = 0.065 (Cox and Snell), 0.103 (Nagelkerke), Model ^{2} (1) = 12.523, df = 7, $p < 0.085$

Farmers reported to us that domestic dogs sometimes detected and cornered slow lorises. I have never observed any flight or freezing reaction of Javan slow lorises towards common palm civets or leopard cats. In contrast, I have witnessed sub-adults feeding unperturbed by an adult male common palm civet within 5m distance.

4. Discussion

4.1 Lunar illumination and predation risk

My model on slow loris activity revealed a negative effect of lunar illumination and relative height on activity, a positive effect of humidity and cloud cover, and an interaction effect of lunar illumination and temperature. Activity was not affected by the number of people observing the slow lorises, neither was an interaction effect with luminosity detected. The predator model was not significant, thus the detection of predators by observers or camera traps was not affected by moonlight or any climatic factors.

Most primate species increase their activity with increasing lunar illumination (Gursky 2003, Kappeler & Erkert 2003, Bearder et al. 2006, Donati & Borgognini-Tarli 2006, Fernandez-Duque &

Erkert 2006). This can be explained by the high visual orientation in primates and higher effectiveness of foraging and detection of potential predators in bright nights (Gursky 2003). Instead of hiding in the dark, some lunarphilic primate species additionally use mobbing and warning calls to deter predators and warn conspecifics (Gursky 2006, Fichtel 2007, Nash et al. 2007, Eberle & Kappeler 2008). In contrast, Javan slow lorises in my study seemed to reduce their activity in brighter nights, as was found for pygmy lorises (Starr et al. 2012), Bengal slow lorises (Rogers & Nekaris 2011) and greater slow lorises (Trent 1977). The logistic regression provides strong evidence for lunarphobia in for Javan slow lorises. Slow lorises thus resemble more the behaviour of other lunarphobic mammals (Prugh & Golden 2014). Starr et al. (2012) explained lunarphobia by their anti-predator behaviour relying on crypsis and concealment, which was likely enhanced by the relatively disturbed and open habitat at my study site.

I did not find any evidence that activity of slow lorises could be negatively affected by human presence, and neither was there any apparent relation between slow loris activity and the behaviour of predators. Slow lorises did not engage in more active behaviour like foraging, feeding and travelling in higher and denser canopy, but in contrast are more active in lower height above ground. They may use the upper parts of the trees, where they are more concealed by the canopy, for vulnerable behaviours such as resting and sleeping. Especially in this human-modified study site they have to use the lower vegetation strata connected by small trees and bushes for lateral travelling, and additionally actively search for lateral routes of travel due to lower connectivity at lower vertical levels. Reduced concealment in lower vegetation strata may force them to be more alert to predators. A higher gum or sap flow at lower heights that may cause higher foraging activity is unlikely and gum or sap pressure is not dependent on height (Nussinovitch 2009, Mauseth 2014). In contrast, although phloem volume may be higher in the trunk, for both, gum and sap, access demands lower gouging energy in smaller branches in higher levels of the tree. Confirmed predators of slow lorises are orang-utans (Utami & van Hooff 1997), snakes (Wiens & Zitzmann 1999), hawk-eagles (Hagey et al. 2007), and monitor lizards (Kenyon et al. 2014). Although all of these taxa may not be sympatric with Javan slow lorises, adaptations to such predators may still be responsible for their behavioural responses (Goodman et al. 1993). The African potto is a slow climber such as slow lorises, and comparable to Javan slow lorises in size and ecology. This species is predated upon by viverrids of relatively small size and by domestic dogs *Canis lupus* (Nash et al. 2007, Nekaris et al. 2007). Animals also showed reactions to viverrids in predation experiments (Charles-Dominique 1977). Due to the similarity of the potto and Javan slow loris it is likely that potential predators of Javan slow lorises are similar to the potto's predators and thus include civets and dogs.

Despite presence of potential predators, slow lorises did not show any fear when encountering potential non-human predators. Similar oblivious reactions to potential predators occurred in red and grey slender lorises and in greater slow lorises (Wiens 2002, Nekaris et al. 2007). Because larger predators are extinct or do not occur on Java, the potential predator species at this field site may not be a real threat to slow lorises. This emphasises the need to study sympatric occurrence of potential predators on Java (CHAPTER 5) to find other potential predators, and investigate the behaviour of slow lorises (also species other than Javan slow loris) towards historical predators or predators still occurring outside of Java, in the wild and captive experiments. These non-invasive experiments may for instance include the presentation of smell or vocalisations of slow lorises to predators and vice versa, but should be conducted in line with current animal welfare guidelines to ensure the wellbeing of animals, especially rescued individuals. Although hunting is the main threat to Javan slow lorises (Nekaris et al. 2009, 2013b), the number of observers had no affect on slow loris activity. Lorises may not fear people because they do not perceive people as predators or they are habituated due to the presence of local farmers.

One alternative explanation to predation pressure is a potential higher availability of prey during either moonlit or dark nights. Lang et al. (2005) attributed high activity during dark moon phases of the lunarphobic Neotropical insectivorous bat *Lophostoma silvicolum* to high prey availability of katydids. Foraging depth of Galapagos fur seals (*Arctocephalus galapagoensis*) followed the moonlight-dependent horizontal migration of fish and squid (Horning & Trillmich 1999). The effect of insect abundance depends on the food preferences of the insectivorous predator. Although these data are not yet available for my field site, it is possible that the higher activity of slow lorises in dark nights follows the higher prey abundance; this possibility should be investigated in future studies.

I suggest that not predator avoidance but alternative factors like higher prey availability cause the slow loris to be more active on darker nights, perhaps due to the extreme morphological adaptations of lorises to avoid predators in the first place. Lorisines rely heavily on crypsis, moving slowly and freezing when feeling threatened (Nekaris et al. 2007). Their fur colour blends in with tree bark and makes animals difficult to detect (Nekaris et al. 2010a). Finally, their venom is suggested to assist in predator defence (Nekaris et al. 2013a), maybe through defensive bites, but possibly also by deterring predators with olfactory cues (Muellerian mimicry) (Hagey et al. 2007) or even concealment when anointing themselves and their offspring (olfactory crypsis) (Alterman 1995). Morphological and behavioural defences against predators can effectively reduce a prey's perception of risk (Stankowich & Blumstein 2005), and the combinations of slow lorises' adaptations might explain their indifferent behaviour when encountering potential predators. If direct encounters with potential predators do cause reaction in slow lorises, low activity in bright nights is unlikely caused by predator avoidance.

4.2 Climatic factors

Of the environmental factors, only humidity and cloudiness had a significant independent effect on slow loris activity. Different effects of humidity on the activity of animals have been found (positive: Fitzgerald & Bider 1974, Orrock et al. 2004, Skutelsky 1996; negative: Kappeler & Erkert 2003, Donati & Borgognini-Tarli 2006). Slow lorises become more active with increasing humidity, possibly because of a higher availability of arthropod prey, which also become more active in higher humidity (Fadamiro & Wyatt 1995). Swifts increase flight height in lower humidity, following flying insects that adapt their flying height to humidity (Shamoun-Baranes et al. 2006). Slow lorises include many flying insects like Coleoptera and Lepidoptera in their diet (Wiens et al. 2006, Starr & Nekaris 2013). As slow lorises cannot leap or fly, they may be more actively foraging when humidity is high and insects fly low. Higher percentage of cloud cover contributes to the darkness that is favoured by Javan slow lorises. As the temperature at my study site can drop to about 10 °C, it is likely that temperature would have affected the activity of Javan slow lorises. Although I could not find an independent effect of temperature, I detected an interaction effect of luminosity and temperature in Javan slow lorises, just like for pygmy lorises (Starr et al. 2012). Indeed, during these inactive bouts, Javan slow lorises, like pygmy lorises, might not move for hours at a time. Many small endotherm species show heterothermy (Heldmeier & Ruf 1992, Heldmaier et al. 2004), including several nocturnal primates such as lemurs of the family Cheirogaleidae and lesser bushbabies (Schmid 2000, Smit et al. 2001, Dausmann et al. 2005, Schuelke & Ostner 2007, Nowack et al. 2010). Slow lorises are able to enter torpor (Whittow et al. 1977, Xiao et al. 2010). Using temperature collars I have already found indication for torpor in one animal at my study site (Rode-Morgano & Nekaris unpub. data), but further investigations are needed if animals at this study site regularly enter torpor during cold temperatures. I attributed the positive effect of higher humidity on activity to an adaptation to the activity of flying insect prey. Although slow lorises do drink in captivity (Ehrlich & Musicant 1977) they drink very little and are able to retrieve their fluids from their food (Mueller 1979, Fitch-Snyder et al. 2001). In the wild they are almost never observed to drink (Nekaris pers. comm.). Potential predators showed no preference for dark or bright nights and I could not detect an effect of climate factors on their activity.

CHAPTER 7

Gastrointestinal parasites and ectoparasites in wild Javan slow loris and implications for captivity and animal rescue

1. Introduction

One proposed ecological function of slow loris venom is the anointment with BGE or its digestion as an ectoparasite defence (Nekaris et al. 2013a). Although slow lorises may be more social than believed (CHAPTER 3 and 4) they spend large parts of the night solitary and allo-grooming by conspecifics may be restricted. Furthermore, high inactivity especially on cold nights (Starr et al. 2012, CHAPTER 6) as well as parking of infants (Nekaris & Bearder 2011) may increase the susceptibility to ectoparasites. The ingestion of secondary metabolites has been associated with the treatment of endoparasites (Forbey et al. 2009), thus, venom may also play a role in endoparasite defence. In captivity, the lack of natural diet including items with secondary plant compounds such as gum, or noxious arthropods, may decrease the effectiveness of venom and cause higher parasite loads. Because they live in highly fragmented and disturbed habitats (CHAPTER 3) Javan slow lorises may be highly susceptible to parasites and infectious diseases that may pose a major threat to their survival and trigger accelerated species and population declines (Lyles & Dobson 1993, Junge & Louis 2005, Wright et al. 2009, Schwitzer et al. 2010a). Living in small and disturbed forest fragments may increase parasite loads due to chronic stress resulting from food shortage, restricted ranging and high population density (Lyles & Dobson 1993, Schwitzer et al. 2010a). This condition makes them more susceptible to parasites, and their infection can be the last trigger leading to deteriorating health (Glaser & Kiecolt-Glaser 2005, Clark et al. 2009, Coe 2011). Inbreeding caused by fragmentation was suggested to be associated with higher parasite prevalence (Schad et al. 2005). Although fragmentation may decrease the diversity of parasite species (Anderson & May 1982), human encroachment results in the sharing of habitat and increased interactions between humans and primates, and thus increases anthropozoonotic transmission (de Thoisy 2001, Graczyk et al. 2001). Animals that are subject to human exploitation or intervention, such as wildlife trade, translocations, and deforestation and fragmentation of their habitat, may also exhibit high levels of stress (Clark et al. 2009, Arroyo-Rodríguez & Dias 2010, Dickens et al. 2010). Thus, gaining insight into baseline patterns of parasite infection in wild populations is of considerable importance with regards to successful conservation management, including small population management or planning of rehabilitation and reintroduction of animals (Cowlishaw & Dunbar 2000, Daszak et al. 2000, Foitova et al. 2009).

Here I describe endo- and ectoparasites exhibited by wild Javan slow lorises and examine the effects of season, sex, age, and diet on the prevalence and intensity of one of the detected endoparasite taxa, the pinworms *Lemuricola* spp. Chabaud & Petter 1959, family Oxyuridae. Although the results cannot directly support that one of the functions of slow loris venom is parasite defence, they may serve as a foundation for future research on venom use. I furthermore use my results to formulate recommendations for the husbandry and release schemes of rescue centres.

2. Methods

The study site is described in CHAPTER 2, section 3.1; capturing and handling in section 4.1.1.

Parasite sampling

I radio-tracked twelve slow lorises over 14 months and re-captured all animals every three months for a health check and the collection of samples. I captured nine additional uncollared animals for sampling purposes. Female adults weighed on average 884 ± 61 g (840 to 974 g) and male adults 905 ± 65 g (820 to 1025 g) (CHAPTER 4). I collected faecal samples (> 2 g) of all animals and stored them in 70% ethanol. I diluted the faeces with water and thoroughly examined them with the naked eye for the presence of adult pinworms, that are easily visible, and food remains. If necessary, I used a microscope (total magnification 50x) for confirmation. I defined parasite prevalence by the number of individuals of a host species infected divided by the total number of hosts examined, and parasite intensity by the number of individuals of a particular parasitic species in each infected host (Stuart & Strier 1995). Although even the number of faecal eggs does not necessarily reflect the severity of infestation (Gillespie 2006) I decided to report the number of adult worms in the faeces. Food remains that were recorded here are tree exudates (gum) and caterpillars, as both diets are known to contain secondary plant components or noxious substances that can potentially be sequestered into venom in slow lorises (CHAPTER 1, section 5.3). Although in almost all samples other arthropod remains were found, the pieces could not yet be identified to a meaningful taxonomic level and thus were not considered here.

In addition to this, in May and June 2012 I examined eight samples in more detail, following a wet lab protocol based on Gillespie (2006) and Hilser (pers. comm.). I subdivided the fresh samples and stored one part in Acetic acid - Formalin solution with triton X-100. Of these samples I placed approximately 1 g of faeces into a 15 ml centrifuge tube using a wooden applicator stick. The tube was filled two third of the way up with de-ionised water and homogenized with the same wooden applicator stick. Then the wooden applicator stick was removed and the tube centrifuged for ten minutes at 1800 rpm. The supernatant was decanted and the faeces re-suspended in Sodium Nitrate

($NaNO_3$-) solution with a specific gravity of 1.18 to 1.20. The faeces were mixed with the solution and poured through a sieve into a 15 ml centrifuge tube and were then spun for 5 minutes to improve separation between faecal matter and parasites. The tube was filled until a slightly positive meniscus formed, where the coverslip was then placed on the tube and the tube was allowed to stand for 20 minutes. The coverslip was removed and placed on a labelled glass slide for microscopic examination. I examined the slides under a total magnification of 100x, and 400x was used when necessary to confirm diagnosis (Dryden et al. 2005, Gillespie 2006). Strongoloid eggs were identified by their size, colour, shape and morula aspect. Nematodes were identified following Do (2009), Huffman & Chapman (2009) and Gillespie et al. (2010). Photos of parasites were sent to Dr Ivona Foitova (Orangutan Health Project) and Dr Lynda Gibbons for confirmation.

During every capture, I thoroughly examined the fur for ectoparasites, parting the hair and especially checking ectoparasite-prone body parts such as ears, face and anogenital area.

Data analysis

Due to small sample sizes and non-normal distribution of data I used descriptive and non-parametric statistics. Confidence limits are given by the standard deviation of the mean. I used one-sided Fisher's Exact Tests to investigate a relationship between pinworm presence in the sample and season, sex, age, presence of gum and presence of caterpillars in the sample (following Field 2009). I set the significance level to $p = 0.05$. I categorised the faecal amount as small (= 1), medium (= 2) and large (= 3). The faecal amount index was calculated by dividing the sum of the faecal amount by n.

3. Results

I collected 43 faecal samples from different captures and 21 individuals. Seven of eight samples that I examined using sodium nitrate flotation were infected with gastrointestinal parasites (Table 7.1). All these parasites were nematodes. In the smear samples and macroscopic examination I found hookworm ***Necator*** spp. (family Ancylostomatidae), eggs (65x40 μm) and adults (10 mm), pinworms ***Lemuricola*** spp. (family Oxyuridae), eggs (60x25 μm) and female adults (11 mm) and ***Trichostrongylus*** spp. (family Trichostrongylidae), eggs (63x40 μm) and adults (8 mm). None of the samples showed blood or mucus.

Table 7.1: Results of sodium nitrate flotation of faecal samples (E = eggs, A = adults) of eight wild Javan slow lorises captured at an agriculture area in West Java in May and June 2002

Sex	Age	Weight (g)	Hookworm	*Trichostrongylus*	Pinworm	Mites
Male	Adult	808		E + A	E + A	
Male	Adult	820	A			
Male	Adult	895		E		
Male	Adult	898	E + A			A
Male	Adult	1025	E		E + A	
Male	Sub-adult	757	A		E + A	
Female	Adult	893	A	E		
Female	Su-adult	850				

The macroscopic examination of all 43 samples revealed a total pinworm prevalence of 69.8 % with an average intensity of 3.0 ± 4.3 worms, range 0 to 21 worms. Details of animals with samples from at least three different captures are shown is Table 7.2. The faeces of one female loris had a pinworm full of eggs in the dry weather period, and another faeces of a female showed many (> 30) pinworms of about 2 to 3 mm as well as 6 pinworms of about 1cm in the wet weather period.

Table 7.2: Prevalence of the pinworm *Lemuricola* spp. (proportion of infected samples) and intensity (mean number of parasites found in the infected hosts) of six adult wild Javan slow lorises with faecal samples from at least three different captures. The faecal amount index (FAI) was calculated by dividing the sum of small (= 1), medium (= 2) and large (= 3) samples by n

Name	Sex	Age	Weight	N	Intensity	sd	Min	Max	Prevalence	FAI
MO	male	adult	915	5	4.6	3.4	1	9	1.00	2.20
AZ	male	adult	870	5	1.2	1.6	0	4	0.60	2.25
YO	male	sub-adult	800	4	1.5	1.7	0	3	0.50	2.25
EN	female	adult	765	3	5	4.6	0	9	0.67	2.00
TE	female	adult	831	3	3.3	3.4	1	5	1.00	2.33
CH	female	adult	920	3	2.3	3.2	0	6	0.67	1.33

None of the variables tested here had a significant relationship with pinworm presence in the sample (Fisher's Exact Test: sex p = 0.204; season p = 0.540; age p = 0.052; caterpillar p = 0.187; gum p = 0.277; Figure 7.1). For worm intensity, none of the variables were significant either (Mann Whitney U Test: sex U = 288, p = 0.131; season U = 257, p = 0.515; age U = 110.5, p = 0.068; caterpillar U = 244.5, p = 0.072; gum U = 185.5 p = 0.880). Age approached significance in both tests, with a lower prevalence and intensity for younger animals.

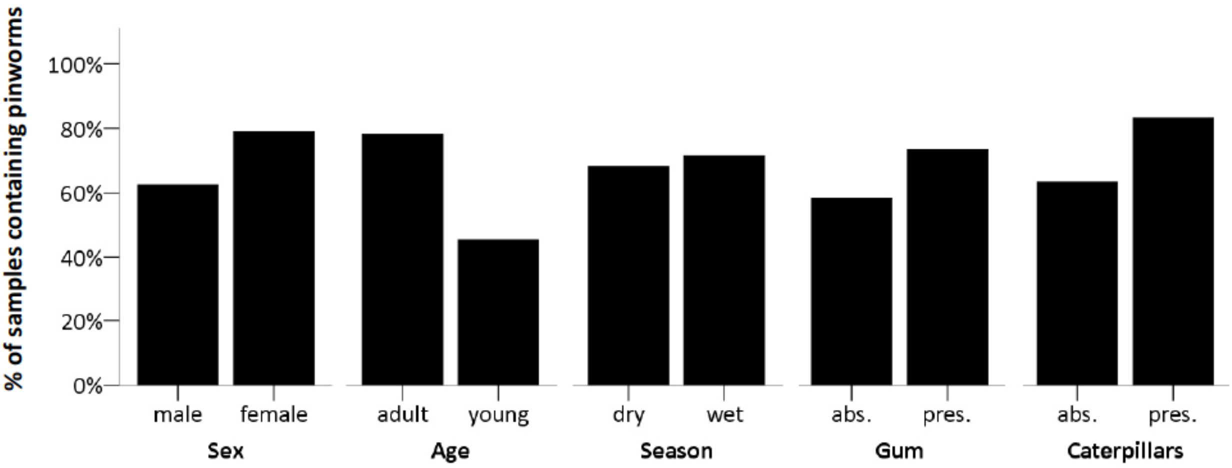


Figure 7.1: Proportions of samples that contained pinworms for different sexes, seasons, age classes, and whether samples contained caterpillar and gum remains. N = 43

Evidence of ectoparasites was only detected a single time in 61 captures of 21 individuals during 14 months. The adult male exhibited an extensive skin rash on the throat, shoulder and upper chest in the dry weather period. The animal lost its fur on the infected area and the skin looked dry and scabby. I took a skin scrape and found an unidentified ectoparasite at a magnification of 40x (Figure 7.2). This parasite was 52 µm in size. Although I could not identify the species, based on the presence of the rash and the shape of the parasite, it might be a skin mite species. I found no eggs, larva, nymphs or signs of reproduction by the skin mite. At the next health check after 3 months, the rash healed completely. No signs of ectoparasites were found on any other Javan slow loris, and in all cases animals had very healthy fur conditions.

Figure 7.2: Ectoparasite of an adult male Javan slow loris, total magnification 100x

4. Discussion

I identified three different gastrointestinal parasites in the wild Javan slow lorises, which were all nematodes: hookworm ***Necator*** spp., pinworms ***Lemuricola*** spp., and ***Trichostrongylus*** spp. These parasites are common amongst primates, including toque macaques ***Macaca sinica*** (Ekanayake et al. 2006), olive baboons ***Papiocyanocephalus Anubis***, vervet monkeys ***Cercopithecus aethiops*** and Sykes' monkeys ***Cercopithecus albogularis*** (Munene et al. 1998), red-tail guenons ***Cercopithecus ascanius*** and red colobus monkeys ***Piliocolobus tephrosceles*** (Gillespie et al. 2005 a, b), Bornean orang-utans ***Pongo pygmaeus*** (Collet et al. 1986, Foitová 2002, Kilbourn et al. 2003, Foitová et al. 2009, Labes et al. 2010), chimpanzees ***Pan troglodytes*** and sooty mangabeys ***Cercocebus atys*** (Chapman et al. 2005).

Nematodes have been identified in slow lorises, such as ***Trichuris***, ***Strongyloides***, ***Strongylus***, ***Gongylonema***, ***Oxyuris***, ***Enterobius***, ***Physaloptera***, ***Filaria***, ***Spirura***, ***Microfilaria***, Breinlia, ***Pterygo dermatides*** (Sutherland-Smith & Stalis 2001, Streicher 2004). Except for ***Pterygo dermatides*** that causes fatal anaemia (Tuggle & Beehler 1984, Sutherland-Smith & Stalis 2001) most infections seem to be asymptomatic. Only few taxa of protozoan parasites, cestodes, trematodes or acantocephala have been reported for slow lorises (***Giardia***, ***Trichomonas***, ***Cryptosporidia***, ***Trypanomsoma***, ***Hymenolepis***, ***Phaneropsulus***, ***Echinorhynchus***) (Sutherland-Smith & Stalis 2001).

Except for Streicher (2004) who worked on pygmy lorises arriving at a rescue centre, all accounts are from captive animals. Thus, my records of parasites are the first for wild slow lorises. Existing parasite studies of captive slow lorises have never reported ***Lemuricola*** spp. before.

In 69.8 % of 43 faecal samples I found adult pinworms ***Lemuricola*** spp. In pygmy lorises, Streicher (2004) found a related species of the same family Oxyuridae ***Enterobius*** spp. in the faeces and around the anus of some animals that arrived in the rescue centre. Sutherland-Smith and Stalis (2001) found ***Enterobius*** during one of sixteen pygmy lorises health checks but none in 29 health checks of greater slow lorises.

Less than 10 % of rainforest remains in Java (Smiet 1990, 1992, Lavigne & Gunnell 2006). Due to the associated stress level caused by restrictions in food availability, ranging patterns, population sizes as well as anthropozoonotic transmission of pathogens, habitat quality decreases, and habitat disturbance increases the risk of parasite infections and is associated with an overall greater prevalence of parasite infection (Lyles & Dobson 1993, Chapman 2005, Gillespie et al. 2005a,b, Junge & Louis 2005, Gillespie et al. 2008, Wright et al. 2009, Schwitzer et al. 2010a). The field site Cipaganti is subject to high anthropogenic modification, consisting of a mosaic of agriculture fields, interspersed with single trees, small forest and bamboo patches (CHAPTER 2, section 3.1). The majority of primate parasites are transmitted via faecal-oral transmission (Hopkins & Nunn 2007). Local farmers are working in the agricultural fields of the study site every day, sometimes bringing cattle, which perform their daily needs such as eating, drinking and defecating. ***Trichostrongylus*** spp. occur in cattle such as goats that are commonly farmed in Indonesia (Rushton et al. 2002), ***Necator*** (***americanus***) affects humans (Bethony et al. 2006), and ***Lemuricola*** spp. may be hosted by domestic animals (Loudon et al. 2006). Due to the low tree density at this site, Javan slow lorises frequently have to come down to the ground to move across fields (CHAPTER 3), suggesting a higher risk of contamination. If hosts have adequate energy reserves or nutrient supplies, parasite infection may have little effect on the host (Chapman et al. 2005, Gillespie 2006). Disturbed habitat may force animals to feed on a lower quality or quantity of food, and may lead to compromised body condition and reproductive status when parasites inflict substantial energetic costs. However, I had no reason to believe that lorises were confined in their nutrition, as all lorises captured were in good body condition. Due to the lack of information on parasite prevalence and intensity in (Javan) slow lorises, I cannot conclude whether the animals in this study have higher or lower parasite burdens than normal. Additionally, none of the animals showed blood or mucus in the faeces, and although I conducted no special veterinary checks, animals seemed to be asymptotic.

Although several macroscopic ectoparasites have been reported for lorises such as lice, ticks and fleas (Wiens 2002, Streicher 2004), compared to other primates, members of the Lorisidae family are remarkably ectoparasite free (Rode & Nekaris 2011, 2012). Only one of nine wild studies across six taxa found a small amount of ticks in all animals during the wet weather period (Wiens 2002, Nekaris et al. 2013a). In accordance to my results, all other studies rarely or never found any ectoparasites (reviewed by Rode & Nekaris 2011, 2012, Nekaris et al. 2013a).

One of the ecological functions of slow loris venom may be parasite defence (Nekaris et al. 2013a), and it is possible that the slow lorises' venom interrupts the parasites lifecycle by killing the parasites when they are in the mouth or on the skin, thus preventing infection. Animals secrete the venom from the brachial gland (Wilde 1972, Alterman 1995, Krane et al. 2003, Hagey et al. 2007, Ligabue-Braun et al. 2012). By licking their own brachial gland regions and wiping these glands against their heads, lorises combine fluid from the brachial gland with the saliva (Krane et al. 2003, Hagey et al.

2007). Slow lorises exhibit solitary torpor and infant parking in the wild (Wiens & Zitzmann 2003, Xiao et al. 2010, Nekaris & Bearder 2011). Anointment of their own or their infant's fur with a secondary compound of the venom could be crucial in their health maintenance (Nekaris et al. 2013a). Indeed, Nekaris et al. (2013a) applied the combined venom exudates and saliva onto 12 (comparatively large) leeches that all died within minutes. Subsequent experiments have shown that loris venom can kill a wide variety of arthropods (Grow et al. 2015, Nekaris unpublished data). The tendency of immature animals exhibiting a lower prevalence and intensity of pinworms shown in this study supports the anti-parasite function of anointing infants with venom, assuming that they would ingest the venom during subsequent autogrooming. Due to lack of comparative data, I cannot yet conclude that endoparasite prevalence in this study is high or low, nor that ingested venom could also play a role in gastrointestinal parasite defence. Some insectivores (European water shrews, American short-tailed shrews, Haitian solenodons) and lizard species of the clade Toxicofera (e.g. monitor lizards) may use venom for digestive purposes and/or oral hygiene (Blaylock 2000, Arbuckle 2009, Fry et al. 2009b, Folinsbee 2013). Likewise, slow loris venom may kill certain life stages of parasites in the mouth or digestive tract.

Venom in slow lorises may be sequestered from secondary plant compounds and noxious arthropod prey. CHAPTER 3 shows that tree exudates form a substantial component of slow loris diet and noxious arthropod species are present at the study site. However, I could not find a significance relationship between the presence of gum or caterpillars and the presence of endoparasites. This either may indicate that venom is not used to reduce endoparasites, or that it is not sequestered by the considered diet items.

Thorough health checks and risk assessments, especially in respect to parasites, are compulsory for all translocations of wild animals, including reintroductions following the confiscation of rescued animals (IUCN 2002, Leighton 2002, IUCN/SSC 2013). My results could have implications for rescue centres that receive confiscated slow lorises. Poor treatment during trade means that slow lorises arrive in rescue centres in bad health condition, including potentially high stress levels and parasite burdens. Unlike in other primate species, where parasites may be seasonal (Semple et al. 2002), I found endoparasites in Javan slow lorises throughout the year regardless of weather period, whereas macroscopic ectoparasites were virtually absent. Wild slow lorises are known to consume various foods, particularly exudates, which cure human ailments, including parasites (Das et al. 2014). Slow lorises kept in rescue centres may lack dietary choices that would allow them to cope with parasites in the wild. Better mimicking wild diet may improve the welfare and treatment of captive lorises. The fact that I document *Lemuricola* spp. for the first time in slow lorises means that the Javan slow loris may have acquired some resistance to this parasite. Confusing species in captivity or poorly planned releases may transfer the parasites to more sensitive species. This emphasises the importance of the exact knowledge of slow loris taxonomy, the different species' geographic distribution and origin of confiscated animals.

CHAPTER 8

CONCLUSIONS AND RECOMMENDATIONS

1. In relation to venom

Not much is known about most species of venomous mammals due to constraints relating to the body size, protection and conservation status of the species, in addition to a surprising lack of general interest by scientists (Dufton 1992, Ligabue-Brown et al. 2012). With the present project, I intended to collect detailed information on the behaviour and ecology of wild Javan slow lorises, and use it to explain the ecological function of slow loris venom. Several studies investigated the components of BGE (Alterman 1995, Krane et al. 2003, Hagey et al. 2007). In line with the biological definition of venom (Fry et al. 2009a) I can reject the null hypothesis that slow loris BGE is not toxic on the basis of several records of humans and animals been bitten (Wilde 1972, Sutherland-Smith & Stalis 2001, Nekaris et al. 2013, Medani & Nekaris 2014).

I have conducted more than a full year of data collection on wild Javan slow lorises by using radio-tracking and direct observations. In agreement with other studies (Wiens et al. 2006, Swapna et al. 2010, Starr & Nekaris 2013, Streicher et al. 2013, Das et al. 2014) the bulk of easily observable food items taken by Javan slow lorises consist of gum and nectar both of which may contain secondary plant metabolites that can form the basis for sequestration of venom (CHAPTER 3). Although catching insects was not often directly observed due to visibility and methodological constraints, almost all faecal samples contained unidentified arthropod remains. Many noxious arthropods are found at the study site within the slow lorises home ranges, forming another potential source of sequestered toxins. Both chapters reveal that extensive feeding on gum and potentially noxious insects has been observed for all species of slow lorises studied to date. These results support the hypothesis that venom is sequestered, but the analysis of venom and possible seasonal or other variations in diet may reveal more insight. Another part of the venom may still be produced ***de novo***; this hypothesis cannot be proven or rejected without further analysis of the venom itself.

No detailed study has been conducted on slow loris ecology to infer possible functions of their venom. In CHAPTER 4 I found that Javan slow lorises live in a social monogamy, as supported by the overlap of home ranges and social interactions. Similar results were found for greater slow lorises by Wiens and Zitzmann (2006). While observations of agonistic behaviour were almost absent, the only occurrence of aggression was in relation to mating. Although injuries are very frequent, rather low levels of direct aggression may serve the avoidance of dangerous fights involving venom. The social organisation in combination with relatively small testicles and only slightly larger home ranges point to a monogamous mating system usually characterised by high contest competition. I could not detect sexual dimorphism or a difference in venom secretions, possibly due to high non-sexual competition for feeding. Monogamous species systems may show promiscuous tendencies and the actual mating system can only be shown by genetic studies (Isvaran & Clutton-Brock 2007). In conclusion, the social organisation, mating system and ranging behaviour of Javan slow lorises seem to be characterised by a high level of sexual and non-sexual competition, and venom may be used in intraspecific competition.

CHAPTER 5 and 6 explore the possible function of slow loris venom in predator defence. CHAPTER 5 investigates the faunal community of Javan slow lorises and potential predators. Javan slow lorises coexist with leopard cats and common palm civets that may be a threat to slow lorises and their young due to shared habitat. The analysis of factors influencing the detection of small and medium sized carnivores and other similar-sized mammals indicate that surveys should be representative for whole Java in order to find further sites where slow lorises and potential predators can be studied. The results presented in CHAPTER 6 suggest that slow lorises are lunarphobic, as it was also found for the pygmy loris (Starr et al. 2012). While this could be interpreted as a predator avoidance strategy, I did not find a reduction in activity when numbers of human observers increase. Furthermore, individual slow lorises were very indifferent towards the proximity of potential predators and the activity pattern in relation to moon light is not reflected in the behaviour of potential predators. I concluded that lunarphobia is related to factors independent from predators such as availability of food. This result does not interfere with the hypothesis of defence against predators, but may mirror the animals' low vulnerability to predators. While larger predators are extinct or do not occur on Java, the potential predator species at this field site may not be a real threat to slow lorises (CHAPTER 6), and backs up the need for surveys in search of other sites where the predator-prey relation can be studied (CHAPTER 5). Future studies to investigate the behaviour of slow lorises towards historical predators or predators still occurring outside of Java should be conducted in the wild and captive experiments.

In CHAPTER 7 I found that Javan slow lorises – just like other slow lorises - have extremely low numbers of ectoparasites. Although social allogrooming has been observed (CHAPTER 3), grooming frequencies in dispersed social organisations are much lower than in gregarious primates, and may enhance the value of a function in relation to ectoparasite repellence. The role of venom the defence of endoparasites may be a topic to look at in future studies.

In conclusion, the ecological background supports a potential use of slow loris venom in intraspecific competition, predator defence or ectoparasite avoidance. As venom in a certain species can serve multiple purposes (Whittington & Belov 2007, Arbuckle 2009, Casewell et al. 2013), these functions are not mutually exclusive. However, the majority of venomous species in the entire animal kingdom use venom for prey acquisition (Casewell et al. 2013). The fact that the few venomous mammals show signs of a variety of different uses for venom (platypus: sexual competition, predator defence; shrews and solenodons: prey capture, predator defence, digestive aid; vampire bats: facilitation of feeding; slow loris: intraspecific competition, predator defence, ectoparasite avoidance; CHAPTER 1) makes this taxonomic group highly special and interesting.

The findings of this project are limited by the inability of correlating ecological data to toxicity levels in venom composition due to the problems in exporting BGE and saliva for analysis. The collection of evidence for different functions of slow loris venoms was also restricted by the typical difficulties of observing wild and nocturnal species. This leads to the following recommendations in respect to future research on slow loris venom and its ecological function:

- Analysis of venom components for extant and future samples
- Compare the variability in venom composition and the actual diet of animals in relation to different factors such as seasons, sexes, ontogeny, habitat, wild versus captive animals or other, to explore the role of sequestration from secondary compounds in the food
- Continue captive experiments in relation to the potential functions of venom, including:
    - Monitoring aggressive social behaviour alongside with amounts of venom secretion and variability in venom composition. As social stress is known to affect the level of glucocorticoids, parallel measurements of cortisol levels may give additional clues.
    - Presenting scents of slow lorises and BGE as well as vocalisations to potential predators and vice versa
    - Presenting scents of BGE to conspecifics to explore whether they show certain different reactions in relation to characteristics of the sender
    - Testing the effect of venom on ectoparasites and endoparasites
    - Conducting prey capture experiments to explore the possible venom function of prey capture, that I did not examine specifically in this project

2. In relation to conservation

All species of slow loris that are assessed on the IUCN Red List are listed in one of the threatened categories (IUCN 2014). The Javan slow loris is considered as Critically Endangered (Nekaris et al. 2013b) and one of the 25 most endangered primate species of the world (Mittermeier et al. 2009, 2012, Schwitzer et al. 2014). Apart from some habitat assessments, a distribution survey and one reintroduction study involving post-monitoring of animals rescued from the pet trade (Winarti 2003, 2011, Moore 2012, Wirdateti 2012, Nekaris et al. 2014a), Javan slow lorises have never been studied in the wild. Similarly, almost nothing is known about other Javan (and Bali) endemics such as the Javan chevrotain, the Javan ferret badger or the Javan colugo (IUCN 2014, CHAPTER 5). Javan populations of most small- to medium-sized mammal species are not well studied either (CHAPTER 5). Indonesia forms a large part of the Sundaland biodiversity hotspot, with high levels of endemic species and habitat loss (Myers et al. 2000, Brooks et al. 2002). Not only destruction and conversion of natural habitat poses a high threat to wildlife in Indonesia (Sodhi et al. 2004, Santilli et al. 2005), but trade of animals and their parts for food, medicines, raw materials, and pets (Shepherd et al. 2004, Corlett 2007, Shepherd 2009, 2012a,b, Nijman 2010). Enforcement of conservation legislation is often ineffective (Shepherd et al. 2004, Lee et al. 2005, Bickford et al. 2007, Corlett 2007). Finally, captive care of slow lorises in zoos and rescue centres often proves difficult (Nekaris & Campbell 2012, Fuller et al. 2014) and rescued animals are often released without the consideration of the IUCN Reintroduction Guidelines. Even professional reintroduction programmes often work on the basis of insufficient knowledge of behaviour, ecology and habitat needs of wild animals. Thus, the data presented here bears important implications for the protection and conservation of Javan slow lorises and other mammals. Apart from the application in conservation, I presented the first ecological data on wild Javan slow lorises that can be integrated into the general body of knowledge in behaviour, ecology and evolution.

Although slow loris species differ in aspects of their ecology, in CHAPTER 3 I found Javan slow lorises to have similar needs in terms of fundamental feeding and social activities to other slow loris species (Wiens et al. 2006, Wiens & Zitzmann 2006, Swapna et al. 2010, Starr & Nekaris 2013, Streicher et al. 2013, Das et al. 2014). I described the natural diet (mainly gum, nectar and insects, but also small amounts of fruit), the activity budget and habitat use of wild lorises, indicating a preference for bamboo, and gum- and nectar-producing plant species. The importance of bamboo is supported by Voskamp et al. (2014). These data can help to improve husbandry of animals in zoos and rescue centres to adapt captive diets, assess the presence of natural behaviour, and find suitable release sites for rescued animals. ***In situ*** the information can be used to select priority sites for habitat protection and design reforestation plans. Javan slow lorises can thrive in human-altered habitat that is very different from dense rainforest and are adaptable to exotic plant species.

The monogamous social organisation and mating system described in CHAPTER 4 gives information for the forming of social groups in captivity and pre-release preparations in reintroduction programmes. Similar to what was found for greater slow lorises (Wiens & Zitzmann 2006), wild Javan slow lorises seem to live in pairs with their offspring and show surprisingly low levels of aggression. Relatively small home ranges in this study and their comparison to larger home ranges in other more naturally forested sites (Wiens & Zitzmann 2006) can give indications of space requirements for reintroduction, and may assist in predicting population densities.

Javan slow lorises coexist with a wide range of mammal species (CHAPTER 5). Thus they are a suitable flagship species for conservation programmes, such as it is the case for the LFP. The sympatric distribution and natural reactions of slow lorises towards potential carnivore predators (CHAPTER 5 and 6) seemingly indicate that no special precaution in relation to pre-release training and selection of release site has to be taken. However, some potential predator species (snakes, hawk eagles, monitor lizards) have not been considered here, and the IUCN Reintroduction Guidelines strongly advice conducting thorough assessment of the release site. The data on small- to medium-sized carnivores and mammals indicates that some species are relatively flexible towards the presence of and modification of land by humans (e.g. common palm civet), but distribution results raise the concern about the conservation status of some species, e.g. the Sunda porcupine and the small-toothed palm civet.

Finally, in CHAPTER 7 I documented the surprising low prevalence of ectoparasites in wild Javan slow lorises, possibly indicating the importance of natural diet to produce gland exudates aiding parasite defence. The knowledge of endoparasites found in faecal matter can help in the medical care and husbandry of captive animals.

To ensure the applications of my findings to the conservation of (Javan) slow lorises, I make the following recommendations:

- Integrate data on (Javan) slow loris behaviour, ecology and distribution into the first global “Slow and Slender Loris Conservation Action Plan” to make results widely available to science and practitioners

- Use information of habitat requirements, such as the preference for bamboo and feeding plants (green wattle, red calliandra), into habitat protection and reforestation schemes
- Use information from the wild to improve captive care and management, such as diet (gum and opportunities for gouging, arthropods, nectar), lighting and temperature management, enclosure furnishing (e. g. bamboo), social composition of groups (pairs), or monitoring of natural behaviour
- Use information from the wild for reintroduction planning. Data can help to follow the IUCN Reintroduction Guidelines by providing a better basis for selection and assessment of release site and their habitats, as they can be very different from the origin, and plant equivalents of exotic agricultural and native rainforest species must be identified. Further aspects of release schemes include space requirements in different habitats, social composition of release groups and post-release monitoring of natural behaviour including feeding, activity budget and ranging
- Integrate findings into education efforts, and evaluate the possible use of toxicity in slow lorises to combat the threats posed by wildlife trade, e. g. by deterring hunters, middle-man and potential buyers from hunting, trading and buying a slow loris, and reinforcing traditional myths and beliefs on local community level
- Conduct further studies that seek to improve the knowledge on slow loris diet, life history patterns, dispersal and its effect on the individual and the population structure, and genetic diversity on population level. Detailed and meaningful data in these areas are critical in the establishment and continuation of long-term projects such as LFP. Further studies should focus on studying Javan slow loris populations in the east of Java, their comparison to western populations, and the effect of human-modified landscapes on the behaviour and ecology of animals
- Conduct further surveys on the geographic distribution and abundance of lorises in the wild, and regularly monitor the abundance of animals sold on wildlife markets

Recommendations for other mammals studied in the scope of this project:

- Conduct regular surveys on the geographic distribution and abundance of populations in the wild, and abundance on animals sold on wildlife markets
- In terms of conservation priorities, intensify surveys of Sunda porcupines and small-toothed palm civets to ensure that their absence in my surveys is not a general trend
- Integrate findings into assessments of species on the IUCN Red List and consider the re-assessment of the Sunda porcupine

- Include unprotected sites with human-altered habitats and locations in the east of Java into island-wide surveys. Repeat previous surveys to cover all possible locations and to avoid bias due to untested assumptions about the distribution and abundance of their focus species.
- Conduct more detailed long-term studies in relatively easy and high abundance study sites identified by this project (e.g. Garut regency and Tasikmalaya regency) especially on little studied and endemic species such as the Javan ferret badger or Javan colugo
- Conduct taxonomic review of warranted genetic sampling kits, international cooperation to save costs and the export of DNA data (owned by an Indonesian institute) rather than the export of complete samples may facilitate analysis.

In terms of project management I recommend:

- Due to the apparent ability of Javan slow lorises to live in human-altered and unprotected habitat the success of conservation depends on the support of the local community. Thus, LFP and other conservation projects should continue and intensify the integration of the local community by environmental education, conservation awareness activities, and small side projects that benefit the rural development of communities. The development and maintenance of professional local scientists and field workers should be intensified.
- The slow loris can be used as a flagship species for conservation projects that cover a wide range of Javan mammals

REFERENCES

REFERENCES

Abramov A, Timmins RJ, Roberton S, Long B, Zaw T, Duckworth JW. 2008. *Martes flavigula*. IUCN Red List of Threatened Species. Version 2013.1 Online: www.iucnredlist.org. Accessed: 12 December 2013.

Alterman L. 1995. Toxins and toothcombs: potential allospecific chemical defenses in *Nycticebus* and *Perodicticus*. In: Alterman L, Doyle GA, Izard MK, editors. Creatures of the dark: the nocturnal prosimians. New York: Plenum Press. p 413-424.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour 49(3/4):227-267.

Ancrenaz M, Lackman-Ancrenaz I, Mundy N. 1994. Field observations of aye-Ayes (*Daubentonia madagascariensis*) in Madagascar. Folia Primatologica 62(1-3):22-36.

Anderson RM, May RM. 1982. Coevolution of hosts and parasites. Parasitology 85(02): 411-426.

Andrade DV, Abe AS. 1999. Relationship of venom ontogeny and diet in *Bothrops*. Herpetologica 55(2):200-204.

Arbuckle K. 2009. Ecological function of venom in *Varanus*, with a compilation of dietary records from the literature. Biawak 3(2):46-56.

Ario A, Sunarto S, Sanderson J. 2008. *Panthera pardus* ssp. *melas*. IUCN Red List of Threatened Species. Version 2013.2. Online: www.iucnredlist.org. Accessed 12 December 2013.

Arroyo-Rodríguez V, Dias PAD. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. American Journal of Primatology 72(1):1-16.

Ashdown RA, McKechnie AE. 2008. Environmental correlates of freckled nightjar (*Caprimulgus tristigma*) activity in a seasonal, subtropical habitat. Journal of Ornithology 149(4):615-619.

Atsalis S. 2000. Spatial distribution and population composition of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar, and its implications for social organization. American Journal of Primatology 51(1):61-78.

Attems C. 1907. Javanische Myriapoden gesammelt von Direktor Dr K. Kroepelin im Jahre 1903. Mitteilungen Naturhistorisches Museum Hamburg 24:77-142.

Bali A, Kumar A, Krishnaswamy J. 2007. The mammalian communities in coffee plantations around a protected area in the Western Ghats, India. Biological Conservation 139(1):93-102.

Balogh ACV, Gamberale-Stille G, Leimar O. 2008. Learning and the mimicry spectrum: from quasi-Bates to super-Müller. Animal Behaviour 76(5):1591-1599.

Barrett EBM. 1984. The ecology of some nocturnal arboreal mammals in the rain forest of peninsular Malaysia. PhD thesis. Cambridge, UK: University of Cambridge.

Barua M. 2011. Mobilizing metaphors: the popular use of keystone, flagship and umbrella species concepts. Biodiversity and Conservation 20(7):1427-1440.

Basset Y. 2003. Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy. Cambridge, UK: Cambridge University Press.

Bearder SK, Ambrose L, Harcourt C, Honess P, Perkin A, Pimley E, Pullen S, Svoboda N. 2003. Species-typical patterns of infant contact, sleeping site use and social cohesion among nocturnal primates in Africa. Folia Primatologica 74(5-6):337-354.

Bearder SK, Martin RD. 1980. Acacia gum and its use by bushbabies, *Galago senegalensis* (Primates: Lorisidae). International Journal of Primatology 1(2):103-128.

Bearder SK, Nekaris KAI, Buzzell CA. 2001. Dangers in the night: are some nocturnal primates afraid of the dark? In: Miller LE, editor. Eat or be eaten: predator sensitive foraging among primates. Cambridge, UK: Cambridge University Press. p 21-43.

Bearder SK, Nekaris KAI, Curtis DJ. 2006. A re-evaluation of the role of vision in the activity and communication of nocturnal primates. Folia Primatologica 77(1-2):50-71.

Behnke JM. 1990. Parasites: immunity and pathology: the consequences of parasitic infections in mammals. London, UK: Taylor and Francis.

Beier P. 2006. Effects of artificial night lighting on terrestrial mammals. In: Rich C, Loncore T, editors. Ecological consequences of artificial night lighting. Washington, DC: Island Press. p 19-42.

Bekoff M, Daniels TJ, Gittleman JL. 1984. Life history patterns and the comparative social ecology of carnivores. Annual Review of Ecology and Systematics 15:191-232.

Berglund A. 2013. Why are sexually selected weapons almost absent in females? Current Zoology 59(4):564-568.

Bernede L. 2009. A study of the social and behavioural ecology of the red slender loris (*Loris tardigradus tardigradus*) in Masmullah Proposed Forest Reserve, Sri Lanka. PhD thesis. Oxford, UK: Oxford Brookes University.

Bernede L, Davies R, Nekaris KAI, Gunawardene A, Bearder SK. 2013. Vocalizations of red slender lorises (*Loris tardigradus tardigradus*) in Masmullah Proposed Forest Reserve, Sri Lanka. In: Masters J, Gamba M, Génin F, editors. Leaping ahead. New York: Springer. p271-278.

Bethony J, Brooker S, Albonico M, Geiger SM, Loukas A, Diemert D, Hotez PJ. 2006. Soil-transmitted helminth infections: ascariasis, trichuriasis, and hookworm. The Lancet 367(9521):1521-1532.

Bickford D, Supriatna J, Nanda Y, Iskandar D, Evans B, Brown R, Umilaela Townsend T, Azhari D, McGuire J. 2007. Indonesia's protected areas need more protection – suggestions from island examples. In: Sodhi NS, Acciaioli G, Erb M, Tan AKJ, editors. Biodiversity and human livelihoods in protected areas: case studies from the Malay Archipelago. Cambridge, UK: Cambridge University Press. p 53-77.

Bigger M. 1976. Oscillations of tropical insect populations. Nature 259:207-209.

Bird MI, Taylor D, Hunt C. 2005. Palaeoenvironments of insular Southeast Asia during the last glacial period: a savanna corridor in Sundaland? Quaternary Science Reviews 24(20):2228-2242.

Birkhead T. 2000. Promiscuity: an evolutionary history of sperm competition. London, UK: Faber & Faber.

Blaylock RSM. 2000. Antibacterial properties of KwaZulu Natal snake venoms. Toxicon 38(11):1529-1534.

Borgatti SP, Everett MG, Freeman LC. 2002. UCInet for Windows: software for social network analysis. Natick, MA: Analytic Technologies, Inc.

Brennan EJ, Else JG, Altmann J. 1985. Ecology and behaviour of a pest primate: vervet monkeys in a tourist-lodge habitat. African Journal of Ecology 23(1):35-44.

Brickle N. 2007. Sightings of Javan Ferret Badger *Melogale orientalis*. Small Carnivore Conservation 36:50.

Brodie ED. 1977. Hedgehogs use toad venom in their own defence. Nature 268:627-628.

Brooks TM, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16(4):909-923.

Brown JL, Orians GH. 1970. Spacing patterns in mobile animals. Annual Review of Ecology and Systematics 1:239-262.

Bruehl CA, Gunsalam G, Linsenmair KE. 1998. Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. Journal of Tropical Ecology 14(3):285-297.

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford, UK: Oxford University Press.

Burt WH. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24(3):346-352.

Campos WG, Pereira D, Schoereder JH. 2000. Comparison of the efficiency of flight-interception trap models for sampling Hymenoptera and other insects. Anais da Sociedade Entomológica do Brasil 29(3):381-389.

Cannon T, Musing L, Nekaris KAI. 2013. The modern social organisation of human primates and its implications for primate conservation. Poster presentation. Primate Society of Great Britain Winter Meeting, 11 December 2013. London, UK.

Caro T. 2005. Antipredator defenses in birds and mammals. Chicago: University of Chicago Press.

Caro T. 2010. Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species. Washington, DC: Island Press.

Casewell NR, Wüster W, Vonk FJ, Harrison RA, Fry BG. 2013. Complex cocktails: the evolutionary novelty of venoms. Trends in Ecology & Evolution 28(4):219-229.

Casey JM, Myers RA. 1998. Near extinction of a large, widely distributed fish. Science 281(5377):690-692.

Ceballos G, Ehrlich PR. 2002. Mammal population losses and the extinction crisis. Science 296(5569):904-907.

Chapman CA, Gillespie TR, Goldberg TL. 2005. Primates and the ecology of their infectious diseases: how will anthropogenic change affect host-parasite interactions? Evolutionary Anthropology: Issues, News, and Reviews 14(4):134-144.

Charles-Dominique P. 1977. Ecology and behaviour of nocturnal primates: prosimians of equatorial West Africa. New York: Columbia University Press.

Charles-Dominique P, Petter JJ. 1980. Ecology and social life of *Phaner furcifer*. In: Charles-Dominique P, Cooper HM, Hladik A, Pages E, Pariente GF, Petter-Rousseaux A, Petter JJ, Schilling A, editors. Nocturnal Malagasy primates: ecology, physiology and behavior. New York: Academic Press. p 75-96.

Charnov EL. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9(2):129-136.

Chauhan A, Pirta RS. 2010. Agonistic interactions between humans and two species of monkeys (rhesus monkey *Macaca mulatta* and hanuman langur *Semnopithecus entellus*) in Shimla, Himachal Pradesh. Journal of Psychololg 1: 9-14.

Chen B, Xia X. 2001. The genus *Schevodera* Borchmann: phylogeny and historical biogeography, with description of a new species (Coleoptera: Tenebrionidae: Lagriinae). Oriental Insects 35(1):3-27.

Cheyne SM, Husson SJ, Chadwick RJ, Macdonald DW, Hutan S. 2010. Diversity and activity of small carnivores of the Sabangau Peat-swamp Forest, Indonesian Borneo. Small Carnivore Conservation 43:1-7.

Cristóbal-Azkarate J, Dias PAD, Veà JJ. 2004. Causes of intraspecific aggression in *Alouatta palliata mexicana*: evidence from injuries, demography, and habitat. International Journal of Primatology 25(4):939-953.

CIA World Factbook. 2013. The World Factbook. Online: https://www.cia.gov/library/publications/the-world-factbook/fields/2103.html. Accessed 20 June 2014.

Clark AB. 1982. Scent marks as social signals in *Galago crassicaudatus* I. Sex and reproductive status as factors in signals and responses. Journal of Chemical Ecology 8(8):1133-1151.

Clark AB. 1982. Scent marks as social signals in *Galago crassicaudatus* II. Discrimination between individuals by scent. Journal of Chemical Ecology 8(8):1153-1165.

Clark L, Thai NV, Phuong TQ. 2009. A long way from home: the health status of Asian pangolins confiscated from the illegal wildlife trade in Viet Nam. In: Pantel S, Yun CS, editors. Proceedings of the workshop on trade and conservation of pangolins native to South and Southeast Asia. Petaling Jaya, Selangor, Malaysia: TRAFFIC Southeast Asia. p 101-118.

Clay K, Marks S, Cheplick GP. 1993. Effects of insect herbivory and fungal endophyte infection on competitive interactions among grasses. Ecology 74(6):1767-1777.

Clucas B, Rowe MP, Owings DH, Arrowood PC. 2008. Snake scent application in ground squirrels, *Spermophilus* spp.: a novel form of antipredator behaviour? Animal Behaviour 75(1):299-307.

Coe CL. 2011. Immunity in primates within a psychobiological perspective. In: Demas G, Nelson RJ, editors. Ecoimmunology. Oxford, UK: Oxford University Press. p 144-164.

Collet JY, Galdikas BM, Sugarjito J, Jojosudharmo S. 1985. A coprological study of parasitism in orangutans (*Pongo pygmaeus*) in Indonesia. Journal of Medical Primatology 15(2):121-129.

Collins RL. 2007. Behavioural data of captive greater slow loris (*Nycticebus coucang*) & Javan slow loris (*N. javanicus*), and a survey of Javan slow loris in Mt. Salak, West Java, Java. MSc thesis. Oxford, UK: Oxford Brookes University.

Colón CP. 2002. Ranging behaviour and activity of the Malay civet (*Viverra tangalunga*) in a logged and an unlogged forest in Danum Valley, East Malaysia. Journal of Zoology 257(4):473-485.

Colquhoun IC. 2011. A review and interspecific comparison of nocturnal and cathemeral strepsirhine primate olfactory behavioural ecology. International Journal of Zoology DOI: 10.1155/2011/362976.

Combes C. 2001. Parasitism: the ecology and evolution of intimate interactions. Chicago: University of Chicago Press.

Corlett RT. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. Biological Reviews 73(4):413-448.

Corlett RT. 2007. The impact of hunting on the mammalian fauna of tropical Asian forests. Biotropica 39(3):292-303.

Corlett RT. 2011. Vertebrate carnivores and predation in the oriental (Indomalayan) region. Raffles Bulletin of Zoology 59(2):325–360.

Coultas DS. 2002. Bioacoustic analysis of the loud call of two species of slender loris (*Loris tardigradus* and *L. lydekkerianus nordicus*) from Sri Lanka. MSc thesis. Oxford, UK: Oxford Brookes University.

Cowlishaw G, Dunbar RIM. 2000. Primate conservation biology. Chicago: University of Chicago Press.

Crompton RH, Sellers WI, Gunther MM. 1993. Energetic efficiency and ecology as selective factors in the saltatory adaptation of prosimian primates. Proceedings of the Royal Society of London Series B: Biological Sciences 254(1339):41-45.

Cuenca-Bescós G, Rofes J. 2007. First evidence of poisonous shrews with an envenomation apparatus. Naturwissenschaften 94(2):113-116.

Curran LM, Trigg SN, McDonald AK, Astiani D, Hardiono Y, Siregar P, Caniago I, Kasischke E. 2004. Lowland forest loss in protected areas of Indonesian Borneo. Science 303(5660):1000-1003.

Dahrudin H, Wirdateti. 2008. Jenis tumbuhan dan tempat bersarang kukang (*Nycticebus coucang menagensis*) di hutan lindung pegunungan Merratus, Kalimantan Selatan. Zoo Indonesia 17(1):7-14.

Daltry JC, Wuester W, Thorpe RS. 1996. Diet and snake venom evolution. Nature 379(6565):537-540.

Daly JW. 1995. The chemistry of poisons in amphibian skin. Proceedings of the National Academy of Sciences 92(1):9-13.

Daly JW, Secunda SI, Garraffo HM, Spande TF, Wisnieski A, Cover Jr JF. 1994. An uptake system for dietary alkaloids in poison frogs (Dendrobatidae). Toxicon 32(6):657-663.

Daly JW, Secunda SI, Garraffo HM, Spande TF, Wisnieski A, Nishihira C, Cover Jr JF. 1992. Variability in alkaloid profiles in neotropical poison frogs (Dendrobatidae): genetic versus environmental determinants. Toxicon 30(8):887-898.

Darwin C. 1871. The descent of man, and selection in relation to sex. London, UK: John Murray.

Das N, Biswas J, Das J, Ray PC, Sangma A, Bhattacharjee PC. 2009. Status of Bengal slow loris *Nycticebus bengalensis* (Primates: Lorisidae) in Gibbon Wildlife Sanctuary, Assam, India. Journal of Threatened Taxa 1(11):558-561.

Das N, Nekaris KAI, Bhattacharjee PC. 2014. Medicinal plant exudativory by the Bengal slow loris *Nycticebus bengalensis*. Endangered Species Research 23:149-157.

Daschbach NJ, Schein MW, Haines DE. 1981. Vocalizations of the slow loris, *Nycticebus coucang* (Primates, Lorisidae). International Journal of Primatology 2(1):71-80.

Daschbach NJ, Schein MW, Haines DE. 1983. Cage-size effects on locomotor, grooming and agonistic behaviours of the slow loris, *Nycticebus coucang* (Primates, Lorisidae). Applied Animal Ethology 9(3-4):317-330.

Daszak P, Cunningham AA, Hyatt AD. 2000. Emerging infectious diseases of wildlife - threats to biodiversity and human health. Science 287(5452):443-449.

Datta A, Naniwadekar R, Anand MO. 2008. Occurrence and conservation status of small carnivores in two protected areas in Arunachal Pradesh, north-east India. Small Carnivore Conservation 39:1-10.

Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G. 2005. Hibernation in the tropics: lessons from a primate. Journal of Comparative Physiology Biology 175(3):147-155.

Davies NB. 1978. Ecological questions about territorial behaviour. In: Krebs JR, Davies NB, editors. Behavioural Ecology. London, UK: Blackwell. p 317-350.

Dawkins R, Krebs JR. 1979. Arms races between and within species. Proceedings of the Royal Society of London Series B: Biological Sciences 205(1161):489-511.

de Thoisy B, Vogel I, Reynes JM, Pouliquen JF, Carme B, Kazanji M, Vié JC. 2001. Health evaluation of translocated free-ranging primates in French Guiana. American Journal of Primatology 54(1):1-16.

Delpietro HA, Russo RG. 2009. Acquired resistance to saliva anticoagulants by prey previously fed upon by vampire bats *(Desmodus rotundus*): evidence for immune response. Journal of Mammalogy 90(5):1132-1138.

Demling RH. 2009. Nutrition, anabolism, and the wound healing process: an overview. Eplasty 9:65-94.

Despommier DD, Gwadz RW, Hotez PJ. 1994. Parasitic diseases. New York: Springer.

Dickens MJ, Delehanty DJ, Romero LM. 2010. Stress: an inevitable component of animal translocation. Biological Conservation 143(6):1329-1341.

Dickman CR. 1987. Habitat fragmentation and vertebrate species richness in an urban environment. Journal of Applied Ecology 224:337-351.

Do HV. 2009. Gastrointestinal parasites of the Delacour's langur (*Trachypithecus delacouri*): comparison between caged, semi-wild, and free-ranging individuals. Vietnamese Journal of Primatology 3:83-88.

Donati G, Borgognini-Tarli SM. 2006. Influence of abiotic factors on cathemeral activity: the case of *Eulemur fulvus collaris* in the littoral forest of Madagascar. Folia Primatologica 77(1-2):104-122.

Donati G, Ricci E, Baldi N, Morelli V, Borgognini-Tarli SM. 2011. Behavioral thermoregulation in a gregarious lemur, *Eulemur collaris*: effects of climatic and dietary-related factors. American Journal of Physical Anthropology 144(3):355-364.

Douglas III HD. 2008. Prenuptial perfume: alloanointing in the social rituals of the crested auklet (*Aethia cristatella*) and the transfer of arthropod deterrents. Naturwissenschaften 95(1):45-53.

Dragoo JW. 2009. Family Mephitidae (Skunks). In: Wilson DE, Mittermeier RA, editors. Handbook of the mammals of the world - Volume 1 Carnivores. Barcelona: Lynx. P. 532–563.

Driller C, Perwitasari-Farajallah D, Zischler H, Merker S. 2009. The social system of Lariang tarsiers (*Tarsius lariang*) as revealed by genetic analyses. International Journal of Primatology 30(2):267-281.

Droescher I, Kappeler PM. 2013. Defining the low end of primate social complexity: the social organization of the nocturnal white-footed sportive lemur (*Lepilemur leucopus*). International Journal of Primatology 34(6):1225-1243.

Dryden MW, Payne PA, Ridley R, Smith V. 2005. Comparison of common fecal flotation techniques for the recovery of parasite eggs and oocysts. Veterinary Therapeutics 6(1):15-28.

Duckworth J. 1992. Sighting frequencies of nocturnal mammals in an Ethiopian Rift Valley national park. African Journal of Ecology 30(1):90-97.

Duckworth JW, Brickle NW. 2008. *Melogale orientalis.* IUCN Red List of Threatened Species. Version 2013.2. Online: www.iucnredlist.org. Accessed 12 December 2013.

Duckworth JW, Roberton SI, Brickle NW. 2008. Further notes on Javan Ferret Badger *Melogale orientalis* at Gunung Gede Pangrango National Park, Java. Small Carnivore Conservation 39:39-40.

Duffey SS. 1980. Sequestration of plant natural products by insects. Annual Review of Entomology 25(1):447-477.

Dufton MJ. 1992. Venomous mammals. Pharmacology & Therapeutics 53(2):199-215.

Dugon MM, Arthur W. 2012. Comparative studies on the structure and development of the venom-delivery system of centipedes, and a hypothesis on the origin of this evolutionary novelty. Evolution & Development 14(1):128-137.

Dumbacher JP, Menon GK, Daly JW. 2009. Skin as a toxin storage organ in the endemic New Guinean genus *Pitohui*. The Auk 126(3):520-530.

Dumbacher JP, Wako A, Derrickson SR, Samuelson A, Spande TF, Daly JW. 2004. Melyrid beetles (Choresine): a putative source for the batrachotoxin alkaloids found in poison-dart frogs and toxic passerine birds. Proceedings of the National Academy of Sciences of the United States of America 101(45):15857-15860.

Dutertre S, Lewis RJ. 2010. Use of venom peptides to probe ion channel structure and function. Journal of Biological Chemistry 285(18):13315-13320.

Dytham C. 2007. Choosing and using statistics: a biologist's guide. Malden: Wiley-Blackwell.

Eaton JA, Wüst R, Wirth R, Shepherd CR, Semiadi G, Hall J, Duckworth JW. 2010. Recent records of the Javan Small-toothed Palm Civet *Arctogalidia (trivirgata) trilineata*. Small Carnivore Conservation 43:16-22.

Eberle M, Kappeler PM. 2002. Mouse lemurs in space and time: a test of the socioecological model. Behavioral Ecology and Sociobiology 51(2):131-139.

Eberle M, Kappeler PM. 2004. Sex in the dark: determinants and consequences of mixed male mating tactics in *Microcebus murinus*, a small solitary nocturnal primate. Behavioral Ecology and Sociobiology 57(1):77-90.

Eberle M, Kappeler PM. 2008. Mutualism, reciprocity, or kin selection? Cooperative rescue of a conspecific from a boa in a nocturnal solitary forager the gray mouse lemur. American Journal of Primatology 70(4):410-414.

Edgecombe GD, Giribet G. 2007. Evolutionary biology of centipedes (Myriapoda: Chilopoda). Annual Review of Entomology 52:151-170.

Ehrlich A. 1974. Infant development in two prosimian species: greater galago and slow loris. Developmental Psychobiology 7(5):439-454.

Ehrlich A, Macbride L. 1989. Mother-infant interactions in captive slow lorises (*Nycticebus coucang*). American Journal of Primatology 19(4):217-228.

Ehrlich A, Musicant A. 1977. Social and individual behaviors in captive slow lorises. Behaviour 60(3/4):195-220.

Eisner T, Alsop D, Hicks K, Meinwald J. 1978. Defensive secretions of millipeds. In: Bettini S, editor. Arthropod venoms. New York: Springer. p 41-72.

Eisner T, Rossini C, Eisner M. 2000. Chemical defense of an earwig (*Doru taeniatum*). Chemoecology 10(2):81-87.

Ekanayake DK, Arulkanthan A, Horadagoda NU, Sanjeejani GKM, Kieft R, Gunatilake S, Dittus WPJ. 2006. Prevalence of Cryptosporidium and other enteric parasites among wild non-human primates in Polonnaruwa, Sri Lanka. The American Journal of Tropical Medicine and Hygiene 74(2):322-329.

Elliot O, Elliot M. 1967. Field notes on the slow loris in Malaya. Journal of Mammalogy 48:497-498.

Emlen DJ. 2008. The evolution of animal weapons. Annual Review of Ecology, Evolution, and Systematics 39:387-413.

Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197(4300):215-223.

Erkert HG. 2003. Chronobiological aspects of primate research. In: Setchell JM, Curtis DJ, editors. Field and laboratory methods in primatology. Cambridge, UK: Cambridge University Press. p 252-270.

Erkert HG, Cramer B. 2006. Chronobiological background to cathemerality: circadian rhythms in *Eulemur fulvus albifrons* (Prosimii) and *Aotus azarai boliviensis* (Anthropoidea). Folia Primatologica 77(1-2):87-103.

Espmark Y. 1964. Studies in dominance-subordination relationship in a group of semi-domestic reindeer (*Rangifer tarandus* L.). Animal Behaviour 12(4):420-426.

Fadamiro HY, Wyatt TD. 1995. Flight initiation by *Prostephanus truncatus* in relation to time of day, temperature, relative humidity and starvation. Entomologia Experimentalis et Applicata 75(3):273-277.

Fenner PJ, Williamson JA, Myers D. 1992. Platypus envenomation - a painful learning experience. The Medical Journal of Australia 157(11-12):829-832.

Fernandez-Duque E, Erkert HG. 2006. Cathemerality and lunar periodicity of activity rhythms in owl monkeys of the Argentinian Chaco. Folia Primatologica 77(1-2):123-138.

Fernando P, Polet G, Foead N, Ng LS, Pastorini J, Melnick DJ. 2006. Genetic diversity, phylogeny and conservation of the Javan rhinoceros (*Rhinoceros sondaicus*). Conservation Genetics 7(3):439-448.

Fichtel C. 2007. Avoiding predators at night: antipredator strategies in red-tailed sportive lemurs (*Lepilemur ruficaudatus*). American Journal of Primatology 69(6):611-624.

Fichtel C, Hilgartner R. 2013. Noises in the dark: vocal communication in *Lepilemur ruficaudatus* and other nocturnal pair-living primates. In: Masters J, Gamba M, Génin F, editors. Leaping ahead. New York: Springer. p 297-304.

Field A. 2009. Discovering statistics using SPSS. London, UK: Sage publications.

Fietz J. 1999b. Mating system of *Microcebus murinus*. American Journal of Primatology 48(2):127-133.

Fietz J. 1999a. Monogamy as a rule rather than exception in nocturnal lemurs: the case of the fat tailed dwarf lemur, *Cheirogaleus medius*. Ethology 105(3):255-272.

Fietz J, Zischler H, Schwiegk C, Tomiuk J, Dausmann KH, Ganzhorn JU. 2000. High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. Behavioral Ecology and Sociobiology 49(1):8-17.

Fisher HS, Swaisgood R, Fitch-Snyder H. 2003. Countermarking by male pygmy lorises (*Nycticebus pygmaeus*): do females use odor cues to select mates with high competitive ability? Behavioral Ecology and Sociobiology 53(2):123-130.

Fisher HS, Swaisgood RR, Fitch-Snyder H. 2003. Odor familiarity and female preferences for males in a threatened primate, the pygmy loris *Nycticebus pygmaeus*: applications for genetic management of small populations. Naturwissenschaften 90(11):509-512.

Fitch-Snyder H, Ehrlich A. 2003. Mother-infant interactions in slow lorises (*Nycticebus bengalensis*) and pygmy lorises (*Nycticebus pygmaeus*). Folia Primatologica 74:259-271.

Fitch-Snyder H, Jurke M. 2003. Reproductive patterns in pygmy lorises (*Nycticebus pygmaeus*): behavioral and physiological correlates of gonadal activity. Zoo Biology 22(1):15-32.

Fitch-Snyder H, Schulze H. 2001. Management of lorises in captivity: a husbandry manual for Asian lorisines (*Nycticebus* & *Loris* spp.). San Diego: Center for Reproduction of Endangered Species, Zoological Society of San Diego.

FitzGerald GJ, Bider JR. 1974. Influence of moon phase and weather factors on locomotory activity in *Bufo americanus*. Oikos 25:338-340.

Fleagle JG. 2013. Primate Adaptation and Evolution. San Diego: Academic Press.

Fogden MPL. 1972. The seasonality and population dynamics of equatorial forest birds East Sarawak. Ibis 114(3):307-343.

Foitová I. 2002. Parasites in orangutans (*Pongo pygmaeus* Linnaeus 1760) with connection to the ecology and ethology factors. PhD thesis. Brno, Czech Republic: Veterinary and Pharmaceutical University Brno.

Foitová I, Huffman MA, Wisnu N, Olsansky M. 2009. Parasites and their impacts on orangutan health. In: Wich SA, Atmoko SSU, Setia TM, editors. Orangutans: geographic variation in behavioral ecology and conservation. Oxford, UK: Oxford University Press. p 157-169.

Folinsbee KE. 2013. Evolution of venom across extant and extinct eulipotyphlans. Comptes Rendus Palevol 12(7):531-542.

Folinsbee KE, Müller J, Reisz RR. 2007. Canine grooves: morphology, function, and relevance to venom. Journal of Vertebrate Paleontology 27(2):547-551.

Forbey JS, Harvey AL, Huffman MA, Provenza FD, Sullivan R, Tasdemir D. 2009. Exploitation of secondary metabolites by animals: a response to homeostatic challenges. Integrative and Comparative Biology 49(3):314.

Fox RC, Scott CS. 2005. First evidence of a venom delivery apparatus in extinct mammals. Nature 435(7045):1091-1093.

Frith DW. 1975. A preliminary study of insect abundance on West Island, Aldabra Atoll, Indian Ocean. Transactions of the Royal Entomological Society of London 127(3):209-225.

Fry BG, Casewell NR, Wüster W, Vidal N, Young B, Jackson TN. 2012. The structural and functional diversification of the Toxicofera reptile venom system. Toxicon 60(4):434-448.

Fry BG, Roelants K, Champagne DE, Scheib H, Tyndall JD, King GF, Nevalainen TJ, Norman JA, Lewis RJ, Norton RS. 2009a. The toxicogenomic multiverse: convergent recruitment of proteins into animal venoms. Annual Review of Genomics and Human Genetics 10:483-511.

Fry BG, Scheib H, van der Weerd L, Young B, McNaughtan J, Ramjan SR, Vidal N, Poelmann RE, Norman JA. 2008. Evolution of an arsenal structural and functional diversification of the venom system in the advanced snakes (Caenophidia). Molecular & Cellular Proteomics 7(2):215-246.

Fry BG, Vidal N, Norman JA, Vonk FJ, Scheib H, Ramjan SR, Kuruppu S, Fung K, Hedges SB, Richardson MK. 2005. Early evolution of the venom system in lizards and snakes. Nature 439(7076):584-588.

Fry BG, Vidal N, Van der Weerd L, Kochva E, Renjifo C. 2009b. Evolution and diversification of the Toxicofera reptile venom system. Journal of Proteomics 72(2):127-136.

Fuller G, Lukas KE, Kuhar C, Dennis PM. 2014. A retrospective review of mortality in lorises and pottos in North American zoos, 1980–2010. Endangered Species Research 23:205-217.

Furió M, Agustí J, Mouskhelishvili A, Sanisidro Ó, Santos-Cubedo A. 2010. The paleobiology of the extinct venomous shrew *Beremendia* (Soricidae, Insectivora, Mammalia) in relation to the geology and paleoenvironment of Dmanisi (Early Pleistocene, Georgia). Journal of Vertebrate Paleontology 30(3):928-942.

Ganzhorn JU, Abraham JP, Razanahoera-Rakotomalala M. 1985. Some aspects of the natural history and food selection of *Avahi laniger*. Primates 26(4):452-463.

Ganzhorn JU, Jacques S, Rakotondranary, Ratovonamana YR. 2011. Habitat description and phenology. In: Setchell JM, Curtis DJ, editors. Field and laboratory methods in primatology: a practical guide. Cambridge, UK: Cambridge University Press. p. 51-68.

Gao X, Zhang X, Yang J, Chen G, Shi A, Song J, Li Q. 2011. Relationships between arthropod community characteristic and meteorological factors in *Zanthoxylum bungeanum* gardens. Acta Ecologica Sinica 31(10):2788-2796.

Gardner JL, Serena M. 1995. Spatial-organization and movement patterns of adult male platypus, *Ornithorhynchus anatinus* (Monotremata, Ornithorhynchidae). Australian Journal of Zoology 43(1):91-103.

Gaston KJ, Fuller RA. 2007. Biodiversity and extinction: losing the common and the widespread. Progress in Physical Geography 31(2):213-225.

Gebo DL. 1986. Miocene lorisids – the foot evidence. Folia Primatologica 47(4):217-225.

Gilbert FS. 1985. Diurnal activity patterns in hoverflies (Diptera, Syrphidae). Ecological Entomology 10(4):385-392.

Gillespie TR. 2006. Noninvasive assessment of gastrointestinal parasite infections in free-ranging primates. International Journal of Primatology 27(4):1129-1143.

Gillespie TR, Chapman CA, Greiner EC. 2005a. Effects of logging on gastrointestinal parasite infections and infection risk in African primates. Journal of Applied Ecology 42(4):699-707.

Gillespie TR, Greiner EC, Chapman CA. 2005b. Gastrointestinal parasites of the colobus monkeys of Uganda. Journal of Parasitology 91(3):569-573.

Gillespie TR, Lonsdorf EV, Canfield EP, Meyer DJ, Nadler Y, Raphael J, Pusey AE, Pond J, Pauley J, Mlengeya T, Travis DA. 2010. Demographic and ecological effects on patterns of parasitism in eastern chimpanzees (*Pan troglodytes schweinfurthii*) in Gombe National Park, Tanzania. American Journal of Physical Anthropology 143(4):534-544.

Gillespie TR, Nunn CL, Leendertz FH. 2008. Integrative approaches to the study of primate infectious disease: implications for biodiversity conservation and global health. American Journal of Physical Anthropology 137(S47):53-69.

Gjershaug JO, Røv N, Nygård T, Prawiradilaga DM, Afianto M, Hapsoro M, Supriatna A. 2004. Home-range size of the Javan Hawk-Eagle (*Spizaetus bartelsi*) estimated from direct observations and radiotelemetry. Journal of Raptor Research 38:343-349.

Glander KE. 1982. The impact of plant secondary compounds on primate feeding behavior. American Journal of Physical Anthropology 25(S3):1-18.

Glaser R, Kiecolt-Glaser JK. 2005. Stress-induced immune dysfunction: implications for health. Nature Reviews Immunology 5(3):243-251.

Gomendio M, Harcourt AH, Roldán ERS. 1998. Sperm competition in mammals. In Birkhead TR, Møller AP, editors. Sperm competition and sexual selection. London, UK: Academic Press. p 667-756.

Goodman SM, O'Connor S, Langrand O. 1993. A review of predation on lemurs: implications for the evolution of social behavior in small, nocturnal primates. In: Kappeler PM, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum Press. p 51-66.

Goossens B, Graziani L, Waits LP, Farand E, Magnolon S, Coulon J, Bel M-C, Taberlet P, Allainé D. 1998. Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. Behavioral Ecology and Sociobiology 43(4-5):281-288.

Gould L, Sauther M. 2011. Lemuriformes. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf R, editors. Primates in Perspective. New York: Springer. p 46-72.

Graczyk TK, Mudakikwa AB, Cranfield MR, Eilenberger U. 2001. Hyperkeratotic mange caused by *Sarcoptes scabiei* (Acariformes: Sarcoptidae) in juvenile human-habituated mountain gorillas (*Gorilla gorilla beringei*). Parasitology Research 87(12):1024-1028.

Grant TR. 1995. The platypus. Sydney, Australia: UNSW Press.

Grant TR, Temple–Smith PD. 1998. Field biology of the platypus (*Ornithorhynchus anatinus*): historical and current perspectives. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences 353(1372):1081-1091.

Grassman Jr LI, Tewes ME, Silvy NJ. 2005. Ranging, habitat use and activity patterns of binturong *Arctictis binturong* and yellow-throated marten *Martes flavigula* in north-central Thailand. Wildlife Biology 11(1):49-57.

Gray A. 2013. Stress reduction through environmental enrichment: improving welfare for captive slow lorises (*Nycticebus* spp.) rescued from the illegal pet trade in Indonesia. MSc thesis. Oxford, UK: Oxford Brookes University.

Greenhall AM, Schmidt U. 1988. Natural history of vampire bats. Boca Raton, Florida: CRC Press.

Groves C, Grubb P. 2011. Ungulate Taxonomy. Baltimore, Maryland: John Hopkins University Press.

Grow NB, Wirdateti, Nekaris KAI. 2015. Does toxic defence in *Nycticebus* spp. relate to ectoparasites? The lethal effects of slow loris venom on arthropods. Toxicon 95:1-5.

Grubb P, Butynski TM, Oates JF, Bearder SK, Disotell TR, Groves CP, Struhsaker TT. 2003. Assessment of the diversity of African primates. International Journal of Primatology 24(6):1301-1357.

Guércio RAP, Shevchenko A, Shevchenko A, López-Lozano JL, Paba J, Sousa MV, Ricart CAO. 2006. Ontogenetic variations in the venom proteome of the Amazonian snake *Bothrops atrox*. Proteome Science 4(1):11.

Gursky S. 1998. Conservation status of the spectral tarsier *Tarsier spectrum*: Population density and home range size. Folia Primatologica 69:191-203.

Gursky S. 2003. Lunar philia in a nocturnal primate. International Journal of Primatology 24(2):351-367.

Gursky S. 2006. Function of snake mobbing in spectral tarsiers. American Journal of Physical Anthropology 129(4):601-608.

Gursky SL. 2007. The response of spectral tarsiers toward avian and terrestrial predators. In: Gursky SL, Nekaris KAI, editors. Primate anti-predator strategies. New York: Springer. p 241-252.

Gursky-Doyen S. 2010. Intraspecific variation in the mating system of spectral tarsiers. International Journal of Primatology 31(6):1161-1173.

Hagey L, Fry B, Fitch-Snyder H. 2007. Talking defensively, a dual use for the brachial gland exudate of slow and pygmy lorises. In: Gursky S, Nekaris KAI, editors. Primate anti-predator strategies. New York: Springer. p 253-272.

Hanya G. 2004. Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: effects of food and temperature. American Journal of Primatology 63(3):165-177.

Harcourt AH, Harvey PH, Larson SG, Short RV. 1981. Testis weight, body weight and breeding system in primates. Nature 293(5827):55-57.

Harcourt AH, Purvis A, Liles L. 1995. Sperm competition: mating system, not breeding season, affects testes size of primates. Functional Ecology 9(3):468-476.

Harcourt C. 1991. Diet and behaviour of a nocturnal lemur, *Avahi laniger*, in the wild. Journal of Zoology 223(4):667-674.

Harcourt CS, Nash LT. 1986. Social organization of Galagos in Kenyan coastal forests: I. *Galago zanzibaricus*. American Journal of Primatology 10(4):339-355.

Harris S, Cresswell WJ, Forde PG, Trewhella WJ, Woollard T, Wray S. 1990. Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20(2-3):97-123.

Harrison RA, Cook DA, Renjifo C, Casewell NR, Currier RB, Wagstaff SC. 2011. Research strategies to improve snakebite treatment: challenges and progress. Journal of Proteomics 74(9):1768-1780.

Hayes WK, Lavín-Murcio P, Kardong KV. 1995. Northern Pacific rattlesnakes (*Crotalus viridis oreganus*) meter venom when feeding on prey of different sizes. Copeia 1995(2):337-343.

Heaney LR. 1991. A synopsis of climatic and vegetational change in Southeast Asia. Climatic change 19(1-2):53-61.

Hebard M. 1929. Studies in Malayan Blattidae (Orthoptera). Proceedings of the Academy of Natural Sciences of Philadelphia 81:1-109.

Hecker KR, Brigham RM. 1999. Does moonlight change vertical stratification of activity by forest-dwelling insectivorous bats? Journal of Mammalogy 80(4):1196-1201.

Heldmaier G, Ortmann S, Elvert R. 2004. Natural hypometabolism during hibernation and daily torpor in mammals. Respiratory Physiology & Neurobiology 141(3):317-329.

Heldmaier G, Ruf T. 1992. Body temperature and metabolic rate during natural hypothermia in endotherms. Journal of Comparative Physiology Biology 162(8):696-706.

Herr J, Schley L, Roper TJ. 2009. Socio-spatial organization of urban stone martens. Journal of Zoology 277(1):54-62.

Heydon MJ, Bulloh P. 1996. The impact of selective logging on sympatric civet species in Borneo. Oryx 30(1):31-36.

Heymann EW. 2006. Scent marking strategies of New World primates. American Journal of Primatology 68(6):650-661.

Hilgartner R, Fichtel C, Kappeler PM, Zinner D. 2012. Determinants of pair-living in red-tailed sportive lemurs (*Lepilemur ruficaudatus*). Ethology 118(5):466-479.

Hill D, Fasham M, Tucker G, Shewry M, Shaw P. 2005. Handbook of biodiversity methods. Survey, evaluation and monitoring. Cambridge, UK: Cambridge University Press.

Hill T, Lewicki P. 2006. Statistics: methods and applications: a comprehensive reference for science, industry, and data mining. Tulsa: StatSoft, Inc.

Hill WCO. 1953. Primates: comparative anatomy and taxonomy I. Strepsirhini. Edinburgh: Edinburgh University Press.

Hirzel AH, Hausser J, Chessel D, Perrin N. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83(7):2027-2036.

Hladik CM. 1979. Diet and ecology of prosimians. In: Doyle GA, editor. The study of prosimian behavior. New York, Academic Press. p 307-357.

Hladik CM, Charles-Dominique P, Petter JJ. 1980. Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In: Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pages E, Pariente GF, Petter-Rousseaux A, Schilling A, Petter JJ, editors. Nocturnal Malagasy primates: ecology, physiology and behaviour. New York: Academic Press. p 41-73.

Hoffman RL. 1975. Studies on spirostreptoid millipeds. XI. A review of some Indonesian genera of the family Harpagophoridae. Journal of Natural History 9(2):121-152.

Hoogerwerf A. 1970. Udjung Kulon: the land of the last Javan rhinoceros. Leiden, the Netherlands: Brill Archive.

Hopkins ME, Nunn CL. 2007. A global gap analysis of infectious agents in wild primates. Diversity and Distributions 13(5):561-572.

Horning M, Trillmich F. 1999. Lunar cycles in diel prey migrations exert a stronger effect on the diving of juveniles than adult Galapagos fur seals. Proceedings of the Royal Society of London Series B: Biological Sciences 266(1424):1127-1132.

Huck M, Fernandez-Duque E, Babb P, Schurr T. 2014. Correlates of genetic monogamy in socially monogamous mammals: insights from Azara's owl monkeys. Proceedings of the Royal Society B: Biological Sciences 281(1782):20140195.

Huffman MA. 1997. Current evidence for self-medication in primates: a multidisciplinary perspective. American Journal of Physical Anthropology 104(25):171-200.

Huffman MA, Chapman CA. 2009. Methods to study primates and parasites interactions. In: Huffman MA, Chapman CA, editors. Primate parasite ecology - the dynamics and study of host-parasite relationships. Cambridgie, UK: Cambridge University Press. p. 5-10.

Hutchinson DA, Mori A, Savitzky AH, Burghardt GM, Wu X, Meinwald J, Schroeder FC. 2007. Dietary sequestration of defensive steroids in nuchal glands of the Asian snake *Rhabdophis tigrinus*. Proceedings of the National Academy of Sciences 104(7):2265-2270.

Hutchinson DA, Savitzky AH, Mori A, Burghardt GM, Meinwald J, Schroeder FC. 2012. Chemical investigations of defensive steroid sequestration by the Asian snake *Rhabdophis tigrinus*. Chemoecology 22(3):199-206.

Inceoglu B, Lango J, Jing J, Chen L, Doymaz F, Pessah IN, Hammock BD. 2003. One scorpion, two venoms: prevenom of *Parabuthus transvaalicus* acts as an alternative type of venom with distinct mechanism of action. Proceedings of the National Academy of Sciences 100(3):922-927.

Internet World Stats. 2014. Asia. Online: http://www.internetworldstats.com/asia.htm#id. Accessed 20 June 2014.

Ishida H, Hirasaki E, Matano S. 1992. Locomotion of the slow loris between discontinuous substrates. Topics in Primatology 3:139-152.

Ishikawa T, Susila W, Okajima S. 2007. The thread-legged assassin bug genus *Calphurnioides distant* (Hemiptera: Heteroptera Reduviidae) from eastern Java and Bali, Indonesia. Proceedings of the Entomological Society of Washington 109(2):277-285.

Iskandar DT, Erdelen WR. 2006. Conservation of amphibians and reptiles in Indonesia: issues and problems. Amphibian and Reptile Conservation 4(1):60-87.

Isvaran K, Clutton-Brock T. 2007. Ecological correlates of extra-group paternity in mammals. Proceedings of the Royal Society B: Biological Sciences 274(1607):219-224.

IUCN. 2002. Guidelines for the placement of confiscated animals. Gland, Switzerland: IUCN Species Survival Commission.

IUCN. 2014. IUCN red list of threatened species. Version 2014.1. Online: www.iucnredlist.org. Accessed 20 June 2014.

IUCN & UNEP. 2014. The World Database on Protected Areas (WDPA). Cambridge, UK: UNEP-WCMC. Online: www.protectedplanet.net. Accessed 20 June 2014.

IUCN/SSC. 2013. Guidelines for reintroductions and other conservation translocations. Gland, Switzerland: IUCN Species Survival Commission.

Izard MK, Weisenseel K, Ange R. 1988. Reproduction in the slow loris (*Nycticebus coucang*). American Journal of Primatology 16(4):331-339.

Jackson BC, Thompson DC, Wright MW, McAndrews M, Bernard A, Nebert DW, Vasiliou V. 2011. Update of the human secretoglobin (SCGB) gene superfamily and an example of'evolutionary bloom'of androgen-binding protein genes within the mouse Scgb gene superfamily. Human Genomics 5(6):691–702.

Jackson K. 2003. The evolution of venom-delivery systems in snakes. Zoological Journal of the Linnean Society 137(3):337-354.

Janečka JE, Helgen KM, Lim NT-L, Baba M, Izawa M, Murphy WJ. 2008. Evidence for multiple species of Sunda colugo. Current Biology 18(21):R1001-R1002.

Joshi AR, Smith JLD, Cuthbert FJ. 1995. Influence of food distribution and predation pressure on spacing behavior in palm civets. Journal of Mammalogy 76(7):1205-1212.

Jothish P. 2011. Diet of the common palm civet *Paradoxurus hermaphroditus* in a rural habitat in Kerala, India, and its possible role in seed dispersal. Small Carnivore Conservation 45:14-17.

Junge RE, Louis EE. 2005. Biomedical evaluation of two sympatric lemur species (*Propithecus verreauxi deckeni* and *Eulemur fulvus rufus*) in Tsiombokibo Classified Forest, Madagascar. Journal of Zoo and Wildlife Medicine 36(4):581-589.

Jurke MH, Czekala NM, Fitch-Snyder H. 1997. Non-invasive detection and monitoring of estrus, pregnancy and the postpartum period in pygmy loris (*Nycticebus pygmaeus*) using fecal estrogen metabolites. American Journal of Primatology 41(2):103-115.

Kappeler PM. 1997a. Intrasexual selection in *Mirza coquereli*: evidence for scramble competition polygyny in a solitary primate. Behavioral Ecology and Sociobiology 41(2):115-127.

Kappeler PM. 1997b. Intrasexual selection and testis size in strepsirhine primates. Behavioral Ecology 8(1):10.

Kappeler PM. 1997c. Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. Biological Reviews 72(1):111-151.

Kappeler PM, Erkert HG. 2003. On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs (*Eulemur fulvus rufus*). Behavioral Ecology and Sociobiology 54(4):359-369.

Kappeler PM, Rasoloarison RM, Razafimanantsoa L, Walter L, Roos C. 2005. Morphology, behaviour and molecular evolution of giant mouse lemurs (*Mirza* spp.) GRAY, 1870, with description of a new species. Primate Report 71:3-26.

Kappeler PM, van Schaik CP. 2002. Evolution of primate social systems. International Journal of Primatology 23(4):707-740.

Kellaway CH, LeMessurier DH. 1935. The venom of the platypus (*Ornithorhynchus anatinus*). Australian Journal of Experimental Biology & Medical Science 13:205-221.

Kenward R. 2001. A manual for wildlife radio tagging. London, UK: Academic Press.

Kenyon M, Streicher U, Loung H, Tran T, Tran M, Vo B, Cronin A. 2014. Survival of reintroduced pygmy slow loris *Nycticebus pygmaeus* in South Vietnam. Endangered Species Research DOI: 10.3354/esr00607.

Kilbourn AM, Karesh WB, Wolfe ND, Bosi EJ, Cook RA, Andau M. 2003. Health evaluation of free-ranging and semi-captive orangutans (*Pongo pygmaeus pygmaeus*) in Sabah, Malaysia. Journal of Wildlife Diseases 39(1):73-83.

King GF. 2011. Venoms as a platform for human drugs: translating toxins into therapeutics. Expert Opinion on Biological Therapy 11(11):1469-1484.

Kingdon J, Agwanda B, Kinnaird M, O'Brien T, Holland C, Gheysens T, Boulet-Audet M, Vollrath F. 2011. A poisonous surprise under the coat of the African crested rat. Proceedings of the Royal Society B: Biological Sciences 279:675–680.

Kita M, Nakamura Y, Okumura Y, Ohdachi SD, Oba Y, Yoshikuni M, Kido H, Uemura D. 2004. Blarina toxin, a mammalian lethal venom from the short-tailed shrew *Blarina brevicauda*: isolation and characterization. Proceedings of the National Academy of Sciences of the United States of America 101(20):7542-7547.

Klotz JH, Klotz SA, Pinnas JL. 2009. Animal bites and stings with anaphylactic potential. The Journal of Emergency Medicine 36(2):148-156.

Knapp LA, Robson J, Waterhouse JS. 2006. Olfactory signals and the MHC: a review and a case study in Lemur catta. American journal of primatology 68(6):568-584.

Koenig A, Scarry CJ, Wheeler BC, Borries C. 2013. Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. Philosophical Transactions of the Royal Society B: Biological Sciences 368:20120348.

Kool KM. 1993. The diet and feeding behavior of the silver leaf monkey *(Trachypithecus auratus sondaicus*) in Indonesia. International Journal of Primatology 14(5):667-700.

Krane S, Itagaki Y, Nakanishi K, Weldon PJ. 2003. "Venom" of the slow loris: sequence similarity of prosimian skin gland protein and Fel d 1 cat allergen. Naturwissenschaften 90(2):60-62.

Krause WJ. 2009. Morphological and histochemical observations on the crural gland-spur apparatus of the echidna (*Tachyglossus aculeatus*) together with comparative observations on the femoral gland-spur apparatus of the duckbilled platypus (*Ornithorhyncus anatinus*). Cells Tissues Organs 191(4):336-354.

Kuhn-Nentwig L, Schaller J, Nentwig W. 2004. Biochemistry, toxicology and ecology of the venom of the spider *Cupiennius salei* (Ctenidae). Toxicon 43(5):543-553.

Kumar A, Sarma K, Panvor J, Mazumdar K, Devi A, Krishna M, Ray PC. 2014. Threats to the Bengal slow loris *Nycticebus bengalensis* in and around Itanagar Wildlife Sanctuary, Arunachal Pradesh, India: impediments to conservation. Endangered Species Research 23:99-106.

Labes E, Hegglin D, Grimm F, Nurcahyo W, Harrison M, Bastian M, Deplazes P. 2010. Intestinal parasites of endangered orangutans (*Pongo pygmaeus*) in Central and East Kalimantan, Borneo, Indonesia. Parasitology 137(1):123-135.

Lang AB, Kalko EK, Römer H, Bockholdt C, Dechmann DK. 2005. Activity levels of bats and katydids in relation to the lunar cycle. Oecologia 146(4):659-666.

Lavigne F, Gunnell Y. 2006. Land cover change and abrupt environmental impacts on Javan volcanoes, Indonesia: a long-term perspective on recent events. Regional Environmental Change 6(1-2):86-100.

Le Boeuf BJ. 1974. Male-male competition and reproductive success in elephant seals. American Zoologist 14(1):163-176.

Lee RJ, Gorog AJ, Dwiyahreni A, Siwu S, Riley J, Alexander H, Paoli GD, Ramono W. 2005. Wildlife trade and implications for law enforcement in Indonesia: a case study from North Sulawesi. Biological Conservation 123(4):477-488.

Lehtinen J. 2013. Distribution of the Javan slow loris (*Nycticebus javanicus*): assessing the presence in East Java, Indonesia. MSc thesis. Oxford, UK: Oxord Brookes University.

Leighton FA. 2002. Health risk assessment of the translocation of wild animals. Revue Scientifique et Technique - Office International des Epizooties 21(1):187-216.

Lessard JP, Sackett TE, Reynolds WN, Fowler DA, Sanders NJ. 2011. Determinants of the detrital arthropod community structure: the effects of temperature and resources along an environmental gradient. Oikos 120(3):333-343.

Lewis MP. 2009. Ethnologue: languages of the world. Dallas, Texas: SIL International.

Ligabue-Braun R, Verli H, Carlini CR. 2012. Venomous mammals: a review. Toxicon 59(7):680-695.

Lim BL. 1973. The banded linsang and the banded musang of West Malaysia. Malayan Nature Journal 26(3-4):105-111.

Lim NTL. 2007. Autecology of the sunda pangolin (*Manis javanica*) in Singapore. MSc thesis. Singapore: National University of Singapore.

Lim NTL, Ng PKL. 2007. Home range, activity cycle and natal den usage of a female Sunda pangolin *Manis javanica* (Mammalia: Pholidota) in Singapore. Endangered Species Research 3:1-8.

Lim NTL, Ng PKL. 2010. Population assessment methods for the Sunda colugo *Galeopterus variegatus* (Mammalia: Dermoptera) in tropical forests and their viability in Singapore. Raffles Bulletin of Zoology 58(1):157–164

Lisonbee L. 2008. Self-medicative behavior of sheep experiencing gastrointestinal nematode infections and the postingestive effects of tannins. MSc thesis. Logan: Utah State University.

Long CA. 1992. Is the Javan ferret-badger a subspecies or a species? Small Carnivore Conservation 6:17.

Lopez-Jurado LF, Mateo JA. 1996. Evidence of venom in the Canarian shrew (*Crocidura canariensis*): immobilizing effects on the Atlantic lizard (*Gallotia atlantica*). Journal of Zoology 239(2):394-395.

Loudon JE, Sauther ML, Fish KD, Hunter-Ishikawa M, Ibrahim YJ. 2006. One reserve, three primates: applying a holistic approach to understand the interconnections among ring-tailed lemurs (*Lemur catta*), Verreaux's sifaka (*Propithecus verreauxi*), and humans (*Homo sapiens*) at Beza Mahafaly Special Reserve, Madagascar. Ecological and Environmental Anthropology 2:54-74.

Low DH, Sunagar K, Undheim EA, Ali SA, Alagon AC, Ruder T, Jackson TN, Pineda Gonzalez S, King GF, Jones A. 2013. Dracula's children: molecular evolution of vampire bat venom. Journal of Proteomics 89:95-111.

Lowman MD. 1982. Seasonal variation in insect abundance among three Australian rain forests, with particular reference to phytophagous types. Australian Journal of Ecology 7(4):353-361.

Lozano GA. 1998. Parasitic stress and self-medication in wild animals. Advances in the Study of Behavior 27:291-317.

Lukas D, Clutton-Brock TH. 2013. The evolution of social monogamy in mammals. Science 341(6145):526-530.

Lyles AM, Dobson AP. 1993. Infectious disease and intensive management: population dynamics, threatened hosts, and their parasites. Journal of Zoo and Wildlife Medicine 24(3):315-326.

Mackessy SP, Williams K, Ashton KG. 2003. Ontogenetic variation in venom composition and diet of *Crotalus oreganus concolor*: a case of venom paedomorphosis? Copeia 2003(4):769-782.

MacKinnon K, Wardojo W. 2001. ICDPs: Imperfect solutions for imperilled forests in South-East Asia. Parks 11(2):50-59.

Madani G, Nekaris KAI. 2014. Anaphylactic shock following the bite of a wild Kayan slow loris (*Nycticebus kayan*): implications for slow loris conservation. Journal of Venomous Animals and Toxins Including Tropical Diseases 20(1):43.

Malli H, Kuhn-Nentwig L, Imboden H, Nentwig W. 1999. Effects of size, motility and paralysation time of prey on the quantity of venom injected by the hunting spider *Cupiennius salei*. Journal of Experimental Biology 202(15):2083-2089.

Manley GH. 1966. Reproduction in lorisoid primates. Symposium of the Zoological Society of London 15:493-509.

Marliana SN, Ruehe F. 2012. Biodiversity of the Dieng Mountains ecosystem, Java, Indonesia: floristic composition of the vegetation and species richness of the mammalian and avifauna communities. In: Feit U, Korn H, editors. Treffpunkt Biologische Vielfalt XI. Bonn, Germany: Bundesamt fuer Naturschutz. p 31-38.

Marshall AG. 1977. Interrelationships between *Arixenia emu* (Dermaptera) and molossid bats and their ectoparasites in Malaysia. Ecological Entomology 2(4):285-291.

Martin CJ, Tidswell F. 1895. Observations on the femoral gland of *Ornithorhynchus* and its secretion; together with an experimental enquiry concerning its supposed toxic action. Proceedings of the Linnean Society of New South Wales 9:471-500.

Martin IG. 1981. Venom of the short-tailed shrew (*Blarina brevicauda*) as an insect immobilizing agent. Journal of Mammalogy 62(1):189-192.

Martin RD. 1990. Primate origins and evolution: a phylogenetic reconstruction. Princeton, NJ: University Press Princeton.

Maschwitz U, Dorow W, Buschinger A, Kalytta G. 2000. Social parasitism involving ants of different subfamilies: *Polyrhachis lama* (Formicinae) an obligatory inquiline of *Diacamma* sp. (Ponerinae) in Java. Insectes Sociaux 47(1):27-35.

Mauseth JD. 2014. Botany: an introduction to plant biology. Burlington, MA: Jones & Bartlett Publishers.

McGavin GC, McGavin G. 2001. Essential entomology: an order-by-order introduction. Oxford, UK: Oxford University Press.

McKinney ML. 2002. Urbanization, Biodiversity, and Conservation. The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. BioScience 52(10):883-890.

McKinney ML. 2008. Effects of urbanization on species richness: a review of plants and animals. Urban ecosystems 11(2):161-176.

Mebs D. 1999. Studies on biological and enzymatic activities of salivary glands from the European hedgehog (*Erinaceus europaeus*). Toxicon 37(11):1635-1638.

Meijaard E, Groves C. 2004. A taxonomic revision of the *Tragulus* mouse-deer (Artiodactyla). Zoological Journal of the Linnean Society 140(1):63-102.

Meiri S. 2005. Small carnivores on small islands. New data based on old skulls. Small Carnivore Conservation 33:21-23.

Melisch R, Asmoro P, Lubis I, Kusumawardhani L. 1996. Distribution and status of the Fishing Cat (*Prionailurus viverrinus rhizophoreus* Sody, 1936) in West Java, Indonesia (Mammalia: Carnivora: Felidae). Faunistische Abhandlungen Staatliches Museum für Tierkunde Dresden 20(17):311-319.

Melisch R, Asmoro PB, Kusumawardhani L. 1994. Major steps taken towards otter conservation in Indonesia. IUCN/SSC Otter Specialist Group Bulletin 10:21-24.

Méndez-Cárdenas MG, Zimmermann E. 2009. Duetting - a mechanism to strengthen pair bonds in a dispersed pair-living primate (*Lepilemur edwardsi*)? American Journal of Physical Anthropology 139(4):523-532.

Merritt JF. 1986. Winter survival adaptations of the short-tailed shrew (*Blarina brevicauda*) in an Appalachian montane forest. Journal of Mammalogy 67(3):450-464.

Michalski F, Norris D. 2011. Activity pattern of *Cuniculus paca* (Rodentia: Cuniculidae) in relation to lunar illumination and other abiotic variables in the southern Brazilian Amazon. Zoologia (Curitiba) 28(6):701-708.

Miettinen J, Shi C, Liew SC. 2011. Deforestation rates in insular Southeast Asia between 2000 and 2010. Global Change Biology 17(7):2261-2270.

Miller JC. 1993. Insect natural history, multi-species interactions and biodiversity in ecosystems. Biodiversity & Conservation 2(3):233-241.

Mittermeier RA, Rylands AB, Schwitzer C, Taylor LA, Chiozza F, Williamson EA. 2012. Primates in peril: the world's 25 most endangered primates 2010-2012. Arlington, VA: IUCN/SSC Primate Specialist Group (PSG), International Primatological Society (IPS), and Conservation International (CI).

Mittermeier RA, Wallis J, Rylands AB, Ganzhorn JU, Oates JF, Williamson EA, Palacios E, Heymann EW, Kierulff MCM, Yongcheng L, Supriatna J, Roos C, Walker S, Cortes-Ortiz L, Schwitzer C. 2009. Primate in peril: the world's 25 most endangered primates 2008-2010. Primate Conservation 24:1-57.

Mohamed A, Samejima H, Wilting A. 2009. Records of five Bornean cat species from Deramakot Forest Reserve in Sabah, Malaysia. Cat News 51:12-15.

Moore R. 2012. Ethics, ecology and evolution of Indonesian slow lorises (*Nycticebus* spp.) rescued from the pet trade. PhD thesis. Oxford, UK: Oxford Brookes University.

Moore RS. 2011. Sightings of Javan small-toothed palm civets *Arctogalidia trivirgata trilineata* on Gunung Salak, West Java, Indonesia. Small Carnivore Conservation 44:38-39.

Moore RS, Nekaris KAI, Eschmann C. 2010. Habitat use by western purple-faced langurs *Trachypithecus vetulus nestor* (Colobinae) in a fragmented suburban landscape. Endangered Species Research 12(3):227-234.

Moore RS, Wihermanto, Nekaris KAI. 2014. Compassionate conservation, rehabilitation and translocation of Indonesian slow lorises. Endangered Species Research DOI: 10.3354/esr00620.

Mueller AE, Thalmann URS. 2000. Origin and evolution of primate social organisation: a reconstruction. Biological Reviews 75(3):405-435.

Mueller EF. 1979. Energy metabolism, thermoregulation and water budget in the slow loris (*Nycticebus coucang*, Boddaert 1785). Comparative Biochemistry and Physiology Part A: Physiology 64(1):109-119.

Mueller AE. 1999. Aspects of social life in the fat tailed dwarf lemur (*Cheirogaleus medius*): inferences from body weights and trapping data. American Journal of Primatology 49(3):265-280.

Mueller AE. 1998. A preliminary report on the social organisation of *Cheirogaleus medius* (Cheirogaleidae; Primates) in North-West Madagascar. Folia Primatologica 69(3):160-166.

Munds RA, Ali R, Nijman V, Nekaris KAI, Goossens B. 2013b. Living together in the night: abundance and habitat use of sympatric and allopatric populations of slow lorises and tarsiers. Endangered Species Research 22:269-277.

Munds RA, Nekaris K, Ford SM. 2013a. Taxonomy of the Bornean slow loris, with new species *Nycticebus kayan* (Primates, Lorisidae). American Journal of Primatology 75(1):46-56.

Munene E, Otsyula M, Mbaabu D, Mutahi W, Muriuki S, Muchemi G. 1998. Helminth and protozoan gastrointestinal tract parasites in captive and wild-trapped African non-human primates. Veterinary Parasitology 78(3):195-201.

Munshi-South J. 2007. Extra-pair paternity and the evolution of testis size in a behaviorally monogamous tropical mammal, the large treeshrew (*Tupaia tana*). Behavioral Ecology and Sociobiology 62(2):201-212.

Murphy F, Murphy J. 2000. An introduction to the spiders of South East Asia. Kuala Lumpur, Malaysia: Malaysian Nature Society.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403(6772):853-858.

Nash LT. 2007. Moonlight and behavior in nocturnal and cathemeral primates, especially *Lepilemur leucopus*: illuminating possible anti-predator efforts. In: Gursky SL, Nekaris KAI, editors. Primate anti-predator strategies. New York: Springer. p 173-205.

Nash L, Gursky SL, Nekaris KAI. 2007. Moonlight and behavior in nocturnal and cathemeral primates, especially *Lepilemur leucopus*: illuminating possible anti-predator efforts. In: Gursky S, Nekaris KAI, editors. Primate anti-predator strategies. New York: Springer. p 173-205.

Nash LT. 1993. Juveniles in nongregarious primates. In: Pereira ME, Fairbanks LA, editors. Juvenile primates: life history, development, and behavior. Oxford, UK: Oxford University Press. p 119-137.

Nash LT, Burrows AM. 2010. Introduction: advances and remaining sticky issues in the understanding of exudativory in primates. In: Burrows AM, Nash LT, editors. The evolution of exudativory in primates. New York: Springer. p 1-24.

Nash LT, Harcourt CS. 1986. Social organization of galagos in Kenyan coastal forests: II. *Galago garnettii*. American Journal of Primatology 10(4):357-369.

Navarro-Montes A, Nekaris KAI, Parish TJ, Compton J, Shepherd C, Asia TE, Asia TS, Corner S, Aiwu J. 2009. Trade in Asian slow lorises (*Nycticebus*): using education workshops to counter an increase in illegal trade. Living Forests 15. Online: http://www.kfbglivingforests.org/content/issue15/feature1.php. Accessed 20 June 2014.

Nekaris KAI. 2014. Extreme primates: Ecology and evolution of Asian lorises. Evolutionary Anthropology: Issues, News, and Reviews 23(5):177-187.

Nekaris KAI, Bearder SK. 2011. The lorisiform primates of Asia and mainland Africa: diversity shrouded in darkness. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM, editors. Primates in perspective. Oxford, UK: Oxford University Press. p 34-54.

Nekaris KAI, Blackham GV, Nijman V. 2008. Conservation implications of low encounter rates of five nocturnal primate species (*Nycticebus* spp.) in Asia. Biodiversity and Conservation 17(4):733-747.

Nekaris KAI, Campbell N. 2012. Media attention promotes conservation of threatened Asian slow lorises. Oryx 46(2):169-170.

Nekaris KAI, Jaffe S. 2007. Unexpected diversity of slow lorises (*Nycticebus* spp.) within the Javan pet trade: implications for slow loris taxonomy. Contributions to Zoology 76(3):187-196.

Nekaris KAI, Jayewardene J. 2003. Pilot study and conservation status of the slender loris (*Loris tardigradus* and *Loris lydekkerianus*) in Sri Lanka. Primate Conservation 19:83-90.

Nekaris KAI, Moore RS, Rode J, Fry BG. 2013a. Mad, bad and dangerous to know: the biochemistry, ecology and evolution of slow loris venom. Journal of Venomous Animals and Toxins including Tropical Diseases 19(1):21.

Nekaris KAI, Munds R. 2010. Using facial markings to unmask diversity: the slow lorises (Primates: Lorisidae: *Nycticebus* spp.) of Indonesia. In: Gursky S, Supriatna J, editors. Indonesian Primates. New York: Springer. p 383-396.

Nekaris KAI, Nijman V. 2007. CITES proposal highlights rarity of Asian nocturnal primates (Lorisidae: *Nycticebus*). Folia Primatologica 78:211-214.

Nekaris KAI, Nijman V. 2008. Survey on the abundance and conservation of Sumatran slow lorises (*Nycticebus coucang hilleri*) in Aceh, Northern Sumatra. Folia Primatologica 79(5):365-365.

Nekaris KAI, Pambudi JAA, Susanto D, Ahmad RD, Nijman V. 2014a. Densities, distribution and detectability of a small nocturnal primate (Javan slow loris *Nycticebus javanicus*) in a montane rainforest. Endangered Species Research 24:95-103.

Nekaris KAI, Pimley ER, Ablard KM. 2007. Predator defense by slender lorises and pottos. In: Gursky SL, Nekaris KAI, editors. Primate anti-predator strategies. New York: Springer. p 222-240.

Nekaris KAI, Rode EJ, Nijman V. 2014b. Javan slow loris. In: Schwitzer C, Mittermeier RA, Rylands AB, Taylor LA, Chiozza F, Williamson EA, Wallis J., Clark FE., editors. Primates in peril: the world's 25 most endangered primates 2012-2014. Arlington, US: IUCN/SSC Primate Specialist Group (PSG), International Primatological Society (IPS), Conservation International (CI), and Bristol Zoological Society, p. 51-54.

Nekaris KAI, Sanchez KL, Thorn JS, Winarti I, Nijman V. 2009. Javan slow loris. In: Mittermeier RA, Wallis J, Rylands AB, Ganzhorn JU, Oates JF, Williamson EA, Palacios E, Heymann EW, Kierulff MCM, Yongcheng L, Supriatna J, Roos C, Walker S, Cortes-Ortiz L, Schwitzer C. et al., editors. Primates in peril: the world's 25 most endangered primates 2008–2010. Primate Conservation 24: 1-57. p 44-46.

Nekaris KAI, Shekelle M, Wirdateti, Rode EJ, Nijman V. 2013b. *Nycticebus javanicus.* IUCN Red List of Threatened Species. Version 2013.1. Online: www.iucnredlist.org. Accessed 1 March 2014.

Nekaris KAI, Campbell N, Coggins TG, Rode EJ, Nijman V. 2013c. Tickled to death: analysing public perceptions of 'cute' videos of threatened species (slow lorises - *Nycticebus* spp.) on Web 2.0 sites. PLoS ONE 8(7):e69215.

Nekaris KAI, Starr CR, Collins RL, Wilson A. 2010a. Comparative ecology of exudate feeding by lorises (*Nycticebus, Loris*) and pottos (*Perodicticus, Arctocebus*). In: Burrows AM, Nash LT, editors. The evolution of exudativory in primates. New York: Springer. p 155-168.

Nekaris KAI, Shepherd CR, Starr CR, Nijman V. 2010b. Exploring cultural drivers for wildlife trade via an ethnoprimatological approach: a case study of slender and slow lorises (*Loris* and *Nycticebus*) in South and Southeast Asia. American Journal of Primatology 72(10):877-886.

Nekaris KAI, Stevens NJ. 2007. Not all lorises are slow: rapid arboreal locomotion in *Loris tardigradus* of southwestern Sri Lanka. American Journal of Primatology 69(1):113-121.

Nekaris KAI. 2000. The socioecology of the Mysore slender loris (*Loris tardigradus lydekkerianus*) in Dindigul, Tamil Nadu, south India. PhD thesis. St. Louis: Washington University.

Nekaris KAI. 2001. Activity budget and positional behavior of the Mysore slender loris (*Loris tardigradus lydekkerianus*): implications for slow climbing locomotion. Folia Primatologica 72(4):228-241.

Nekaris KAI. 2003. Spacing system of the Mysore slender loris (*Loris lydekkerianus lydekkerianus*). American Journal of Physical Anthropology 121(1):86-96.

Nekaris KAI. 2012. Lethal loris. BBC Wildlife February:52-56.

Nettelbeck AR. 1997. Sightings of binturongs in the Khao Yai National Park, Thailand. Small Carnivore Conservation 16:22-24.

Nickle DA, Castner JL, Smedley SR, Attygalle AB, Meinwald J, Eisner T. 1996. Glandular Pyrazine emission by a tropical katydid: an example of chemical aposematism? (Orthoptera: Tettigoniidae: Copiphorinae: Vestria Stål). Journal of Orthoptera Research 5:221-223.

Nijman V. 2000. Geographic distribution of ebony leaf monkey *Trachypithecus auratus* (E. Geoffroy Saint-Hilaire, 1812) (Mammalia: Primates: Cercopithecidae). Contributions to Zoology 69(3):157-178.

Nijman V. 2006. In-situ and ex-situ status of the Javan gibbon and the role of zoos in conservation of the species. Contributions to Zoology 75(3/4):161-168.

Nijman V. 2010. An overview of international wildlife trade from Southeast Asia. Biodiversity and Conservation 19(4):1101-1114.

Nijman V. 2013. One hundred years of solitude: effects of long-term forest fragmentation on the primate community of Java, Indonesia. In: Marsh LK, Chapman CA, editors. Primates in fragments. New York: Springer. p 33-45.

Nijman V, Nekaris KAI. 2014. Traditions, taboos and trade in slow lorises in Sundanese communities in southern Java, Indonesia. Endangered Species Research DOI: 10.3354/esr00610.

Nijman V, Van Balen SB. 1998. A faunal survey of the Dieng Mountains, Central Java, Indonesia: distribution and conservation of endemic primate taxa. Oryx 32(2):145-156.

Nisani Z, Hayes WK. 2011. Defensive stinging by *Parabuthus transvaalicus* scorpions: risk assessment and venom metering. Animal Behaviour 81(3):627-633.

Nowack J, Wippich M, Mzilikazi N, Dausmann KH. 2013. Surviving the cold, dry period in Africa: behavioral adjustments as an alternative to heterothermy in the African lesser bushbaby (*Galago moholi*). International Journal of Primatology 34(1):49-64.

Nowack J, Mzilikazi N, Dausmann KH. 2010. Torpor on demand: heterothermy in the non-lemur primate *Galago moholi*. PLoS ONE 5(5):e10797.

Nowell K, Jackson P. 1996. Wild cats: status survey and conservation action plan. Gland, Switzerland; Cambridge, UK: IUCN/SSC Cat Specialist Group.

Nowinszky L. 2004. Nocturnal illumination and night flying insects. Applied Ecology and Environmental Research 2:17-52.

Nussinovitch A. 2009. Plant gum exudates of the world: sources, distribution, properties, and applications. Boca Raton, Florida: CRC Press.

O'Connell AF, Nichols JD, Karanth KU. 2011. Camera traps in animal ecology: methods and analyses. Tokyo: Springer.

O'Dea JD. 1990. The mammalian *Rete mirabile* and oxygen availability. Comparative Biochemistry and Physiology Part A: Physiology 95(1):23-25.

Olivera BM, Showers-Corneli P, Watkins M, Fedosov A. 2014. Biodiversity of cone snails and other venomous marine gastropods: evolutionary success through neuropharmacology. Annual Review of Animal Biosciences 2(1):487-513.

Opitz SEW, Müller C. 2009. Plant chemistry and insect sequestration. Chemoecology 19(3):117-154.

Orr CM, Delezene LK, Scott JE, Tocheri MW, Schwartz GT. 2007. The comparative method and the inference of venom-delivery systems in fossil mammals. Journal of Vertebrate Paleontology 27(2):541-546.

Orrock JL, Danielson BJ, Brinkerhoff RJ. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behavioral Ecology 15(3):433-437.

Osterberg P, Nekaris, KAI. 2015. The use of animals as photo propos to attract tourists in Thailand: a case Study of the slow loris *Nycticebus* spp. TRAFFIC Bulletin 27(1):13-18.

Packer C, Swanson A, Ikanda D, Kushnir H. 2011. Fear of darkness, the full moon and the nocturnal ecology of African lions. PloS ONE 6(7):e22285.

Pantel S, Chin SY. 2009. Proceedings of the workshop on trade and conservation of pangolins native to south and southeast Asia. Petaling Jaya, Selangor, Malaysia: TRAFFIC Southeast Asia.

Pawlak J, Mackessy SP, Fry BG, Bhatia M, Mourier G, Fruchart-Gaillard C, Servent D, Ménez R, Stura E, Ménez A. 2006. Denmotoxin, a three-finger toxin from the colubrid snake *Boiga dendrophila* (Mangrove Catsnake) with bird-specific activity. Journal of Biological Chemistry 281(39):29030-29041.

Pawlak J, Mackessy SP, Sixberry NM, Stura EA, Le Du MH, Ménez R, Foo CS, Ménez A, Nirthanan S, Kini RM. 2009. Irditoxin, a novel covalently linked heterodimeric three-finger toxin with high taxon-specific neurotoxicity. The FASEB Journal 23(2):534-545.

Payne J, Francis C, Phillipps K. 1985. A field guide to the mammals of Borneo. Kota Kinabalu, Kuala Lumpur, Malaysia: The Sabah Society.

Penteriani V, Kuparinen A, Delgado MdM, Lourenço R, Campioni L. 2011. Individual status, foraging effort and need for conspicuousness shape behavioural responses of a predator to moon phases. Animal Behaviour 82(2):413-420.

Pimley ER. 2002. The behavioural ecology and genetics of two nocturnal prosimians: pottos (*Perodicticus potto edwardsi*) and Allen's bushbabies (*Galago alleni cameronensis*). PhD thesis. Cambridge, UK: University of Cambridge.

Pimley ER, Bearder SK, Dixson AF. 2005. Home range analysis of *Perodicticus potto edwardsi* and *Sciurocheirus cameronensis*. International Journal of Primatology 26(1):191-206.

Plavcan JM, van Schaik CP. 1992. Intrasexual competition and canine dimorphism in anthropoid primates. American Journal of Physical Anthropology 87(4):461-477.

Pliosungneon M, Savani T. 2008. Spatial and feeding behavior of the endangered Bengal slow loris, *Nycticebus bengalensis* in Khao Angrunai Wildlife Sanctuary, Thailand. Report to: Primate Society of Great Britain.

Pliosungnoen M, Gale G, Savini T. 2010. Density and microhabitat use of Bengal slow loris in primary forest and non-native plantation forest. American Journal of Primatology 72(12):1108-1117.

Podgórski T, Bas G, Jedrzejewska B, Sönnichsen L, Sniezko S, Jedrzejewski W, Okarma H. 2013. Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under contrasting conditions of human pressure: primeval forest and metropolitan area. Journal of Mammalogy 94(1):109-119.

Porter LM, Garber PA, Nacimento E. 2009. Exudates as a fallback food for *Callimico goeldii*. American Journal of Primatology 71(2):120-129.

Pough FH. 1988. Mimicry of vertebrates: are the rules different? American Naturalist 131:S67-S102.

Powell RA. 2000. Animal home ranges and territories and home range estimators. In: Boitani L, Fuller TK, editors. Research techniques in animal ecology: controversies and consequences. New York: Columbia University Press. p 65-110.

Pozzi L, Hodgson LA, Burrell AS, Sterner KN, Raaum RL, Disotell TR. 2014. Primate phylogenetic relationships and divergence dates inferred from complete mitochondrial genomes. Molecular phylogenetics and evolution 75:165-183.

Price MV, Waser NM, Bass TA. 1984. Effects of moonlight on microhabitat use by desert rodents. Journal of Mammalogy 65(2):353-356.

Prugh LR, Golden CD. 2013. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. Journal of Animal Ecology 83(2):504-514.

Pucek M. 1968. Chemistry and pharmacology of insectivore venoms. In: Bucherl W, Buckley EAa, Deuloffen V, editors. Venomous animals and their venoms. New York: Academic Press. p 43-50.

Pullen SL. 2000. Behavioural and genetic studies of the mating system in a nocturnal primate: the lesser galago (*Galago moholi*). PhD thesis. Cambridge, UK: University of Cambridge.

Rabb GB. 1959. Toxic salivary glands in the primitive insectivore Solenodon. Natural History Miscellanea 170:1-3.

Radhakrishna S, Datta-Roy A, N. S, Sinha A. 2010. Population Survey of the Bengal Slow Loris, *Nycticebus bengalensis*, in Meghalaya, Northeast India. Primate Conservation 25:105-110.

Radhakrishna S, Goswami AB, Sinha A. 2006. Distribution and conservation of *Nycticebus bengalensis* in northeastern India. International Journal of Primatology 27(4):971-982.

Rajaratnam R, Sunquist M, Rajaratnam L, Ambu L. 2007. Diet and habitat selection of the leopard cat (*Prionailurus bengalensis borneoensis*) in an agricultural landscape in Sabah, Malaysian Borneo. Journal of Tropical Ecology 23(2):209-217.

Ramanankirahina R, Joly M, Zimmermann E. 2011. Peaceful primates: affiliation, aggression, and the question of female dominance in a nocturnal pair-living lemur (*Avahi occidentalis*). American Journal of Primatology 73(12):1261-1268.

Rasmussen DT. 1986. Life history and behavior of slow lorises and slender lorises: implications for the lorisine-galagine divergence. PhD thesis. Durham, NC.: Duke University.

Rasmussen DT, Izard MK. 1988. Scaling of growth and life history traits relative to body size, brain size, and metabolic rate in lorises and galagos (Lorisidae, Primates). American Journal of Physical Anthropology 75(3):357-367.

Rasmussen DT, Nekaris KA. 1998. Evolutionary history of lorisiform primates. Folia Primatologica 69(1):250-285.

Rasoloharijaona S, Randrianambinina B, Braune P, Zimmermann E. 2006. Loud calling, spacing, and cohesiveness in a nocturnal primate, the Milne Edwards' sportive lemur (*Lepilemur edwardsi*). American Journal of Physical Anthropology 129(4):591-600.

Reichard UH, Boesch C. 2003. Monogamy: mating strategies and partnerships in birds, humans and other mammals. Cambridge, UK: Cambridge University Press.

Reithinger V. 2013. Improving welfare and reintroduction schemes of rescued slow lorises (*Nycticebus* spp.). BSc internship report. Leeuwarden, the Netherlands: Applied University Van Hall Larenstein.

Rentz D. 2001. Tettigoniidae of Australia Volume 3: Listroscelidinae, Tympanophorinae, Meconematinae and Microtettigoniinae. Collingwood, Australia: CSIRO Publishing.

Ribble DO. 1991. The monogamous mating system of *Peromyscus californicus* as revealed by DNA fingerprinting. Behavioral Ecology and Sociobiology 29(3):161-166.

Riede K. 1997. Bioacoustic monitoring of insect communities in a Bornean rainforest canopy. In: Stork NE, Adis J, Didham RK, editors. Canopy Arthropods. London, UK: Chapman & Hall. p 442-452.

RISTEK. 2014. Indonesian Science and Technology Portal. Jakarta, Indonesia: Ministry of Research and Technology Republic of Indonesia. Online: http://international.ristek.go.id/. Accessed 20 June 2014.

Robinson MH, Lubin YD, Robinson B. 1974. Phenology, natural history and species diversity of web-building spiders on three transects at Wau, New Guinea. Pacific Insects 16:117-163.

Robson C. 2008. Java & Bali. Birdquest tour report. Online: http://www.birdquest-tours.com/Indonesia-Java-Bali-birding-tour-report/2008. Accessed 12 December 2013.

Rode EJ, Nekaris KAI. 2011. Ectoparasites and anting in lorises. Poster presentation. Primate Society of Great Britain Winter meeting, 1 December 2011. Bristol, UK.

Rode EJ, Nekaris KAI. 2012. Ectoparasites and anting in lorises. Primate Eye 104:19.

Rode EJ, Stengel CJ, Nekaris KAI. 2013a. Habitat assessment and species niche modeling. In: Sterling E, Bynum N, Blair M, editors. Primate ecology and conservation Oxford, UK: Oxford University Press. p 79-102.

Rode EJ, Nekaris KAI, Markolf M, Schliehe-Diecks S, Seiler M, Radespiel U, Schwitzer C. 2013b. Social organisation of the northern giant mouse lemur *Mirza zaza* in Sahamalaza, north western Madagascar, inferred from nest group composition and genetic relatedness. Contributions to Zoology 82:71-83.

Rodgers AR, Kie JG. 2011. HRT: Home Range Tools for ArcGIS. User's Manual. Ontario, Canada: Centre for Northern Forest Ecosystem Research.

Rogers LD, Nekaris KAI. 2011. Behaviour and habitat use of the Bengal slow loris *Nycticebus bengalensis* in the dry dipterocarp forests of Phnom Samkos Wildlife Sanctuary, Cambodia. Cambodian Journal of Natural History 2001(2):104-112.

Rondinini C, Doncaster CP. 2002. Roads as barriers to movement for hedgehogs. Functional Ecology 16(4):504-509.

Roos C. 2003. Molekulare Phylogenie der Halbaffen, Schlankaffen und Gibbons. PhD thesis. Munich, Germany: Technical University Munich.

Ross J, Hearn AJ, Macdonald DW. 2013. Recent camera-trap records of Malay Weasel *Mustela nudipes* in Sabah, Malaysian Borneo. Small Carnivore Conservation 49:20-24.

Rothschild M, Reichstein T, Von Euw J, Aplin R, Harman R. 1970. Toxic lepidoptera. Toxicon 8(4):293-296.

Runcie MJ. 2000. Biparental care and obligate monogamy in the rock-haunting possum, *Petropseudes dahli*, from tropical Australia. Animal Behaviour 59(5):1001-1008.

Rushton J, Pilling D, Heffernan C. 2002. A literature review of livestock diseases and their importance in the lives of poor people. In: Perry B, Randolph J, Madermott KS, Thornton P, editors. Investigation in animal health research to alleviate poverty. Nairobi, Kenya: International Livestock Research Institute. Appendix, 129 p.

Russell-Smith A, Stork NE. 1994. Abundance and diversity of spiders from the canopy of tropical rainforests with particular reference to Sulawesi, Indonesia. Journal of Tropical Ecology 10(4):545-558.

Rustam, Giordano AJ. 2014. Records of Sunda stink-badger *Mydaus javanensis* from Rajuk Forest, Malinau, North Kalimantan, Indonesia. Small Carnivore Conservation 50:74-76.

Ryckman RE, Bentley DG. 1979. Host reactions to bug bites (Hemiptera, Homoptera): a literature review and annotated bibliography. Part II. Californian Vector Views 26:29-45.

Saldaña-Vázquez RA, Munguía-Rosas MA. 2013. Lunar phobia in bats and its ecological correlates: a meta-analysis. Mammalian Biology - Zeitschrift für Saeugetierkunde 78(3):216-219.

Santiapillai C, Ramono WS. 1992. Status of the leopard (*Panthera pardus*) in Java, Indonesia. Tigerpaper 19(2):1-5.

Santiapillai C, Suprahman H. 1986. The proposed translocation of the Javan rhinoceros *Rhinoceros sondaicus*. Biological Conservation 38(1):11-19.

Santilli M, Moutinho P, Schwartzman S, Nepstad D, Curran L, Nobre C. 2005. Tropical deforestation and the Kyoto Protocol. Climatic Change 71(3):267-276.

Saporito RA, Donnelly MA, Norton RA, Garraffo HM, Spande TF, Daly JW. 2007. Oribatid mites as a major dietary source for alkaloids in poison frogs. Proceedings of the National Academy of Sciences 104(21):8885-8890.

Saporito RA, Donnelly MA, Spande TF, Garraffo HM. 2012. A review of chemical ecology in poison frogs. Chemoecology 22(3):159-168.

Saporito RA, Garraffo HM, Donnelly MA, Edwards AL, Longino JT, Daly JW. 2004. Formicine ants: an arthropod source for the pumiliotoxin alkaloids of dendrobatid poison frogs. Proceedings of the National Academy of Sciences of the United States of America 101(21):8045-8050.

Saporito RA, Spande TF, Garraffo HM, Donnelly MA. 2009. Arthropod alkaloids in poison frogs: a review of the dietary hypothesis. Heterocycles 79(1):277-297.

Schmid J. 2000. Daily torpor in the gray mouse lemur (*Microcebus murinus*) in Madagascar: energetic consequences and biological significance. Oecologia 123(2):175-183.

Schmid J, Kappeler PM. 1994. Sympatric mouse lemurs (*Microcebus* spp.) in western Madagascar. Folia Primatologica 63(3):162-170.

Schondube JE, Herrera-M LG, Martínez del Rio C. 2001. Diet and the evolution of digestion and renal function in phyllostomid bats. Zoology 104(1):59-73.

Schreiber A, Wirth R, Van Rompaey H. 1989. Weasels, civets, mongooses, and their relatives: an action plan for the conservation of mustelids and viverrids. Gland, Switzerland: IUCN.

Schuelke O, Kappeler PM. 2003. So near and yet so far: territorial pairs but low cohesion between pair partners in a nocturnal lemur, *Phaner furcifer*. Animal Behaviour 65(2):331-343.

Schuelke O, Kappeler PM, Zischler H. 2004. Small testes size despite high extra-pair paternity in the pair-living nocturnal primate *Phaner furcifer*. Behavioral Ecology and Sociobiology 55(3):293-301.

Schuelke O, Ostner J. 2007. Physiological ecology of cheirogaleid primates: variation in hibernation and torpor. Acta Ethologica 10(1):13-21.

Schulze H, Groves CP. 2004. Asian lorises: taxonomic problems caused by illegal trade. In: Nadler T, Streicher U, Thang LH, editors. Conservation of Primates in Vietnam. Frankfurt, Germany: Frankfurt Zoological Society. p 33-36.

Schwab D. 2000. A preliminary study of spatial distribution and mating system of pygmy mouse lemurs (*Microcebus cf myoxinus*). American Journal of Primatology 51(1):41-60.

Schwitzer C, Glatt L, Nekaris KAI, Ganzhorn JU. 2011. Responses of animals to habitat alteration: an overview focusing on primates. Endangered Species Research 14:31-38.

Schwitzer N, Clough D, Zahner H, Kaumanns W, Kappeler P, Schwitzer C. 2010a. Parasite prevalence in blue-eyed black lemurs *Eulemur flavifrons* in differently degraded forest fragments. Endangered Species Research 12:215–225.

Schwitzer C, Leus K, Byrne M, Lorca L, Yaxley M. 2010b. Feeding. In: Ruivo E, Carroll B, Demoulan A, editors. EAZA husbandry guidelines for callitrichidae. Amsterdam, the Netherlands: EAZA Executive Office. p 80-110.

Schwitzer C, Mittermeier RA, Rylands AB, Taylor LA, Chiozza F, Williamson EA, Wallis J., Clark FE. 2012. Primates in peril: the world's 25 most endangered primates 2012-2014. Arlington, US: IUCN/SSC Primate Specialist Group (PSG), International Primatological Society (IPS), Conservation International (CI), and Bristol Zoological Society.

Scordato ES, Dubay G, Drea CM. 2007. Chemical composition of scent marks in the ringtailed lemur (*Lemur catta*): glandular differences, seasonal variation, and individual signatures. Chemical senses 32(5):493-504.

Seaman DE, Griffith B, Powell RA. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26(1):95-100.

Seastedt TR, Crossley DA. 1984. The influence of arthropods on ecosystems. BioScience 34(3):157-161.

Seena CM, Thomas SK. 2013. Defensive glands of the darkling beetle *Mesomorphus villiger* Blanchard (Coleoptera: Tenebrionidae). Psyche: A Journal of Entomology DOI: 10.1155/2013/201769.

Seidensticker J, Syuono I. 1980. The Javan tiger and the Meru-Betiri Reserve: a plan for management. Gland, Switzerland: IUCN.

Sellers WI. 1996. A biomechanical investigation into the absence of leaping in the locomotor repertoire of the slender loris (*Loris tardigradus*). Folia Primatologica 67(1):1-14.

Selmer J. 1999. Culture shock in China? Adjustment pattern of western expatriate business managers. International Business Review 8(5):515-534.

Sémah A-M, Sémah F. 2012. The rain forest in Java through the Quaternary and its relationships with humans (adaptation, exploitation and impact on the forest). Quaternary International 249:120-128.

Semiadi G, Meijaard E. 2006. Declining populations of the Javan warty pig *Sus verrucosus*. Oryx 40(1):50-56.

Semple S, Cowlishaw G, Bennett PM. 2002. Immune system evolution among anthropoid primates: parasites, injuries and predators. Proceedings of the Royal Society of London Series B: Biological Sciences 269(1495):1031-1037.

Serena M. 1994. Use of time and space by platypus (*Ornithorhynchus anatinus*: Monotremata) along a Victorian stream. Journal of Zoology 232(1):117-131.

Shamoun-Baranes J, van Loon E, van Gasteren H, van Belle J, Bouten W, Buurma L. 2006. A comparitive analysis of the influence of weather on the flight altitudes of birds. Bulletin of the American Meteorological Society 87(1):47-61.

Shapiro LJ, Demes B, Cooper J. 2001. Lateral bending of the lumbar spine during quadrupedalism in strepsirhines. Journal of Human Evolution 40(3):231-259.

Shepherd CR. 2009. Overview of pangolin trade in southeast Asia. In: Pantel S, Chin SY, editors. Proceedings of the workshop on trade and conservation of pangolins native to south and southeast Asia. Petaling Jaya, Selangor, Malaysia: TRAFFIC Southeast Asia.

Shepherd CR. 2010. Illegal primate trade in Indonesia exemplified by surveys carried out over a decade in North Sumatra. Endangered Species Research 11(3):201-205.

Shepherd CR. 2012. Observations of small carnivores in Jakarta wildlife markets, Indonesia, with notes on trade in Javan Ferret Badger *Melogale orientalis* and on the increasing demand for Common Palm Civet *Paradoxurus hermaphroditus* for civet coffee production. Small Carnivore Conservation 47:38-41.

Shepherd CR. 2012. The owl trade in Jakarta, Indonesia: a spot check on the largest bird markets. BirdingASIA 18 58-59.

Shepherd CR, Sukumaran J, Wich SA, Asia TS. 2004. Open season: an analysis of the pet trade in Medan, Sumatra, 1997-2001. Kuala Lumpur, Malaysia: TRAFFIC Southeast Asia.

Sherratt TN. 2008. The evolution of Müllerian mimicry. Naturwissenschaften 95(8):681-695.

Siebert L, Simkin T, Kimberly P. 2010. Volcanoes of the world. Berkeley and Los Angeles, California: University of California Press.

Siswowidjoyo S, Sudarsono U, Wirakusumah AD. 1997. The threat of hazards in the Semeru volcano region in East Java, Indonesia. Journal of Asian Earth Sciences 15(2):185-194.

Sitprija V, Suteparak S. 2008. Animal toxins: an overview. Asian Biomedicine 2(6):451-457.

Sjare B, Stirling I. 1996. The breeding behavior of Atlantic walruses, *Odobenus rosmarus rosmarus*, in the Canadian High Arctic. Canadian Journal of Zoology 74(5):897-911.

Skutelsky O. 1996. Predation risk and state-dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus*. Animal Behaviour 52(1):49-57.

Smiet AC. 1990. Forest ecology on Java: conversion and usage in a historical perspective. Journal of Tropical Forest Science 2(4):286-302.

Smiet AC. 1992. Forest ecology on Java: human impact and vegetation of montane forest. Journal of Tropical Ecology 8(2):129-152.

Smit B, Boyles JG, Brigham RM, McKechnie AE. 2011. Torpor in dark times: patterns of heterothermy are associated with the lunar cycle in a nocturnal bird. Journal of Biological Rhythms 26(3):241-248.

Smith AC. 2010. Exudativory in primates: interspecific patterns. In: Burrows AM, Nash LT, editors. The evolution of exudativory in primates. New York: Springer. p 45-87.

Smith WL, Wheeler WC. 2006. Venom evolution widespread in fishes: a phylogenetic road map for the bioprospecting of piscine venoms. Journal of Heredity 97(3):206-217.

Sodhi NS, Koh LP, Brook BW, Ng PKL. 2004. Southeast Asian biodiversity: an impending disaster. Trends in Ecology & Evolution 19(12):654-660.

Sodhi NS, Posa MRC, Lee TM, Bickford D, Koh LP, Brook BW. 2010. The state and conservation of Southeast Asian biodiversity. Biodiversity and Conservation 19(2):317-328.

Sommer S. 2003. Social and reproductive monogamy in rodents: the case of the Malagasy giant jumping rat (*Hypogeomys antimena*). Cambridge, UK: Cambridge University Press.

Sotavalta O. 1947. The flight-tone (wing-stroke frequency) of insects. Acta Entomologica Fennica 4:1-117.

Southwood TRE, Henderson PA. 2009. Ecological methods. Oxford, UK: Blackwell.

Spruijt BM, Van Hooff JA, Gispen WH. 1992. Ethology and neurobiology of grooming behavior. Physiological Reviews 72(3):825-852.

Stankowich T. 2011. Armed and dangerous: predicting the presence and function of defensive weaponry in mammals. Adaptive Behavior 20(1):32-43.

Stankowich T, Blumstein DT. 2005. Fear in animals: a meta-analysis and review of risk assessment. Proceedings of the Royal Society B: Biological Sciences 272(1581):2627-2634.

Stankowich T, Caro T. 2009. Evolution of weaponry in female bovids. Proceedings of the Royal Society B: Biological Sciences 276(1677):4329-4334.

Starr C. 2011. The conservation and ecology of the pygmy slow loris (*Nycticebus pygmaeus*) in eastern Cambodia. PhD thesis. Brisbane, Australia: University of Queensland.

Starr C, Nekaris KAI. 2013. Obligate exudativory characterizes the diet of the pygmy slow loris *Nycticebus pygmaeus*. American Journal of Primatology 75(10):1054-1061.

Starr C, Nekaris KAI, Leung L. 2012. Hiding from the moonlight: luminosity and temperature affect activity of Asian nocturnal primates in a highly seasonal forest. PloS ONE 7(4):e36396.

Starr C, Nekaris KAI, Streicher U, Leung LKP. 2011. Field surveys of the Vulnerable pygmy slow loris *Nycticebus pygmaeus* using local knowledge in Mondulkiri Province, Cambodia. Oryx 45(1):135-142.

Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41(5):291-309.

Sterling EJ. 1993. Patterns of range use and social organization in aye-ayes (*Daubentonia madagascariensis)* on Nosy Mangabe. In: Kappeler PM, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum Press. p 1-9.

Sterling EJ. 1994. Evidence for nonseasonal reproduction in wild aye-ayes (*Daubentonia madagascariensis*). Folia Primatologica 62(1-3):46-53.

Sterling EJ, Nguyen N, Fashing PJ. 2000. Spatial patterning in nocturnal prosimians: a review of methods and relevance to studies of sociality. American Journal of Primatology 51:3-19.

Streicher U. 2004. Aspects of ecology and conservation of the pygmy loris *Nycticebus pygmaeus* in Vietnam. PhD thesis. Munich, Germany: Ludwig-Maximilian-Universität München.

Streicher U. 2009. Diet and feeding behaviour of pygmy lorises (*Nycticebus pygmaeus*) in Vietnam. Vietnamese Journal of Primatology 3:37-44.

Streicher U, Wilson A, Collins RL, Nekaris KAI. 2013. Exudates and animal prey characterize slow loris (*Nycticebus pygmaeus*, *N. coucang* and *N. javanicus*) diet in captivity and after release into the wild. In: Masters J, Gamba M, Génin F, editors. Leaping ahead. New York: Springer. p 165-172.

Stuart MD, Strier KB. 1995. Primates and parasites: a case for a multidisciplinary approach. International Journal of Primatology 15(5):577-593.

Su Su S, Sale J. 2007. Niche differentiation between Common Palm Civet *Paradoxurus hermaphroditus* and Small Indian Civet *Viverricula indica* in regenerating degraded forest, Myanmar. Small Carnivore Conservation 36:30-34.

Sulistyawati E, Rosleine D, Sungkar R, Gurnita. 2005. Struktur komunitas dan keanekaragaman tumbuhan di G. Papandayan. Conference presentation. Annual Meeting of the Association of Indonesian Plant Taxonomist, 18-19 November 2005. Universitas Pendidikan Indonesia, Bandung, Indonesia.

Sulistyawati E, Sungkar RM, Maryani E, Aribowo M, Rosleine D. 2006. The biodiversity of Mount Papandayan and the threats. International Interdisciplinary Conference in Volcano International Gathering, 4-10 September 2006. Yogyakarta, Indonesia.

Sulistyawati E, Ulumuddin YI, Zuhri M. 2008. Landuse change in Mount Papandayan: its associated impacts on biodiversity and carbon stock. International Conference of Environmental Research and Technology, 28-30 May 2008. Penang, Malaysia.

Sunquist ME, Sunquist FC. 2009. Family Felidae (cats). In: Wilson DE, Mittermeier RA, editors. Handbook of the mammals of the world - Volume 1 Carnivores. Barcelona: Lynx. p. 54–168

Supriatna J. 2006. Conservation programs for the endangered Javan gibbon (*Hylobates moloch*). Primate Conservation 21:155-162.

Sutherland WJ. 2006. Ecological census techniques: a handbook. Cambridge, UK: Cambridge University Press.

Sutherland-Smith M, Stalis I. 2001. Health. In: Fitch-Snyder H, Schulze H, Larson L, editors. Management of lorises in captivity. A husbandry manual for Asian lorisines. San Diego, UK: Center for Reproduction of Endangered Species (CRES) Zoological Society of San Diego.

Sutrisno H. 2010. The impact of human activities to dynamic of insect communities: a case study in Gunung Salak, West Java. HAYATI Journal of Biosciences 17(4):161.

Swapna N. 2008. Assessing the feeding ecology of the Bengal slow loris (*Nycticebus bengalensis*) in Trishna Wildlife Sanctuary, Tripura. MSc thesis. Bangalore, India: National Centre for Biological Sciences.

Swapna N, Gupta A, Radhakrishna S. 2008. Distribution survey of Bengal slow loris *Nycticebus bengalensis* in Tripura, northeastern India. Asian Primates 1(1):37-40.

Swapna N, Radhakrishna S, Gupta AK, Kumar A. 2010. Exudativory in the Bengal slow loris (*Nycticebus bengalensis*) in Trishna Wildlife Sanctuary, Tripura, Northeast India. American Journal of Primatology 72(2):113-121.

Takeshita F, Wada S. 2012. Morphological comparison of the second gnathopod in males of four *Caprellid* species (Amphipoda: Caprellidae). Journal of Crustacean Biology 32(4):673-676.

Tan CL, Drake JH. 2001. Evidence of tree gouging and exudate eating in pygmy slow lorises (*Nycticebus pygmaeus*). Folia Primatologica 72(1):37-39.

Tanaka L, Tanaka S. 1982. Rainfall and seasonal changes in arthropod abundance on a tropical oceanic island. Biotropica 14(2):114-123.

Tati-Subahar SS, Amasya AF, Choesin DN. 2007. Butterfly (Lepidoptera: Rhopalocera) distribution along an altitudinal gradient on Mount Tangkuban Parahu, West Java, Indonesia. The Raffles Bulletin of Zoology 55(1):175-178.

Taylor LR. 1963. Analysis of the effect of temperature on insects in flight. Journal of Animal Ecology 32(1):99-117.

Temple-Smith PD. 1973. Seasonal breeding biology of the platypus, *Ornithorhynchuasn atinus* Shaw 1799, with special reference to the male. PhD thesis. Canberra, Australia: Australian National University.

The Embassy of the Republic of Indonesia. 2014. Facts and Figures. Online: http://www.embassyofindonesia.org/wordpress/?page_id=494. Accessed 4 June 2014.

Thies W, Kalko EK, Schnitzler H-U. 2006. Influence of environment and resource availability on activity patterns of *Carollia castanea* (Phyllostomidae) in Panama. Journal of Mammalogy 87(2):331-338.

Thomas RM. 1998. MoonDV software. Moon version 1.

Thorn JS, Nijman V, Smith D, Nekaris KAI. 2009. Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). Diversity and Distributions 15(2):289-298.

Thorson JM, Morgan RA, Brown JS, Norman JE. 1998. Direct and indirect cues of predatory risk and patch use by fox squirrels and thirteen-lined ground squirrels. Behavioral Ecology 9(2):151-157.

Tigar BJ, Osborne PE. 1999. The influence of the lunar cycle on ground-dwelling invertebrates in an Arabian desert. Journal of Arid Environments 43(2):171-182.

Tiuria R, Primawidyawan A, Pangihutan J, Warsito J, Hariyadi A, Handayani S, Priosoeryanto B. 2006. Identification of endoparasites from faeces of Javan rhino (*Rhinoceros sondaicus*) in Ujung Kulon National Park, Indonesia. Asian Zoo and Wildlife Medicine Convention, 26-29 October 2006. Chulalongkam University, Bangkok, Thailand.

Tobias JA, Montgomerie R, Lyon BE. 2012. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. Philosophical Transactions of the Royal Society B: Biological Sciences 367(1600):2274-2293.

Tomasi TE. 1978. Function of venom in the short-tailed shrew, *Blarina brevicauda*. Journal of Mammalogy 59(4):852-854.

Topping C, Sunderland K. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. Journal of Applied Ecology 29(2):485-491.

Torres AFC, Quinet YP, Havt A, Rádis-Baptista G, Martins AMC. 2013. Molecular pharmacology and toxinology of venom from ants. An integrated view of the molecular recognition and toxinology. Analytical Procedures to Biomedical Applications DOI: 10.5772/53539.

Townes H. 1962. Design for a Malaise trap. Proceeding of the Entomological Society Washington 64(4):253-262.

Trent BK, Tucker ME, Lockard JS. 1977. Activity changes with illumination in slow loris *Nycticebus coucang*. Applied Animal Ethology 3(3):281-286.

Trillmich F, Mohren W. 1981. Effects of the lunar cycle on the Galapagos fur seal, *Arctocephalus galapagoensis*. Oecologia 48(1):85-92.

Tuggle BN, Beehler BA. 1984. The occurrence of *Pterygodermatites nycticebi* (Nematoda: Rictulariidae) in a captive slow loris, *Nycticebus coucang*. Proceedings of the Helminthological Society of Washington 51(1):162-163.

Tuttle MD, Ryan MJ. 1982. The role of synchronized calling, ambient light, and ambient noise, in anti-bat-predator behavior of a treefrog. Behavioral Ecology and Sociobiology 11(2):125-131.

UNESCO Institute for Statistics. 2013. International literacy data. Online: http://www.uis.unesco.org/literacy/Pages/data-release-map-2013.aspx. Accessed 20 June 2014.

Upham NS, Hafner JC. 2013. Do nocturnal rodents in the Great Basin Desert avoid moonlight? Journal of Mammalogy 94(1):59-72.

Utami SS, Van Hooff JA. 1997. Meat-eating by adult female Sumatran orangutans (*Pongo pygmæus abelii*). American Journal of Primatology 43(2):159-165.

Vahed K, Parker DJ. 2012. The evolution of large testes: sperm competition or male mating rate? Ethology 118(2):107-117.

van Balen SB, Nijman V, Prins H. 2000. The Javan hawk-eagle: misconceptions about rareness and threat. Biological Conservation 96(3):297-304.

van Bemmel AC. 1952. Contribution to the knowledge of the genera *Muntiacus* and *Arctogalidia* in the Indo-Chinese archipelago (Mammalia, Cervidae & Viverridae). Beaufortia 2(16):1-50.

van Rompaey H. 1993. The banded linsang. Small Carnivore Conservation 9:11-15.

van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley R, editors. Comparative socioecology: the behavioral ecology of humans and other mammals. Oxford, UK: Blackwell. p 195-218.

van Schaik CP, Griffiths M. 1996. Activity periods of Indonesian rain forest mammals. Biotropica 28(1):105-112.

van Vuren D. 1996. Ectoparasites, fitness, and social behaviour of yellow-bellied marmots. Ethology 102(4):686-694.

van Welzen PC, Parnell JAN, Slik JWF. 2011. Wallace's Line and plant distributions: two or three phytogeographical areas and where to group Java? Biological Journal of the Linnean Society 103(3):531-545.

Vasquez RA. 1994. Assessment of predation risk via illumination level: facultative central place foraging in the cricetid rodent *Phyllotis darwini*. Behavioral Ecology and Sociobiology 34(5):375-381.

Vickery WL, Bider JR. 1981. The influence of weather on rodent activity. Journal of Mammalogy 62(1):140-145.

Villalba JJ, Provenza FD. 2009. Learning and dietary choice in herbivores. Rangeland Ecology & Management 62(5):399-406.

Vinyard CJ, Wall CE, Williams SH, Hylander WL. 2003. Comparative functional analysis of skull morphology of tree-gouging primates. American Journal of Physical Anthropology 120:153-170.

Voigt CC, Schneeberger K, Voigt-Heucke SL, Lewanzik D. 2011. Rain increases the energy cost of bat flight. Biology Letters 7(5):793-795.

Voris HK. 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. Journal of Biogeography 27(5):1153-1167.

Voskamp A, Rode EJ, Coudrat CNZ, Wirdateti, Abinawanto, Wilson RJ, Nekaris KAI. 2014. Modelling the habitat use and distribution of the threatened Javan slow loris *Nycticebus javanicus*. Endangered Species Research 23:277-286.

Walker A. 1969. The locomotion of the lorises, with special reference to the potto. African Journal of Ecology 7(1):1-5.

Wallace AR. 1860. On the zoological geography of the Malay Archipelago. Journal of the Proceedings of the Linnean Society of London Zoology 4(16):172-184.

Wallbank BE, Waterhouse DF. 1970. The defensive secretions of *Polyzosteria* and related cockroaches. Journal of Insect Physiology 16(11):2081-2096.

Warren RD, Crompton RH. 1997. A comparative study of the ranging behaviour, activity rhythms and sociality of *Lepilemur edwardsi* (Primates, Lepilemuridae) and *Avahi occidentalis* (Primates, Indriidae) at Ampijoroa, Madagascar. Journal of Zoology 243(2):397-415.

Waser PM, Jones WT. 1983. Natal philopatry among solitary mammals. Quarterly Review of Biology 58(3):355-390.

Weidt A, Hagenah N, Randrianambinina B, Radespiel U, Zimmermann E. 2004. Social organization of the golden brown mouse lemur (*Microcebus ravelobensis*). American Journal of Physical Anthropology 123(1):40-51.

Weisenseel KA, Izard MK, Nash LT, Ange RL, Poorman-Allen P. 1998. A comparison of reproduction in two species of *Nycticebus*. Folia Primatologica 69(1):321-324.

Weldon J. 2004. Defensive anointing: extended chemical phenotype and unorthodox ecology. Chemoecology 14(1):1-4.

Wells M. 1999. Investing in biodiversity: a review of Indonesia's integrated conservation and development projects. Washington, DC: World Bank Publications.

Whitten T, Soeriaatmadja RE, Afiff SA. 1996. Ecology of Java & Bali. The ecology of Indonesia series 2. Singapore: Perplus Editions.

Whittington C, Belov K. 2007. Platypus venom: a review. Australian Mammalogy 29(1):57-62.

Whittow GG, Scammell CC, Manuel JK, Rand D, Leong M. 1977. Temperature regulation in a hypometabolic primate, the slow loris (*Nycticebus coucang*). Archives of Physiology and Biochemistry 85(1):139-151.

Wiens F. 2002. Behavior and ecology of wild slow lorises (*Nycticebus coucang*): social organization, infant care system, and diet. PhD thesis. Bayreuth, Germany: University of Bayreuth.

Wiens F, Zitzmann A. 1999. Predation on a wild slow loris (*Nycticebus coucang*) by a reticulated python (*Python reticulatus*). Folia Primatology 70:362-364.

Wiens F, Zitzmann A. 2003. Social structure of the solitary slow loris *Nycticebus coucang* (Lorisidae). Journal of Zoology 261(1):35-46.

Wiens F, Zitzmann A, Hussein NA. 2006. Fast food for slow lorises: is low metabolism related to secondary compounds in high-energy plant diet? Journal of Mammalogy 87(4):790-798.

Wilde H. 1972. Anaphylactic shock following bite by a 'slow loris', *Nycticebus coucang*. The American Journal of Tropical Medicine and Hygiene 21(5):592.

Willcox DHA, Tran QP, Vu L, Tran VB, Hoang MD. 2012. Small-toothed Palm Civet *Arctogalidia trivirgata* records from human-influenced habitats in Vietnam. Small Carnivore Conservation 47:46-53.

Williams BL, Brodie Jr ED, Brodie III ED. 2003. Coevolution of deadly toxins and predator resistance: self-assessment of resistance by garter snakes leads to behavioral rejection of toxic newt prey. Herpetologica 59(2):155-163.

Williams C. 1940. An analysis of four years of insects in a light trap. Part II. The effect of weather conditions on insect activity; and the estimation and forecasting of changes in the insect populations. Transactions of the Royal Entomological Society of London 90(8):227-306.

Wilting A, Samejima H, Mohamed A. 2010. Diversity of Bornean viverrids and other small carnivores in Deramakot Forest Reserve, Sabah, Malaysia. Small Carnivore Conservation 42:10-13.

Winarti I. 2003. Distribusi dan struktur vegetasi habitat kukang (*Nycticebus coucang* Boddaert, 1785) di desa Marga Mekar, kecamatan Sumedang selatan, Sumedang, Jawa Barat. BSc thesis. Bandung, Indonesia: Universitas Padjadjaran.

Winarti I. 2008. Field research on Javan slow loris' population in Sukakerta Ciamis and Kawungsari Tasikmalaya, West Java, Indonesia. Report to International Animal Rescue Indonesia. Bogor, Indonesia.

Winarti I. 2011. Habitat, populasi, dan seberan kukang Jawa (*Nycticebus javanicus* Geoffroy 1812) di talun Tasikmalaya dan Ciamis, Jawa Barat. MSc thesis. Bogor, Indonesia: Institut Pertanian Bogor.

Wirdateti. 2012. Sebarandan habitat kukang jawa (*Nycticebus javanicus*) di perkebunan sayur Gunung papandayan, Kabupaten Garut. Berita Biologi 11:113-120.

Wirdateti, Okayama T, Kurniati H. 2006. Genetic diversity of slow loris (*Nycticebus coucang*) based on mitochondrial DNA. Tropics 15(4):377-381.

Wolda H. 1977. Fluctuations in abundance of some Homoptera in a neotropical forest. Geo-Eco-Trop 3:229-257.

Wolda H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. Journal of Animal Ecology 47:369-381.

Wong ESW, Belov K. 2012. Venom evolution through gene duplications. Gene 496(1):1-7.

Wong ESW, Nicol S, Warren WC, Belov K. 2013. Echidna venom gland transcriptome provides insights into the evolution of monotreme venom. PloS ONE 8(11):e79092.

Woods CP, Brigham RM. 2008. Common poorwill activity and calling behavior in relation to moonlight and predation. The Wilson Journal of Ornithology 120(3):505-512.

World Health Organization. 2013. Life expectancy: life expectancy data by country Online: http://apps.who.int/gho/data/node.main.688. Accessed 20 June 2014.

World Weather Online. 2014. Bandung Monthly Climate Average, Indonesia. Online: http://www.worldweatheronline.com/. Accessed 25 June 2014.

Worldbank. 2014. Population density. Online: http://data.worldbank.org/indicator/EN.POP.DNST. Accessed 20 June 2014.

Wright PC, Arrigo-Nelson SJ, Hogg KL, Bannon B, Morelli TL, Wyatt J, Harivelo AL, Ratelolahy F, Huffman MA, Chapman CA. 2009. Habitat disturbance and seasonal fluctuations of lemur parasites in the rain forest of Ranomafana National Park, Madagascar. In: Chapman C, Huffman MA, editors. Primate parasite ecology The dynamics and study of host-parasite relationships. Cambridge, UK: Cambridge University Press. p 311-330.

Xiao C, Wang Z, Zhu W, Chu Y, Liu C, Jia T, Meng L, Cai J. 2010. Energy metabolism and thermoregulation in pygmy lorises (*Nycticebus pygmaeus*) from Yunnan Daweishan Nature Reserve. Acta Ecologica Sinica 30(3):129-134.

Yanoviak S, Kaspari M. 2000. Community structure and the habitat templet: ants in the tropical forest canopy and litter. Oikos 89(2):259-266.

Yepez P, De La Torre S, Snowdon CT. 2005. Interpopulation differences in exudate feeding of pygmy marmosets in Ecuadorian Amazonia. American Journal of Primatology 66(2):145-158.

Yossa I, Navy P, Dolly P, Yudha N, Aswar, Yosias M. 1991. Survey of the carnivores of Gunung Halimun nature reserve, Java. Small Carnivore Conservation 5:3.

Young BA, Zahn K. 2001. Venom flow in rattlesnakes: mechanics and metering. Journal of Experimental Biology 204(24):4345-4351.

Zhou J, Wei F, Li M, Zhang J, Wang D, Pan R. 2005. Hainan black-crested gibbon is headed for extinction. International Journal of Primatology 26(2):453-465.

Zimmermann E. 1985. Vocalizations and associated behaviours in adult slow loris (*Nycticebus coucang*). Folia Primatologica 44(1):52-64.

Zimmermann E. 1989. Reproduction, physical growth and behavioral development in slow loris (*Nycticebus coucang*, Lorisidae). Human Evolution 4(2):171-179.

Zimmermann E. 1995a. Acoustic communication in nocturnal prosimians. In: Alterman L, Doyle GA, Izard MK, editors. Creatures of the dark: the nocturnal prosimians. New York: Plenum Press. p 311-330.

Zimmermann E. 1995b. Loud calls in nocturnal prosimians: structure, evolution and ontogeny. In: Zimmermann E, Newman JD, Jürgens U, editors. Current topics in primate vocal communication. New York: Plenum Press. p 47-72.

Zimmermann E. 2009. Vocal expression of emotion in a nocturnal prosimian primate group, mouse lemurs. In: Brudzynski SM, editor. Handbook of Mammalian Vocalization. Oxford, UK: Academic Express. p 215-225.

Zimmermann E. 2013. Primate serenades: call variation, species diversity, and adaptation in nocturnal strepsirhines. In: Masters J, Gamba M, Génin F, editors. Leaping Ahead. New York: Springer. p 287-295.

Zimmermann E, Bearder SK, Doyle GA, Andersson AB. 1988. Variations in vocal patterns of Senegal and South African lesser bushbabies and their implications for taxonomic relationships. Folia Primatologica 51(2-3):87-105.

Zinner D, Hilgartner RD, Kappeler PM, Pietsch T, Ganzhorn JU. 2003. Social organization of *Lepilemur ruficaudatus*. International Journal of Primatology 24(4):869-888.

Zuhri M, Sulistyawati E. 2007. Pengelolaan Perlindungan Cagar Alam Gunung Papandayan. Protection management of Mount Papandayan Nature Reserve Presented on Seminar Nasional Penelitian Lingkungan di Perguruan Tinggi, 20 June 2007. Jakarta, Indonesia.

APPENDICES

APPENDIX 1
Permit application process

Pre-arrival procedure

All foreign researchers conducting research in Indonesia need an official counterpart in an Indonesian Institution. In my case this was Mrs. Wirdateti, a senior researcher from the Indonesian Institute of Sciences LIPI (*Lembaga Ilmu Pengetahuan Indonesia*), Bogor. The research permit is called SIP (*Surat Izin Penelitian*), but is also known as RISTEK permit (*Riset dan Teknologi* = Research and Technology). The researcher needs to apply for it at the State Ministry of Research and Technology in Jakarta (Ministry of RISTEK = *Kementerian Riset dan Teknologi Republik Indonesia*) before going to Indonesia (Figure 9.1). Since online applications are possible, the pre-arrival application process is relatively straightforward. The documents currently required for the initial application for the RISTEK permit are listed on the RISTEK website (RISTEK 2014) but the list may be subject to change. In fortnightly meetings the decision whether the RISTEK permit application is accepted or not are taken by a RISTEK coordinating team. Results are published online. After the final approval letter is sent to the Indonesian embassy of the researcher's country the researcher can then apply for his visa. Researchers need to be aware that applications can be postponed. Due to the amount of documents needed, possible delays in the process, the possibility that research permit applications may be postponed, and the additional time needed for the visa application after the research approval has been sent by the embassy, the researcher should allow sufficient time from starting preparations to receiving the research approval and visa (c. 2 months).

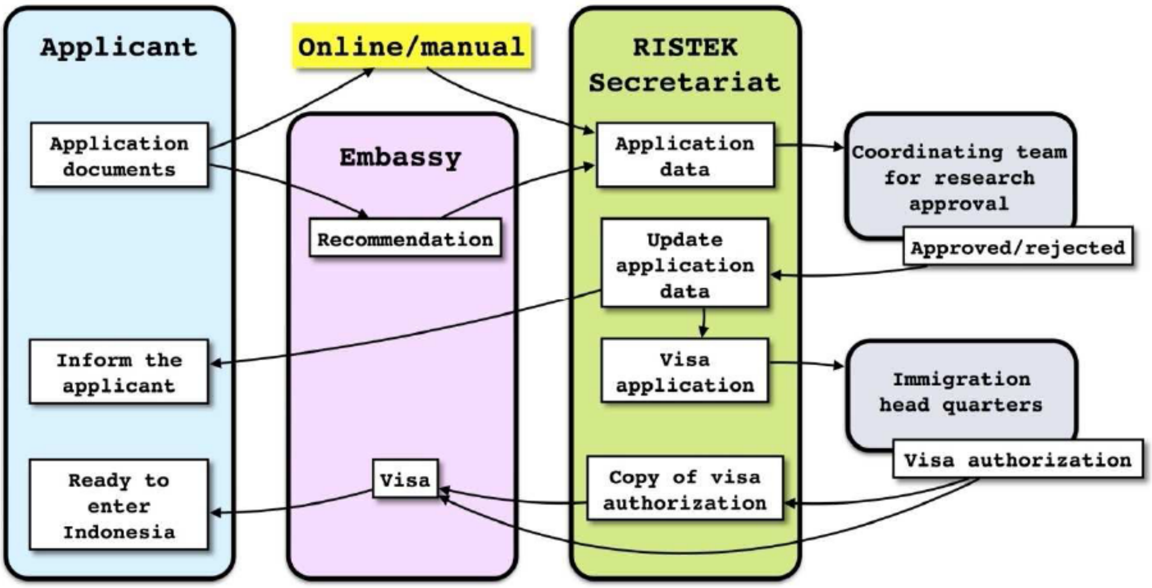


Figure 9.1: Procedure of the research permit application before travelling to Indonesia (RISTEK 2014)

Post-arrival procedure

Before starting the research in Indonesia and upon arrival in Jakarta, the researcher needs to apply for and process several permits and documents (Figure 9.2). These include the following documents:

- **SIP** including a research permit card from the RISTEK office
- Travel Permit from the police office (**SKJ** = *Surat Keterangan Jalan*)
- Police Registration Card from the police office (**SKLD** = *Surat Keterangan Lapor Diri*)[1]
- Limited Stay Residency Permit from the Immigration Office (**KITAS** = *Kartu Izin Tinggal Terbatas*)
- Entrance Permit for Protected Areas (**SIMAKSI** = *Surat Izin Masuk Kawasan Konservasi*) from the office of the office of Forest Protection and Nature Conservation
- Recommendation letter (**SPP central** = *Surat Pemberitahuan Peneliti*) from the Ministry of Home Affairs, needed for the application for a Research Notification Letter at provincial level, and finally presented to the local authorities at the research site

For each application step personal documents (e.g. passport) and recommendation letters from the research counterpart institute and RISTEK office are needed. The application procedure requires visits at the ministry of RISTEK, the National Police Headquarter (*Mabes Polri*), the Indonesian Immigration office (*Direktorat Jenderal Imigrasi – Kantor Imigrasi*), the Ministry of Internal Affairs (*Departement Dalam Negeri*) and the office of Forest Protection and Nature Conservation (PHKA = *Perlindungan Hutan dan Konservasi Alam*) located at the Ministry of Forestry (*Kemenhut = Kementerian kehutanan*). Descriptions of the exact process and costs can be found on the internet (RISTEK 2014). The procedure is complicated and time consuming (c. 1 week). Although it can be done alone or might already be facilitated by larger research institutes, universities or NGOs, it is advisable to request the facilitation service by an agent (such as the company LAHUKA) who leads the researcher through the process, just requiring the actual presence of the researcher during the first day, while final documents can be sent to the field site by the facilitator. The permit documents should be kept safe at the research site, be kept at hand when travelling to different research sites, and the police card and RISTEK card should be taken everywhere if possible.

---

[1] New information from June 2014 indicates that SKLD has been abolished by the police

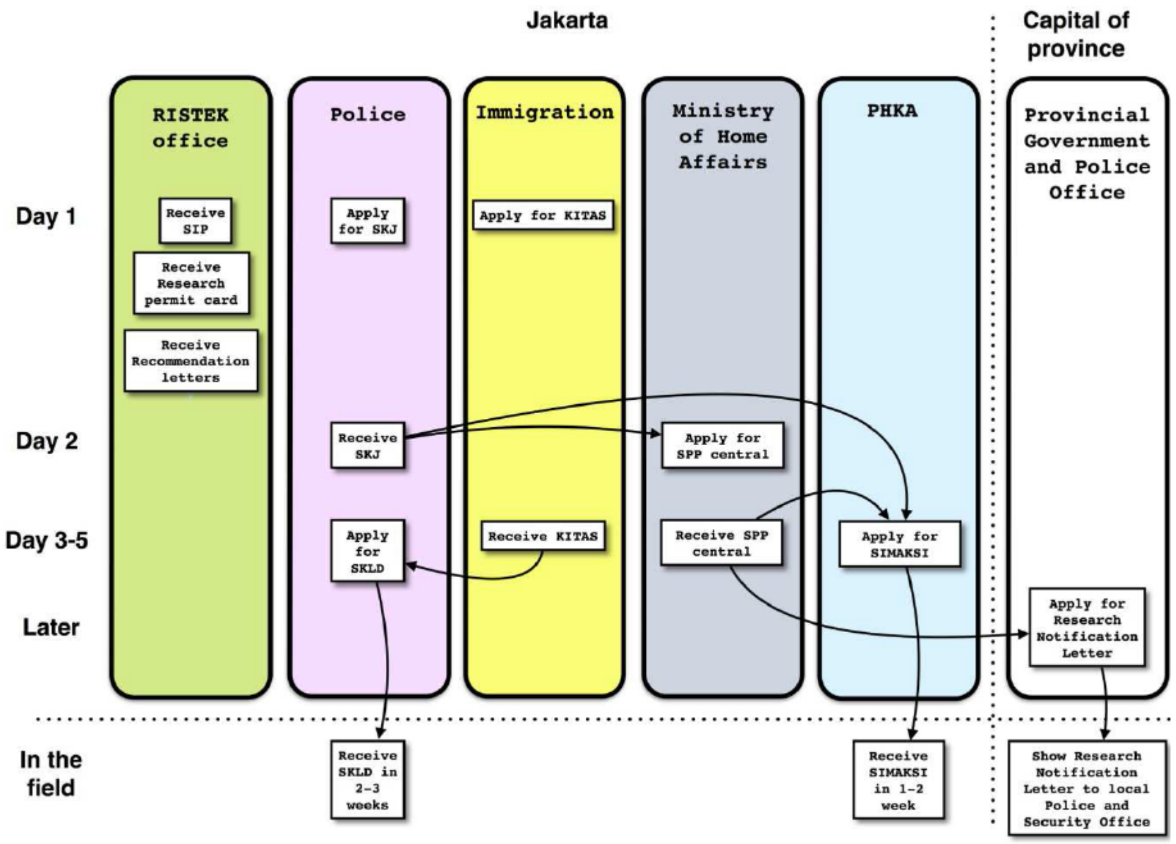


Figure 9.2: Overview of documents needed, offices to be visited and time required for the post-arrival procedure in Indonesia. The documents received from the RISTEK office are needed for all further document applications (no arrows to avoid confusion). After SKJ, SPP and KITAS are received these documents must be presented back to the RISTEK office (RISTEK 2014). Abbreviations see in main text

During and after field work

Upon arrival at the research site, the researcher should report to the Provincial Government Office (*Badan Kesbang Linmas Provinsi*) and the Provincial Police Headquarters to receive the Research Notification Letter for the local authorities; and finally at the village chief (*Kepala Desa*), the local Police and Security Office (Figure 9.2). During the research period, every three months a progress report has to be sent to the research counterpart and the RISTEK office. The report follows a predetermined structure including problems encountered and planned activities for the next three months (RISTEK 2014). When the researcher has finished the project, he needs to apply for an Exit Permit Only (EPO) before leaving the country. This is only necessary if the research lasted longer than 6 months. A tentative final report has to be submitted at the same time, and preferably be sent to the research counterpart before submitting to the RISTEK office.

Export permit

After the arrival in Jakarta the researcher who wants to collect samples in the field has to apply for the Collection Permit (*Surat Keputusan/SK AMBIL*) to PHKA (Figure 9.3). As the application documents for the Collection Permit include the RISTEK permit and SIMAKSI, the application is linked to the RISTEK permit application and can be done at the same time. The process takes one month. While waiting the researcher can already travel to the field and prepare the research. The Collection

Permit is only valid for 3 months and needs to be renewed regularly. It also determines the exact number of samples that can be collected. For the transfer of samples within Indonesia or abroad, further documents are needed. First a BAP stock (*Berita Acara Pemeriksaan Stock*) must be issued by the local Natural Resources Conservation Office (BKSDA = *Balai Konservasi Sumber Daya Alam*) or National Park office if the researcher collects the samples from inside a PA. The BAP stock is an investigation report by the officers of the respective authority who will visit to the field site and inspect and document the samples. If samples are transferred only within Indonesia (e.g. for analysis at the Indonesian research counterpart institute) only a Within Country Transport Permit for Wild Fauna and Flora (SAT-DN = *Surat Angkut Tumbuhan dan Satwa liar - Dalam Negeri*) is needed. It is usually issued by the regional BKSDA (BBKSDA = *Balai Besar Konservasi Sumber Daya Alam*), but the responsibility depends on what office supervises the research site.

If the samples are to be analysed abroad, additionally to the SAT-DN, first an Indonesian export permit or Export Decree Letter (SK Kirim = *Surat Keputusan Kirim*) is needed, applied for at the directorate general of PHKA with a copy to the directorate of Biodiversity and Conservation (KKH = *Konservasi Keanekaragaman Hayati*) at the Ministry of Forestry. The SK Kirim must then be sent to the country of destination to apply for the CITES import permit. Together with the import permit and all the documents above, the researcher finally has to apply for the CITES export permit (SAT-LN = *Surat Izin Angkut Tumbuhan dan Satwa Liar*) at KKH. For each step, the previously received permits, the RISTEK permit, various letters and agreements with the research counterpart and different forms are required. The documents ultimately needed for the final export from Indonesia are the collection permit, the Indonesian export permit and the CITES export permit.

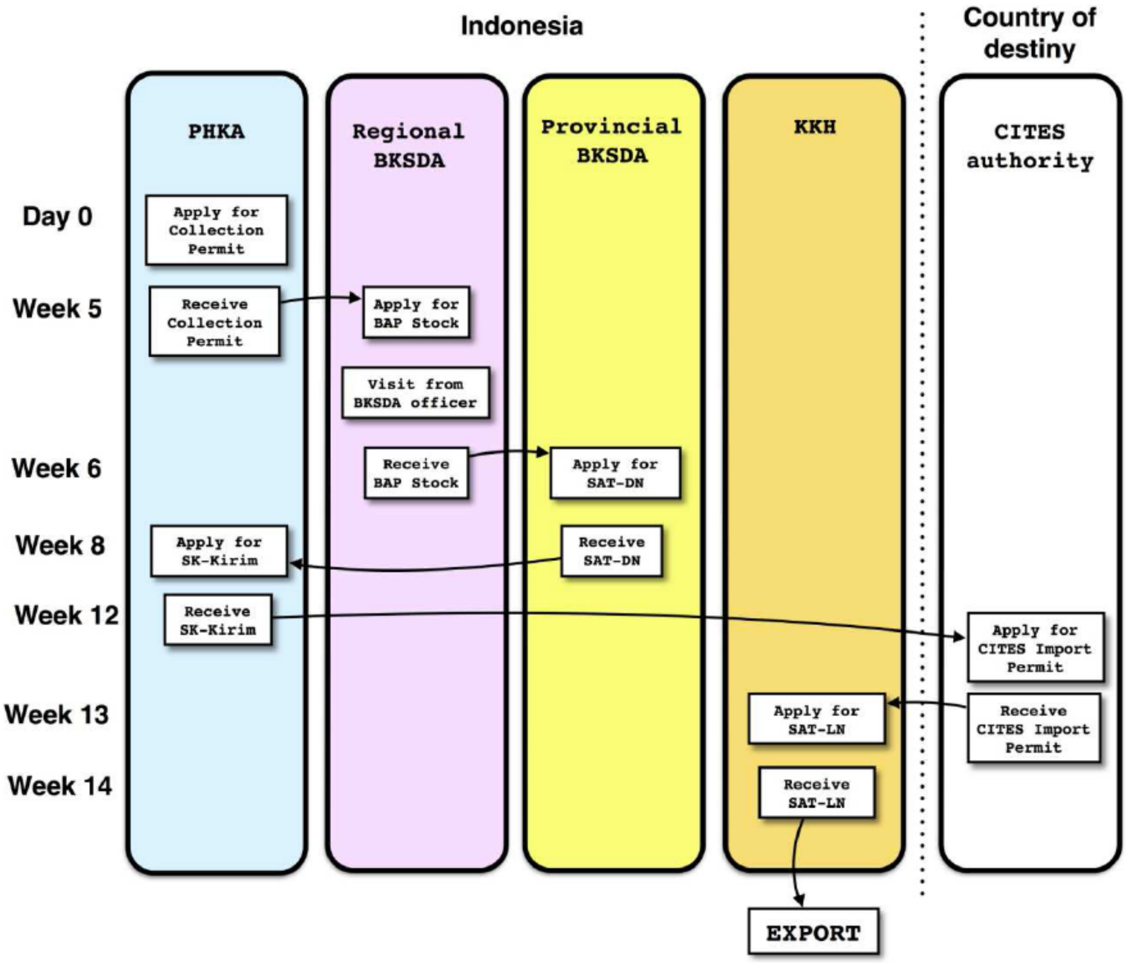


Figure 9.3: Overview of the procedure of applying for an export permit for biological samples in Indonesia. Documents required, authorities to be visited and approximate time required for the different steps are indicated.

Documents needed for the export permit application are:

Documents needed for Collecting Permit:

1. Formal request from the researcher
2. Formal request and recommendation letter from the research counterpart
3. Copy of RISTEK permit /SIP from RISTEK
4. SIMAKSI
5. Research proposal

Documents needed for SAT-DN:

1. All the above
2. Copy of Collection Permit
3. Copy of BAP stock/Investigation letter

Documents needed for SK-Kirim

1. All the above

2. Export form (form C; from PHKA or KSDA)
3. Material Transfer Agreement between related parties (foreign researcher and Indonesian research counterpart)

Documents needed for SAT-LN

1. Copy of SK-Kirim
2. CITES import permit of country of destination

Further problems that may arise during application are confusion between the American and British spelling of dates (better spell out months) and not matching numbers of samples in different letters. If the initial researcher has already left the country, recommendation letters may need to be amended to another name, or authority letters issued.

As evidenced in CHAPTER 5, the Indonesian protection status and the CITES listing on Appendix I do not always match up. In cases where the samples stem from a species that is protected according to Indonesian law, but not on CITES Appendix I, or not protected according to Indonesian law, but listed on CITES Appendix I, documents needed for the export varies and must be discussed with the relevant national authorities.

APPENDIX 2
Information about study sites

Study sites across Java, Indonesia, 2012 to 2014: location, habitat(s), altitudinal range and spotlight transect effort. Total study effort was 126.9 km. Grey shading indicates protected areas, white shading unprotected study sites. The asterisk indicates Cipaganti that was a survey site, but also long-term study site. The altitude range is that surveyed, not necessarily the total of the protected area or other land unit.

Survey site	Location	Regency, province	Habitat(s)	Altitude (m)	Effort (km)
Ujung Kulon National Park	Tamanjaya	Pandeglang, Banten	Secondary forest	0–110	1.8
Carita Nature Recreation Park	Carita	Pandeglang , Banten	Forest plantation	20–220	3.1
Mount Gede Pangrango National Park	Bodogol, Cibodas	Sukabumi / Bogor / Cianjur, West Java	Secondary forest	800–860, 1,150–1,170, 1,370–1,580	18.7
Limbangan	Mount Masgit Kareumbi Game Reserve	Tasikmalaya, West Java	Secondary forest	810–850	2.8
Dieng Plateau, Telaga Sumurup Strict Nature Reserve	Sokokembang	Wonosobo, Central Java	Secondary forest	600–670	5.1
Bromo-Tengger Semeru National Park	Pronojiwo; Mount Bromo	Malang, East Java	Secondary forest	760–910	6.0
Alas Purwo National Park	Rowobendo, Sadengan, Sumurtrong	Banyuwangi, East Java	Forest plantation (teak), secondary forest	10–110	15.4
Meru Betiri National Park	Bandealit, Sumber Salak, Rajegwesi, Sukamade	Banyuwangi, East Java	Late stage secondary forest	10–170	29.2

Survey site	Location	Regency, province	Habitat(s)	Altitude (m)	Effort (km)
Ijen Plateau Strict Nature Reserve / unprotected	Kawah Ijen, Ceding, Kalisat, Sidomulyo	Bondowoso / Jember, East Java	Agricultural area/forest plantation	650–1,740	10.0
Cimungkat	Southeast boarder of Mount Gede Pangrango NP	Cianjur, West Java	Late stage secondary forest	1,150–1,170	3.1
Cipaganti	Mount Papandayan	Garut, West Java	Agricultural area	1,350–1,560	8.9*
Pangalengan	Mount Papandayan	Garut, West Java	Agricultural area	1,690–1,850	Fixed point surveys
Sumedang	Sumedang	Sumedang, West Java	Forest plantation	560–690	7.6
Tasikmalaya	Bantarkalong, Ciamis, Raksajaya	Ciamis / Tasikmalaya, West Java	Agricultural area/ Forest plantation	420–850	15.2

APPENDIX 3
Ethogram for Javan slow lorises

Ethogram for Javan slow lorises, based on observations in this study and from Nekaris (2001), Fitch-Snyder et al. (2001) and Daschbach et al. (1983)

	Behaviour	Definition
1	Alert	Remain stationary like in “rest” but active observation of environment or observer
2	Feed	Actual consumption of a food item
3	Forage	Movement associated with looking for food (often includes visual and olfactory searching)
4	Freeze	Interrupt locomotion to maintain motionless, rigid posture in standing or sitting position for at least three seconds, extremely slow movement not associated with foraging
5	Groom	Autogroom, lick or use tooth comb on own fur
6	Rest	Remain stationary, often with body hunched, eyes open
7	Sleep	Remain stationary in huddled position with head between the knees, or eyes visible but closed
8	Social	All interactions with conspecifics, including aggression, allogrooming, play and other social behaviours
8a	Aggression	Fight, bite (including attempts), threat, chasing; often accompanied by agonistic vocalizations
8b	Allogroom	Lick or comb with toothcomb other loris’ face or fur - usually while clasping him or her
8c	Play	Behaviours serving no immediate, definable purpose, including friendly attempted bites or manual attacks and clasping, dangle by feet, wriggle body with arms over head. No vocalizations as when fighting.
8d	Other social	Social activity while being in contact or close proximity (<5 m), like mating, social follow, sniffing, social explore
9	Travel	Continuous, directed movement from one location to another
10	Other	Other behaviours not included above

APPENDIX 4
Basic morphology, behaviour and ecology data for Javan slow loris

1. Morphology

Research question:	What are morphometric characteristics of Javan slow lorises? Are there differences between sexes?
Methods:	Only adult individuals, descriptive statistics (body weight, head body length and testicle measurements see CHAPTER 5), independent samples t-tests (data normally distributed)
Results:	Table 9.1. No sexual differences detected in any of the variables (statistics not shown).

Table 9.1: Morphological measurements of Javan slow lorises in Cipaganti

Variable (mm)	Males		Female		Both sexes	
	Mean ± sd	Valid N	Mean ± sd	Valid N	Mean ± sd	Valid N
Head length	52.5 ± 8.7	12	51.9 ± 5.3	16	52.1 ± 6.8	28
Head width	48.2 ± 8.4	12	45.8 ± 4.0	16	46.8 ± 6.2	28
Muzzle length	17.8 ± 3.1	11	16.5 ± 2.3	17	17.0 ± 2.7	28
Ear width	10.3 ± 1.4	12	11.0 ± 2.3	17	10.7 ± 2.0	29
Ear length	19.2 ± 3.1	12	19.0 ± 2.4	17	19.1 ± 2.6	29
Neck girth (cm)	13.7 ± 2.5	5	15.5 ± 2.6	11	14.9 ± 2.6	16
Chest girth (cm)	18.8 ± 0.7	14	18.8 ± 0.7	21	18.8 ± 0.7	35
Hand span	59.4 ± 5.9	10	56.9 ± 3.8	17	57.8 ± 4.7	27
Foot span	71.3 ± 7.8	11	72.3 ± 6.5	17	71.9 ± 7.0	28
Tibia	88.0 ± 8.4	11	84.1 ± 10.6	15	85.8 ± 9.7	26
Femur	83.6 ± 9.5	10	81.6 ± 10.0	14	82.4 ± 9.7	24
Radius	73.3 ± 4.5	11	73.2 ± 5.0	17	73.2 ± 4.7	28
Humerus	75.5 ± 6.3	12	77.7 ± 5.2	14	76.7 ± 5.7	26
Tail	18.8 ± 6.1	13	18.0 ± 4.5	15	18.4 ± 5.2	28

2. Activity budget

Research question: What is the general activity budget of Javan slow lorises? Are there differences between sexes, age classes, season or shifts (18:00-00:00; 00:00-06:00)?

Methods: 7169 5-minute observations, from April 2012 to June 2013, descriptive statistics, Chi-Square tests. For testing sex, season and shift only adults and known sexes were used. For comparison, descriptive statistics of activity budget based on (1) all data, (2) only using every 6th observation (see CHAPTER 6), (3) average activity budget of 11 adult Javan slow lorises using all data, (4) average activity budget of 11 adult Javan slow lorises using every 6th observation.

Results: Table 9.2. Statistical significances found in all tests (Table 9.3). Table 9.4 shows that activity budgets are similar between methods used. Means between individuals result in higher frequencies of social activities and lower frequencies of sleeping and resting.

Interpretation:

- For females maintenance behaviour seems to be more important, while for male behaviours related to increased ranging, searching for females, and social activities are more important.
- Immature animals seem to feed more, sleep less and are less alert than adults. Results could be influenced by the majority of observations coming from two individuals (YO and TA).
- The cold temperature in the dry weather period seemed to cause higher inactivity (torpor?), and less feeding, foraging and socialising.
- The second shift is used more for socialising instead of maintenance.

Table 9.2: Activity budget of Javan slow lorises in Cipaganti. Frequencies shown in percentage

		Alert / freeze	Groom	Social	Travel	Feed	Forage	Rest / sleep	Other	Total
Sex	Male	14.7	6.0	4.6	14.7	6.7	27.5	24.1	1.7	2211
	Female	9.8	6.4	1.9	12.7	11.2	32.7	23.5	1.8	3751
	Unknown	11.8	5.0	12.1	7.5	20.7	30.0	9.3	3.6	280
Age	Adult	12.0	6.3	2.9	13.6	7.8	30.7	24.9	1.9	5534
	Immature	8.7	5.1	6.5	10.8	27.9	30.7	8.8	1.4	703
Season	Dry	12.3	6.4	2.4	14.5	7.2	27.2	28.7	1.3	4465
	Wet	9.9	5.6	5.7	10.0	17.5	39.5	8.8	3.1	1756
Shift	First	10.7	6.3	2.6	12.6	9.7	33.6	22.5	2.0	3630
	Second	12.9	6.0	4.7	14.0	10.4	26.1	24.4	1.6	2494
Total (based on sex)		**11.6**	**6.2**	**3.3**	**13.2**	**10.0**	**30.7**	**23.0**	**1.8**	**6242**

Table 9.3: Standardised residuals and results of Chi-Square tests involving behaviour of Javan slow lorises in Cipaganti, and sex, age class, season and night shift

		Alert / freeze	Groom	Social	Travel	Feed	Forage	Rest / sleep	Other	χ	p	n
Sex	Males	3.3	-1.0	4.5	2.2	-2.3	-3.2	0.0	-0.1	84.814	< 0.001	5430
	Females	-2.6	0.8	-3.5	-1.7	1.8	2.5	0.0	0.1			
Age	Adult	0.8	0.4	-1.6	0.6	-5.3	0.0	2.8	0.3	356.679	< 0.001	6237
	Immature	-2.3	-1.1	4.6	-1.8	14.9	0.0	-7.9	-0.8			
Season	Dry	0.9	0.3	-3.0	1.2	-4.4	-3.3	6.1	-2.7	357.931	< 0.001	5409
	Wet	-1.6	-0.6	5.4	-2.1	7.8	5.8	-10.8	4.9			
Shift	First	-1.6	0.1	-1.9	-0.8	0.0	3.0	-1.3	1.0	47.404	< 0.001	5371
	Second	1.9	-0.2	2.4	1.0	0.1	-3.7	1.6	-1.2			

Table 9.4: Activity budget of Javan slow lorises in Cipaganti with different methods used. Frequencies shown in percentage

	Alert / freeze		Groom		Social		Travel		Feed		Forage		Rest / sleep		Other	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd
All data	12.0		6.3		2.9		13.6		7.8		30.7		24.9		1.9	
Every 6th obs.	11.9		7.1		2.4		14.2		7.0		30.2		25.0		2.2	
Means of 11 adults, all data	12.5	4.9	6.1	2.2	4.8	6.2	13.1	5.8	7.7	3.2	32.0	5.5	21.5	9.1	2.2	1.9
Means of 11 adults, every 6th obs.	11.9	5.3	6.5	3.2	4.6	6.6	13.9	5.4	6.5	2.6	33.2	8.2	21.2	10.1	2.1	1.9

3. Feeding observations

Research question:	What are food items eaten by Javan slow lorises in Cipaganti? Are there difference between sexes, age classes and seasons?
Methods:	7169 5-minute observations, from April 2012 to June 2013, descriptive statistics, Chi-Square Tests. For sex differences only cases with known sexes were used. For statistical tests, the food item bark was excluded to meet the assumptions that a maximum of 20 % of the cells should have an expected count of less than 5. I included "insects" as food item, even though insect feeding is rather an event than a state. This should be taking into account when interpreting the data.
Results:	In 526 cases the food item could be identified (Table 9.5). All tests except for sex were significant (sex: χ = 9.094, df = 4, p = 0.059, n = 470) (Table 9.6).
Interpretation:	Nectar was eaten less during the dry season and more during the wet season, probably due to availability. This seems to be compensated for by feeding more on insects and unknown food items.

Table 9.5: Percentages of food items eaten by Javan slow lorises in Cipaganti, per sex, age class, and season

		Gum	Nectar	Insect	Fruit	Unknown	Bark	Total
Sex	Male	52.6 %	27.2 %	10.5 %	0.0 %	8.8 %	0.9 %	114
	Female	64.8 %	18.6 %	6.6 %	1.7 %	7.2 %	1.1 %	361
	Unknown	27.5 %	60.8 %	2.0 %	2.0 %	5.9 %	2.0 %	51
Age	Adult	55.2 %	23.9 %	9.3 %	0.3 %	9.6 %	1.6 %	364
	Immature	66.0 %	25.9 %	1.9 %	3.7 %	2.5 %	0.0 %	162
Season	Dry	58.0 %	14.0 %	12.5 %	0.5 %	14.0 %	1.0 %	200
	Wet	58.9 %	31.0 %	3.7 %	1.8 %	3.4 %	1.2 %	326
Total (based on sex)		**58.6 %**	**24.5 %**	**7.0 %**	**1.3 %**	**7.4 %**	**1.1 %**	**526**

Table 9.6: Standardised residuals and results of Chi-Square tests of food items eaten by Javan slow lorises in Cipaganti, and age class and season

		Gum	Nectar	Insect	Fruit	Unknown	χ	p	n
Age	Adult	-0.8	-0.2	1.7	-1.7	1.6	28.784	< 0.001	520
	Immature	1.1	0.3	-2.5	2.6	-2.3			
Season	Dry	-0.1	-3.0	2.9	-1.0	3.4	48.819	< 0.001	520
	Wet	0.1	2.4	-2.3	0.8	-2.7			

4. Posture and locomotion

Research question:	What is the frequency of different postures and locomotion types used by Javan slow lorises?
Methods:	7169 5-minute observations, from April 2012 to June 2013, descriptive statistics. Drawings of variables see APPENDIX 5.
Results:	Table 9.7.

Table 9.7: Frequencies of different types of locomotion and postures exhibited by Javan slow lorises in Cipaganti

	Count	%
Locomotion		
Climb down	861	15.9
Climb up	519	9.6
Walk	302	5.6
Horizontal climbing	189	3.5
Bridge	167	3.1
Suspensory walk	164	3.0
Posture		
Sit	1200	22.1
Sleeping ball	620	11.4
Vertical suspension	370	6.8
Stand	343	6.3
Suspension 3 or 4	299	5.5
Suspension 1 or 2	159	2.9
Vertical suspension up	99	1.8
Vertical suspension down	78	1.4
Other	59	1.1
TOTAL	**5429**	**100**

5. Individual home ranges

Research question:	What are home range sizes of individual Javan slow lorises during the dry season, wet season and annually?
Methods:	See CHAPTER 4
Results:	Table 9.8.

Table 9.8: Individual homes ranges calculated with different home range estimators, for the dry and wet weather period, and annual home ranges. Asterisks indicate sub-adults.

Name	Season	Fixes	MCP100	MCP95	MCP75	MCP50	Kernel95	Kernel75	Kernel50
Females									
CH	Dry	203	1.89	1.14	0.92	0.46	0.91	0.45	0.25
	Wet	91	1.80	1.28	0.70	0.30	1.12	0.62	0.28
	Both	295	3.13	1.29	1.06	0.54	1.16	0.57	0.31
EN	Dry	270	4.47	2.17	0.83	0.41	2.18	1.26	0.75
	Wet	100	3.52	2.07	0.79	0.46	2.16	1.43	0.86
	Both	370	4.99	2.58	1.01	0.52	2.28	1.39	0.83
ON	Dry	160	3.19	2.91	1.97	0.85	3.24	2.17	1.16
	Wet	92	5.23	2.94	1.94	1.19	4.09	2.75	1.42
	Both	252	5.86	3.20	2.18	1.34	3.78	2.81	1.63
SH	Dry	1							
	Wet	75	2.31	1.88	0.92	0.50	2.48	1.59	1.03
	Both	76	2.31	1.88	0.92	0.50	2.45	1.57	1.01
SI	Dry	11							
	Wet	88	8.63	8.49	2.25	0.53	8.01	3.97	2.22
	Both	104	8.63	8.41	1.69	0.46	6.82	3.42	1.79
TE	Dry	204	3.47	3.28	2.11	0.84	3.56	1.91	0.97
	Wet	66	3.01	2.87	1.36	0.18	3.55	1.82	1.07
	Both	270	4.00	3.82	2.03	0.92	3.62	2.29	1.34
TA*	Dry	49	0.65	0.50	0.24	0.02	0.76	0.42	0.15
	Wet	114	1.75	1.29	0.98	0.08	1.61	0.57	0.26
	Both	163	1.82	1.28	0.57	0.19	1.28	0.65	0.30
Males									
AZ	Dry	139	3.55	2.36	1.42	0.73	2.98	1.89	1.02
	Wet	99	6.04	3.18	1.83	1.07	5.37	3.31	1.87
	Both	238	6.86	3.51	1.77	0.97	4.29	2.65	1.47
GU	Dry	274	4.06	3.84	2.03	1.10	3.23	2.06	1.34
	Wet	79	3.81	3.24	1.72	1.03	4.66	2.76	1.76
	Both	353	6.27	4.13	2.29	1.18	4.75	2.91	1.93
MO	Dry	203	8.11	2.89	1.59	0.30	3.37	2.12	1.02
	Wet	64	2.43	1.85	0.98	0.26	3.02	1.48	0.86
	Both	268	8.76	3.41	1.93	0.65	3.84	2.39	1.28

Name	Season	Fixes	MCP100	MCP95	MCP75	MCP50	Kernel95	Kernel75	Kernel50
TO	Dry	10							
	Wet	66	3.88	3.19	1.73	0.43	4.66	2.40	0.89
	Both	76	4.00	2.86	1.60	0.64	4.45	2.72	1.01
YO*	Dry	21							
	Wet	54	1.29	0.70	0.36	0.16	0.83	0.48	0.26
	Both	75	2.12	1.20	0.70	0.21	1.45	0.85	0.46

6. Position in microhabitat

Research question:	What is the frequency of use of different positions in the microhabitat by Javan slow lorises? Are there differences between sexes, age classes, season or shifts?
Methods:	7169 5-minute observations, from April 2012 to June 2013, descriptive statistics, Chi-Square tests. For testing sex, season and shift only adults and known sexes were used. For drawings of variables see APPENDIX 5.
Results:	Table 9.9. All tests except for sex were significant (sex: χ = 9.041, df = 5, p = 0.107, n = 5763) (Table 9.10)
Interpretation:	During the wet season animals prefer the periphery, and used the centre of the tree less than during the dry season. This could be in relation to seasonal changes in activity pattern, possibly warmer microclimate in the centre is preferred in the dry and colder season, and increased feeding on nectar in the wet season requires more activity in the periphery.

Table 9.9: Percentages of microhabitat positions used by Javan slow lorises in Cipaganti, per sex, age class, season and shift

		Centre	Crown	Periphery	Terrestr.	Trunk	Undergr.	Total
Sex	Male	36.4	21.2	20.4	0.4	20.4	1.3	2353
	Female	36.6	21.3	17.9	0.4	22.3	1.5	3987
	Unknown	32.3	23.9	28.0	1.2	13.7	0.9	322
Age	Adult	37.0	21.6	18.1	0.4	21.4	1.5	5895
	Immature	30.7	19.8	27.4	1.2	20.1	0.8	758
Season	Dry	38.2	20.5	17.2	0.5	22.5	1.2	4728
	Wet	31.1	23.9	24.6	0.3	18.3	1.9	1912
Shift	First	38.2	19.4	18.4	0.2	22.5	1.3	3930
	Second	33.7	24.1	20.1	0.4	20.3	1.3	2593
Total (based on sex)		**36.3**	**21.4**	**19.2**	**0.5**	**21.2**	**1.4**	**6662**

Table 9.10: Standardised residuals and results of Chi-Square tests of microhabitat positions used by Javan slow lorises in Cipaganti, and age class, season and shift

		Centre	Crown	Periph.	Terrestr.	Trunk	Undergr.	χ	p	n
Age	Ad.	0.9	0.3	-1.9	-1.1	0.3	0.5	51.722	< 0.001	6653
	Imm.	-2.6	-1.0	5.2	3.0	-0.7	-1.4			
Season	Dry	2.1	-1.1	-2.7	-0.2	1.2	-1.1	61.908	< 0.001	5742
	wet	-3.6	2.0	4.6	0.4	-2.1	1.9			
Shift	First	2.1	-2.4	-1.5	-0.6	1.0	-0.1	35.021	< 0.001	5702
	Sec.	-2.7	3.0	1.9	0.7	-1.3	0.2			

7. Substrate use

Research question:	What is the frequency of use of different substrate types in Javan slow lorises, the support's size, angle and number of supports involved?
Methods:	7169 5-minute observations, from April 2012 to June 2013, descriptive statistics. For drawings of variables see APPENDIX 5.
Results:	Table 9.11 to 9.13

Table 9.11: Percentages of substrate types used by Javan slow lorises in Cipaganti, per sex, age class, and season

		Bamboo trunk	Tree trunk	Branch	Undergr.	Water pipe	Valid N
Sex	male	13.7 %	20.3 %	64.9 %	0.7 %	0.4 %	2093
	female	11.9 %	26.1 %	61.3 %	0.3 %	0.4 %	3531
	unknown	12.3 %	16.0 %	70.9 %	0.0 %	0.8 %	244
Age	adult	12.9 %	23.8 %	62.5 %	0.4 %	0.4 %	5227
	immature	9.6 %	22.0 %	67.4 %	0.0 %	0.9 %	635
Season	dry	13.5 %	24.9 %	60.8 %	0.4 %	0.4 %	4273
	wet	10.1 %	20.0 %	69.0 %	0.5 %	0.4 %	1573
Total (based on sex)		**12.5 %**	**23.6 %**	**63.0 %**	**0.4 %**	**0.4 %**	**5868**

Table 9.12: Percentages of substrate sizes used by Javan slow lorises in Cipaganti, per sex, age class, and season

		Small	Medium	Large	Valid N
Sex	male	51.7 %	40.7 %	7.5 %	1888
	female	49.1 %	40.2 %	10.7 %	3242
	unknown	67.2 %	23.5 %	9.3 %	204
Age	adult	50.1 %	40.7 %	9.1 %	4744
	immature	55.8 %	31.2 %	13.0 %	584
Season	dry	50.2 %	39.8 %	10.1 %	3874
	wet	52.3 %	39.5 %	8.2 %	1439
Total (based on sex)		**50.7 %**	**39.7 %**	**9.5 %**	**5334**

Table 9.13: Percentages of substrate angles used by Javan slow lorises in Cipaganti, per sex, age class, and season

		-90	-45	0	45	90	Valid N
Sex	Male	13.6 %	10.5 %	33.0 %	27.4 %	15.5 %	1852
	Female	16.6 %	8.4 %	30.1 %	22.6 %	22.3 %	3112
	Unknown	9.8%	4.6 %	35.3 %	30.1 %	20.2 %	173
Age	Adult	15.1 %	9.3 %	31.4 %	24.9 %	19.2 %	4620
	Immature	17.0 %	6.4 %	29.9 %	21.7 %	25.0 %	512
Season	Dry	14.9 %	9.2 %	31.6 %	24.3 %	20.0 %	3853
	Wet	16.2 %	8.5 %	30.3 %	25.7 %	19.3 %	1262
Total (based on sex)		**15.3 %**	**9.0 %**	**31.3 %**	**24.6 %**	**19.8 %**	**5137**

8. Height of animal in tree

Research question:	What heights are Javan slow lorises found in? What heights do they use for different behaviours?
Methods:	7169 5-minute observations, from April 2012 to June 2013, descriptive statistics, Kruskal-Wallis test.
Results:	Table 9.14, Figure 9.4. There is a significant difference in height between different behaviours (H = 564.811, df = 7, p < 0.001, n = 5931)
Interpretation:	Rather stationary and inactive behaviours such as grooming, social activity and resting or sleeping are performed in greater heights, possibly due to lower susceptibility to terrestrial predators and greater concealment in higher positions, e.g. canopy. Travelling is performed on lower heights, possibly due to disconnected microhabitat.

Table 9.14: Heights in meters of Javan slow lorises in Cipaganti during different behaviours

	Mean	sd	Median	Percentile 25	Percentile 75	Min.	Max.	Valid N
Alert / freeze	5.69	2.88	5.5	4.0	7.5	0	17.0	725
Groom	7.22	2.87	7.0	5.0	9.0	1	17.5	387
Social	7.02	2.37	7.0	5.0	9.0	1	14.0	209
Travel	4.72	2.92	4.0	2.5	7.0	0	16.0	826
Feed	5.40	2.32	5.0	4.0	7.0	0	13.5	627
Forage	5.22	2.92	5.0	3.0	7.0	0	19.0	1917
Rest / sleep	7.02	2.90	7.0	5.0	9.0	0.5	17.0	1438
Other	5.05	2.40	5.5	3.0	6.0	0	12.0	114
Total	**5.83**	**2.97**	**6.0**	**4.0**	**8.0**	**0**	**19.0**	**6243**

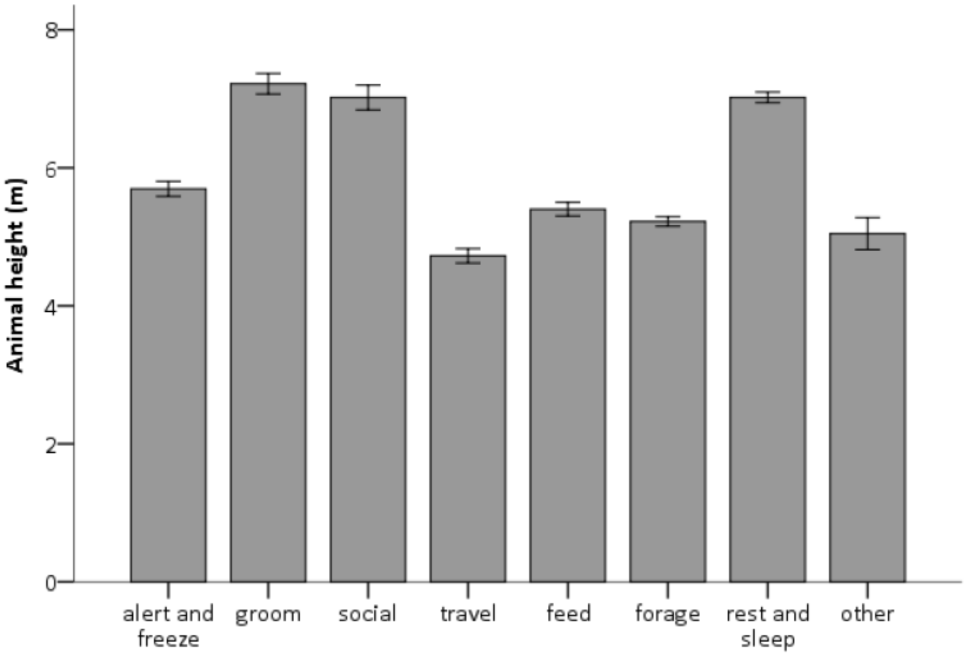


Figure 9.4: Heights in meters of Javan slow lorises in Cipaganti during different behaviours. Error bars denote ± 1SE)

9. Tree height, connectivity of trees and tree species

Research question:	What are heights of trees used by Javan slow lorises in Cipaganti? How well connected are trees? What tree species are mainly used by slow lorises in Cipaganti? Are there differences in frequencies of used tree species between sexes, age classes, seasons and behaviours? Are some tree species better connected than others?
Methods:	7169 5-minute observations, from April 2012 to June 2013, descriptive statistics, Chi-Square Tests. For sex differences only cases with known sexes were used. All tree species with less than 1 % use were considered as "other". Vernacular names used; scientific names can be found in CHAPTER 3.
Results:	Table 9.15 to 9.17. Significant differences found in all tests (Table 9.18 to 9.20).
Interpretation:	Bamboo is especially used for grooming, social and inactive behaviour, in according with results above especially in the dry and cold season. Red calliandra (Kalliandra merah) is especially used for feeding, in the wet season and by immature. Green wattle (Jiengjen) is also especially used for feeding, and especially by females and immature. Although jackfruit (Nangka) has a comparatively small count, this species also seems to be preferred for sleeping and resting. Just looking at the most frequently used tree species, bamboo is significantly more often connected with 5 or more other trees, which provides better concealment when performing grooming, social and inactive behaviours. The nectar-producing Kaliandra merah is of bush-size in Cipaganti and thus well connected. The gum-producing green wattle is little to medium well connected. It is interesting that this species is significantly more isolated from other trees (no trees connected), but still visited by slow lorises, emphasising its high importance as a feeding resource.

Table 9.15: Descriptive values of tree heights of trees used by Javan slow lorises in Cipaganti

	Tree height (m)
Mean	8.37
Standard Deviation	3.18
Median	8.0
Percentile 25	6.0
Percentile 75	10.5
Minimum	0.00
Maximum	23.00
Total N	**7168**

Table 9.16: Connectivity between used and other trees

Connectivity to other trees	Count	%
0	65	1.0
1	425	6.4
2	978	14.8
3	990	15.0
4	517	7.8
5	150	2.3
>5	3474	52.6%
Total	**6599**	**100.0%**

Table 9.17: Percentages of tree species used by Javan slow lorises in Cipaganti, per sex, age class, and season.

		Kayu putih	Bamboo	Jiengjen	Kalliandra merah	Alpukat	Suren	Nangka	Salamandar	Kayu angin	Other	Valid N
Sex	Male	29.0 %	31.2 %	10.2 %	8.2 %	5.6 %	3.5 %	0.6 %	1.5 %	1.7 %	8.6 %	2519
	Female	21.9 %	30.3 %	14.4 %	6.5 %	4.7 %	5.7 %	3.2 %	2.6 %	0.9 %	9.8 %	4297
	Unknown	15.0 %	40.9 %	7.2 %	18.4 %	8.6 %	1.7 %	1.4 %	1.7 %	0.9 %	4.0 %	347
Age	Adult	26.1 %	31.2 %	11.4 %	6.3 %	5.3 %	5.0 %	2.2 %	2.3 %	1.2 %	9.2 %	6320
	Immature	9.1 %	30.0 %	21.5 %	18.1 %	4.6 %	3.2 %	2.4 %	1.3 %	1.1 %	8.7 %	839
Season	Dry	22.8 %	33.8 %	11.9 %	5.8 %	5.9 %	4.8 %	2.7 %	2.7 %	0.8 %	8.8 %	5016
	Wet	26.6 %	24.8 %	14.1 %	12.1 %	3.8 %	4.7 %	0.9 %	1.0 %	2.0 %	9.8 %	2128
Total (based on sex)		**24.1 %**	**31.1 %**	**12.6 %**	**7.7 %**	**5.2 %**	**4.7 %**	**2.2 %**	**2.2 %**	**1.2 %**	**9.1 %**	**7163**

Table 9.18: Standardised residuals and results of Chi-Square tests of tree species used by Javan slow lorises in Cipaganti, and sex, age class and season

		Kayu putih	Bamboo	Jiengjen	Kallian. merah	Alpukat	Suren	Nangka	Salamandar	Kayu angin	Other	χ	p	n
Sex	Males	4.5	0.5	-3.7	2	1.2	-3.3	-5.6	-2.2	2.3	-1.2	149.062	< 0.001	6816
	Females	-3.5	-0.4	2.8	-1.6	-1.0	2.5	4.3	1.7	-1.8	1.0			
Age	Adult	3.2	0.2	-2.6	-4	0.3	0.7	-0.1	0.6	0.1	0.2	249.484	< 0.001	7159
	Immature	-8.9	-0.5	7.3	11.0	-0.8	-2	0.4	-1.7	-0.2	-0.4			
Season	Dry	-1.6	3.4	-1.3	-4.9	1.9	0.0	2.5	2.3	-2.4	-0.7	206.208	< 0.001	7144
	Wet	2.5	-5.3	2.0	7.4	-2.9	0.0	-3.9	-3.6	3.7	1.1			

Table 9.19: Standardised residuals and results of Chi-Square tests of tree species used by Javan slow lorises in Cipaganti, and behaviour

	Kayu putih	Bamboo	Jiengjen	Kallian. merah	Alpukat	Suren	Nangka	Salaman-dar	Kayu angin	Other	χ	p	n
Alert / freeze	4.1	-0.8	-1.6	-2.8	-1.8	1.8	0.2	-2.5	-0.8	1.0	2389.480	< 0.001	6243
Groom	-2.1	5.1	-4.7	-2.6	3.9	1.2	-2.3	-0.9	-0.2	0.0			
Social	-3.1	7.5	-5.2	-3.3	-1.9	-0.7	-1.7	0.2	11.3	-0.7			
Travel	0.5	-0.5	-4.2	-3.6	-0.7	-0.4	0.8	1.3	4.0	7.7			
Feed	-11.4	-11.9	27.9	22.3	-5.2	-4.8	-0.5	-3.5	-2.7	-4.4			
Forage	2.8	-0.6	-1.2	0.3	1.5	0.9	-2.9	-2.2	-1.9	-0.9			
Rest / sleep	3.3	3.9	-8.2	-7.2	1.8	0.8	5.2	6.5	-2.6	-2.9			
Other	-0.3	0.9	-0.7	-2.0	1.5	0.2	-1.6	-1.6	-0.3	2.2			

Table 9.20: Standardised residuals and results of Chi-Square tests of tree connectivity and tree species used by Javan slow lorises in Cipaganti

	0	1	2-4	5 and more	χ	p	n
Kayu putih	-2.5	2.6	17.3	-14.9	2722.973	< 0.001	6599
Bamboo	-4.1	-7.3	-25.6	24.2			
Jiengjen	9.7	10.5	9.8	-13.0			
Kalliandra merah	-2.3	-4.6	-2.3	3.8			
Alpukat	2.5	-2.2	-1.5	1.7			
Suren	5.0	7.2	4.0	-6.4			
Nangka	-1.2	-2.8	1.8	-0.4			
Salamandar	-1.2	-1.2	9.2	-7.1			
Kayu angin	-0.9	-2.3	5.9	-4.0			
Other	-1.6	.7	1.1	-0.9			
Total		425	2485	3624			

APPENDIX 5

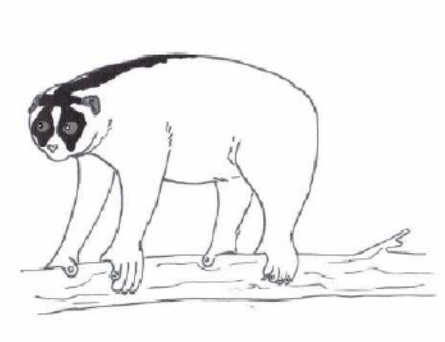
Drawings of posture and locomotion types, position in the tree, support size and support angle

Drawings by Mark Rademaker

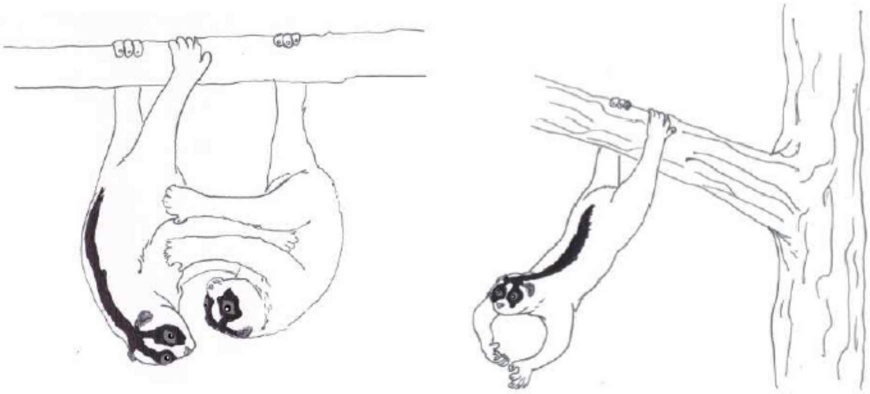
1. Postures

Sit

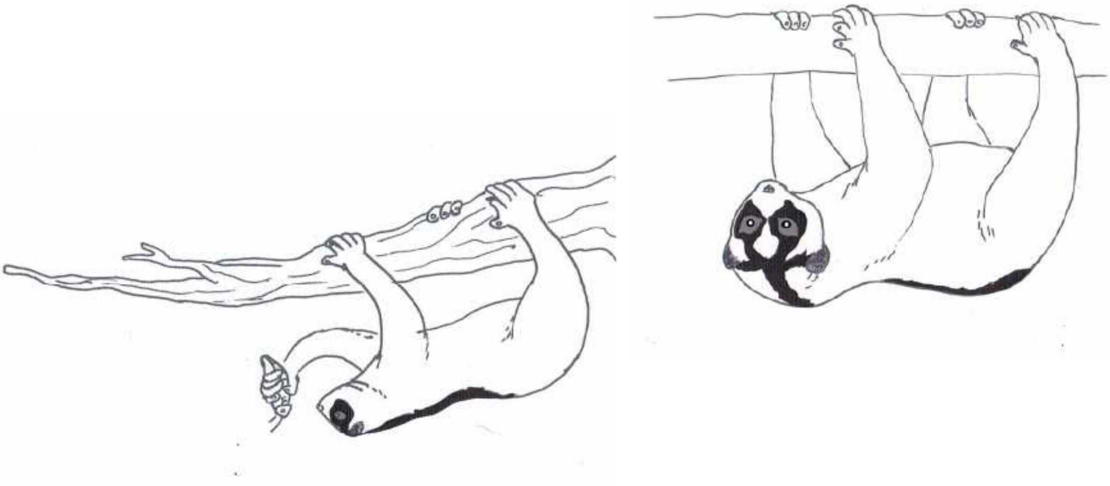
Stand



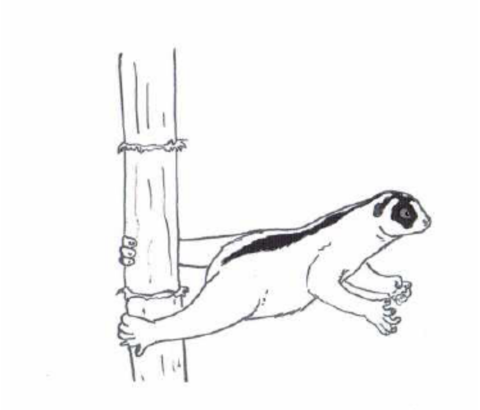
Suspension 1 and 2



Suspension 3 and 4



Vertical suspension 2

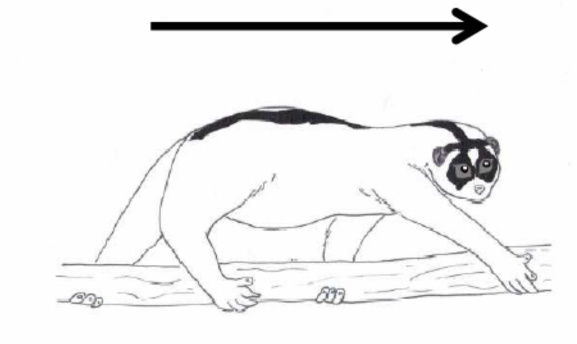


Vertical suspension 3 and 4, up or down (2 different categories)

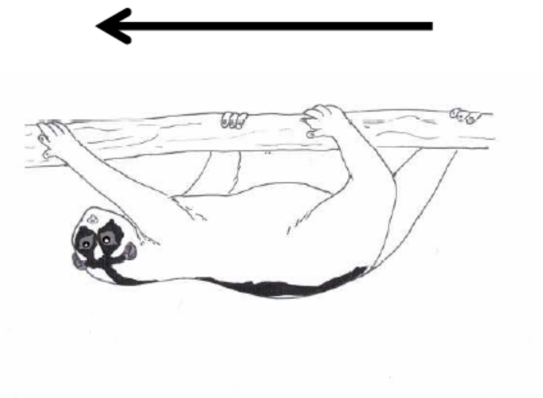
Sleeping ball ("Schlafkugel")

2. Types of locomotion

Walk



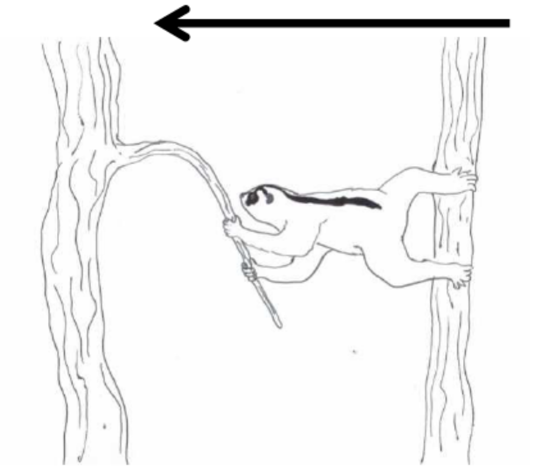
Suspensory walk



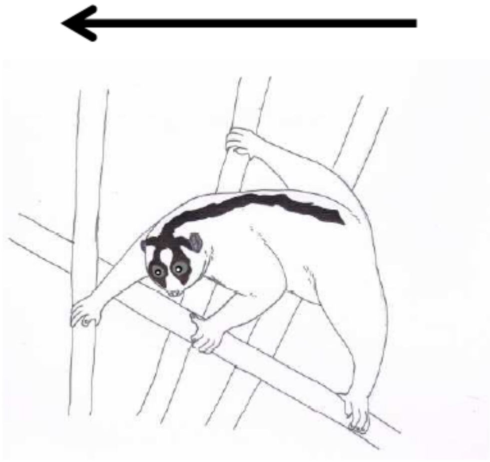
Climb up

Climb down

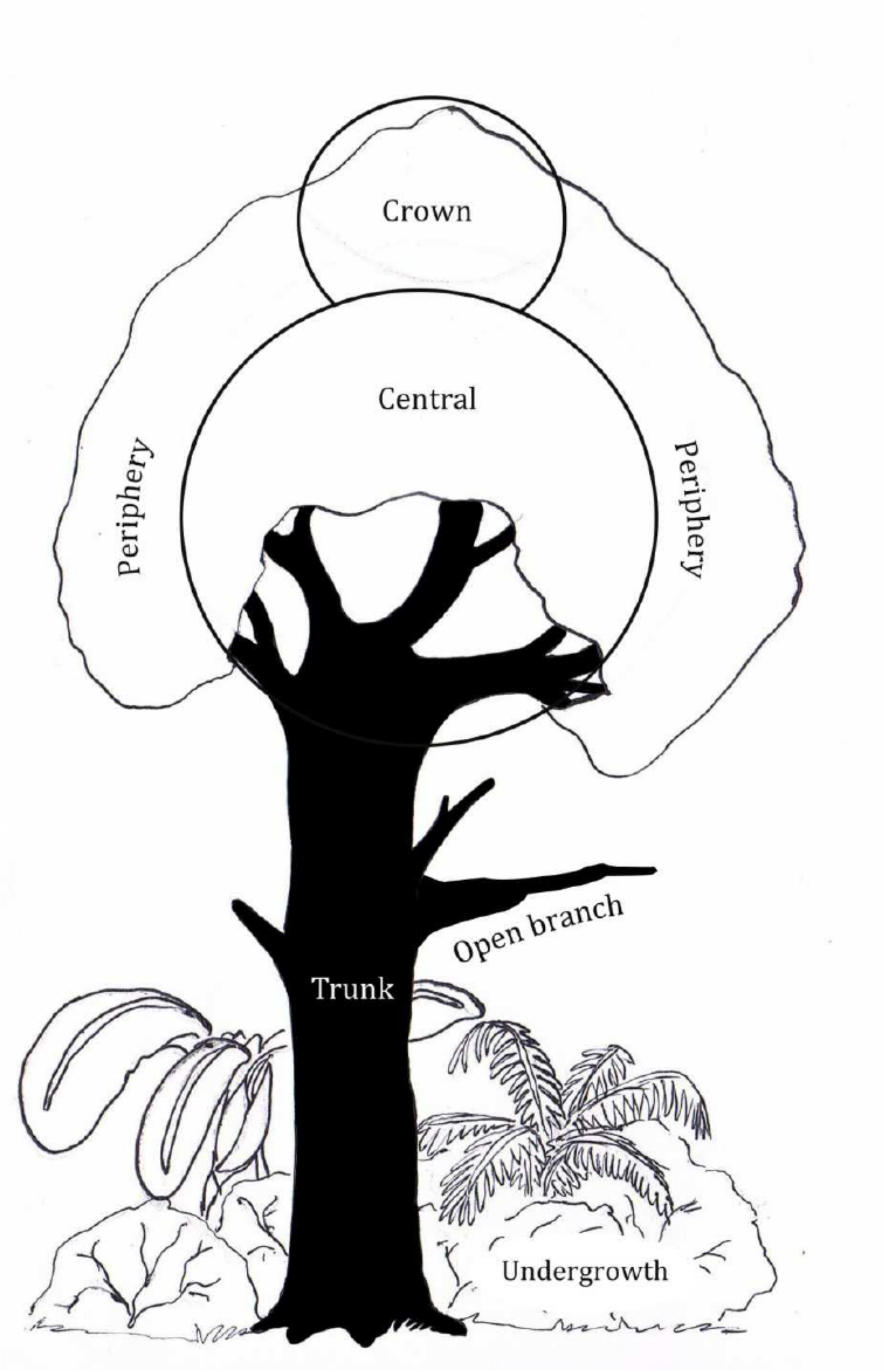
Bridge



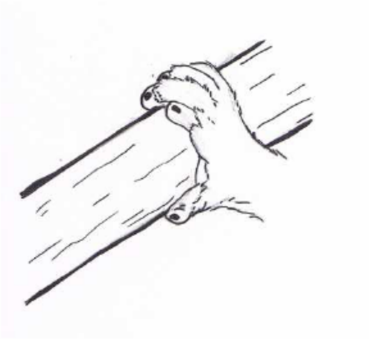
Climb horizontally



3. Position in tree



4. Support size



Small substrate

Hand of animal can fully close around the substrate

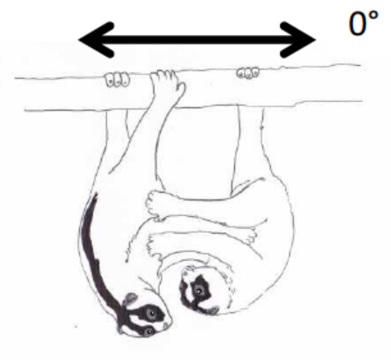
Medium substrate

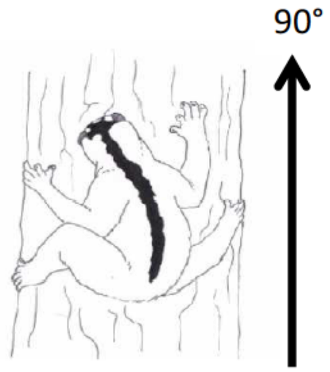
Hand of animal curves around the substrate but cannot close

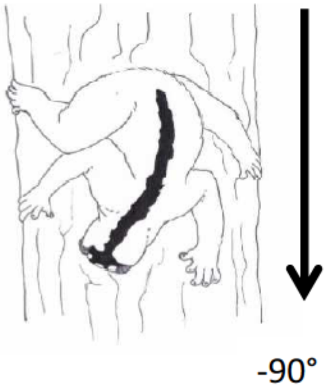
Large substrate

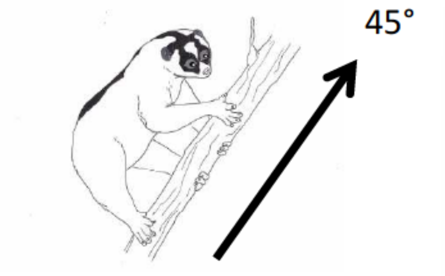
Hand of animal is flat on the surface of the substrate

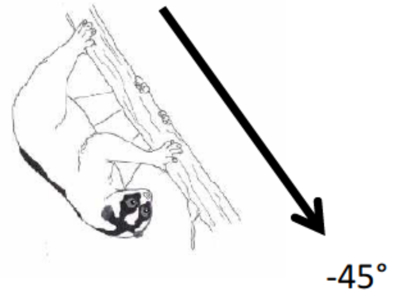
5. Support angle











Ectoparasites and Anting in Lorises

Eva Johanna Rode[1], K.A.I. Nekaris[1]

[1] Nocturnal Primate Research Group, Oxford Brookes University, Oxford, UK

Introduction

- **Ectoparasites** may carry infectious and sometimes lethal diseases; they may remove blood, damage the skin, and cause the host to spend valuable time on grooming leading to decreased reproductive success (Van Vuren 1996)
- Parasites may trigger and accelerate species and population declines particularly in small and isolated populations (Junge & Louis 2005a)
- **Anting**: anointment with chemicals of certain insects for skin protection against ectoparasites or to make such insects edible through camouflage with their chemical signature
- During **passive anting** an animal allows ants to walk over its fur/feathers; during **active anting** it actively applies the ants to its integument (Whitaker 1957)

Aims:

- To compare ectoparasite load in lorises (subfamily Lorisinae) to other primate species
- To investigate how often and how wild lorises 'ant'

Methods

- **Ectoparasite data**: Global Mammal Parasite Database (available online, Nunn & Altizer 2005), PrimateLit database and Google Scholar
- Only wild and healthy animals were considered

- **Anting**: Feeding ecology of the Mysore slender loris (*Loris l. lydekkerianus*) for 10.5 months in 1997/1998 in a dry scrub forest at Ayyalur, Tamil Nadu, South India
- Focal-animal instantaneous point sampling at 5-min intervals

Results

- **Ectoparasites**: We found 29 papers, 38 data points of 13 primate genera
- Many data points had a low sample size and did not address both prevalence and intensity
- Compared to other primates, lorises had a low ectoparasite prevalence (Fig. 1)
- Comparing lorises with all other primates, prevalence was significantly lower (t=2.948, df=25, p=0.007)

- **Anting**: 62.9 % of identified prey items were ants or termites (Nekaris and Rasmussen 2003)
- Anting occurred in 23 % of these feeding bouts
- Lorises ate significantly more ants during anting (t=11.93, df=152, p<0.001) (anting: mean = 7, max. = 26, catching alone: mean = 1, max = 4, Fig. 2)
- Most times (n=26) lorises passively anted, allowing ants to run up and down their arms before consuming them. 10 times, after ants had begun to run up and down their arms, they also urine washed, and seemed to spread the formic acid of the ants further along their integument
- Four times a loris anted in the presence of another loris, once with a juvenile and his mother, suggesting possible social transmission of this behaviour
- Juveniles (n=1) and infants (n=2) anted on their own. An infant both active and passive anted.

Fig. 1: Prevalence of ectoparasites found in different primate groups (compare Tab. 1). Prevalence index shows the difference between the mean prevalence of the respective group from the overall mean prevalence of all studies

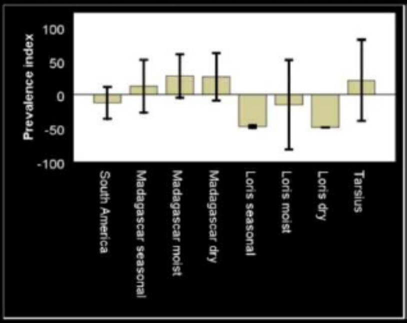


Fig. 2: Number of ants eaten by Mysore slender lorises with anting and without anting observed

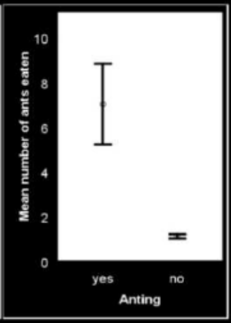


Table 1: Primate species and their ectoparasite prevalence (number of individuals of a host species infected divided by the number of hosts examined) and intensity (number of individuals of a particular parasitic species in each infected host)

Species	Prevalence (%)					Max intensity (mean intensity)	Paper
	Mites	Ticks	Lice	Bot fly	All		
Alouatta caraya			37 (n=302)			1000	1
Alouatta palliata				77.8 (56)		24 (7.5)	2
Alouatta palliata				60 (5496*)		20 (2.6)	3
Alouatta seniculus			32.3 (?)				4
Alouatta spp.		1.1 (88)					5
Ateles paniscus chamek			11.1 (9)				6
Eulemur flavifrons	33.3 (18)					10	7
Eulemur fulvus albifrons	73 (37)						8
Eulemur fulvus rufus					95 (20)		9
Eulemur macaco macaco	21.7 (23)						10
Lemur catta		10.5 (95)	11.6 (95)		23.2 (95)	18	11
Lemur catta		91.7 (24)				20	12
Lemur catta	100 (70)						13
Lemur catta	85 (20)						14
Loris tardigradus					0 (37)		15
Loris lydekkerianus lydekkerianus					0 (26)		15
Loris lydekkerianus nordicus					0 (11)		15
Macaca fuscata			100 (8)			(20^a; 8.5^b)	16
Macaca hecki	95.7 (23)						17
Macaca hecki/M. tonkeana hybrid	82.2 (45)						17
Microcebus rufus						(3.7^c; 2.0^d)	18
Nycticebus pygmaeus					0 (21)		19
Nycticebus pygmaeus					2 (51)		20
Nycticebus bengalensis					0 (7)		21
Nycticebus coucang	10.3 (29)	100 (29)	6.9 (29)		100 (29)		22
Nycticebus javanicus					*		23
Pan troglodytes	40.4 (47)						24
Papio doguera		14 (43)					25
Papio ursinus						>400	26
Propithecus diadema	100 (26)						27
Propithecus edwardsi						175	28
Propithecus verreauxi deckeni	90 (20)	5 (20)			95 (20)		9
Tarsius dianae		39.7 (68)					29
Tarsius dianae						(1.64)	30
Tarsius lariang						(1.00)	30
Tarsius spp.	100 (6)					10	31
Varecia rubra	31.8 (22)						32
Varecia variegata and V. rubra		100 (11)				20	33

N = north, W = west, S = south, N = north; green = moist habitat, blue = seasonal habitat, yellow = dry habitat

^{a} = eggs, ^{b} = adults/nymphs, ^{c} = lice, ^{d} = ticks; * = "extremely rare in >300 lorises

References: 1 = Pope 1966, 2 = Baron et al. 1996, 3 = Milton 1996, 4 = Sánchez-Villagra et al. 2008, 5 = Stuart et al. 1998, 6 = Karesh et al. 1998, 7 = Schwitzer et al. 2010, 8 = Junge et al. 2008, 9 = Junge & Louis 2005b, 10 = Junge & Louis 2007, 11 = Sauther et al. 2002, 12 = Takahata et al. 1998, 13 = Loudon et al. 2006, 14 = Dutton et al. 2003, 15 = Nekaris, 16 = Zamma 2002, 17 = Gotoh et al. 2001, 18 = Durden et al. 2010, 19 = Nekaris, Starr, 20 = Streicher 2004, 21 = Nekaris, Das, 22 = Wiens 2002, 23 = International Animal Rescue Indonesia, 24 = Williams et al. 2008, 25 = Kuntz & Myers 1967, 26 = Brain & Bohrmann 1992, 27 = Irwin et al. 2010, 28 = Wright et al. 2009, 29 = Merker 2003, 30 = Durdon et al. 2008, 31 = Shekelle & Nietsch 2008, 32 = Dutton et al. 2008, 33 = Junge & Louis 2005a

Fig 3. A pygmy loris in Cambodia infected with ticks.

Discussion

- There is a surprising lack of data about ectoparasites in primate species, despite the huge scientific interest in grooming behaviour and parasites in general
- Lorises show an extremely low ectoparasite prevalence compared to other primate species
- This suggests some kind of protection against ectoparasites
- Anting may play an important role in:
  - Protection against ectoparasites (Verderane et al. 2007)
  - Protection from predators, particularly for young lorises who are parked in trees from six weeks, that may be vulnerable to large colonies of ants, by serving as a form of camouflage
  - Preparation of food, e.g. to make ants and termites better edible (Judson & Bennett 1992)
- The slow lorises of Southeast Asia (*Nycticebus* spp.) and possibly other lorisids are among few mammals reported to harbour toxic exudates that are secreted by the brachial gland located proximal to the elbow, and anointment with this secretion might be an ectoparasite defence.

Conclusion

- All studies involving the capture of animals should report on ectoparasites
- The low prevalence of ectoparasites points to a special adaptation of lorises
- Anting might be once mechanism how lorises avoid infestation by ectoparasites but might also serve other functions
- One of the ecological functions of loris venom might be defence against ectoparasites

Presentation 2 of the Little Fireface Project

Contact: anekaris@brookes.ac.uk, eva.rode-2011@brookes.ac.uk

References: Please ask authors for a list of references

OXFORD BROOKES UNIVERSITY

Habitat and substrate use by the Javan slow loris (*Nycticebus javanicus*) in a Talun plantation,
Cipaganti, West Java, Indonesia

Prescilla Rindang Putri[1], Eva Johanna Rode[2]*, N.L. Winarni[1], Wirdateti[3], K. Anne-Isola Nekaris[2]

Introduction

- Many primate populations have suffered from intensive deforestation and anthropogenic habitat modifications on Java, Indonesia (Nijman, 2002)
- Slow lorises (*Nycticebus*) are nocturnal and arboreal primates, rely on camouflage and are believed to depend heavily on connected habitat structure (Nekaris & Bearder, 2011)
- We studied the behaviour and habitat use of a population of Javan slow lorises (*N. javanicus*) in a *Talun* plantation -- a land-use plantation with traditional, rotating system that combines crops with economically high value trees, and forming a multi-strata vegetation.
- **Aims of the study**:
  - To investigate the habitat and substrate use of wild Javan slow lorises in a human-altered habitat and assess the effect of this habitat on their behaviour

Mosaic-like Talun plantation

Radio-tracking

Tab. 1: Basic ethogram for Javan slow lorises

Behavior	Description
Active	No movement, eyes open
Inactive	No movement, eyes closed
Feed	Feeding
Forage	Search, observe, sniff for food
Travel	Travelling
Grooming	Groom oneself
Social	Interact with conspesific
Other	Other behaviors not included above

Methods

- **Study site:** Cipaganti, near Garut, West Java, June 2012 - Jan 2013
- **Study objects:** Six radio-collared adult Javan slow lorises
- Instantaneous behaviour sampling with 5-min interval, during shifts of 1800-0000 and 0000-0600, observation with red head torch
- Variables collected: behaviour (inactive, active, feed, forage, groom, travel, social, other, out of sight; Fitch-Snyder et al 2001, Tab.1), position (central, trunk, periphery, crown, undergrowth, water pipe, terrestrial, other), height of animal
- Used trees marked at beginning, middle and end of night shift
- Descriptive statistics performed with Excel

Results – Behaviour and Habitat

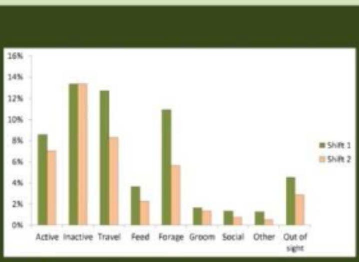


Fig. 1: Activity budget of 6 adult Javan slow lorises during the first and second half of the night

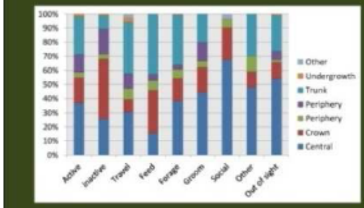


Fig. 2: Different behaviours preformed in different habitat positions by adult Javan slow lorises

- The activity budget depending on the shift can be seen in Figure 1.
- Slow lorises were observed performing different behaviours in all positions, including travelling on the ground (1.3%) and in human artificial substrate (2.5%)
- Substrate was ranging from 0 (ground) to 15 m high. Most of the activities were spent within1-5 m range height (53.5%)
- Only maximum inactive behavior was recorded within 6-10 m high

Top 10 Tree Species

4 % Avocado
Persea americana
Lauraceae

1 % Afrika
Maesopsis eminii
Rhamnaceae

6 % red Kaliandra
Calliandra calothyrsus
Fabaceae

3 % Bamboo surat
Gigantochloa sp.
Poaceae

1 % Kayu angin
Casuarina junghuhniana
Casuarinaceae

6 % Nangka
Actocarpus heterophyllus
Moraceae

4 % Salamandar
Grevillea robust
Proteaceae

21 % Suren
Toona sinensis
Meliaceae

13 % Bamboo temen
Gigantochloa cf. ater
Poaceae

21 % Jiengjen
Acacia decurrens
Fabaceae

Results – Tree species

- We recorded 70 used trees
- Highest percentage Kayu Putih (*Eucalyptus sp.*, Family Myrtaceae 30%)
- *Kayu putih* is know as a highly economically valued tree for the farmers and most of the *kayu putih* trees in the observation area are planted by locals.

Discussion

- Javan slow lorises and slow lorises in general are believed to live in primary and secondary lowland and mountainous forests (Rowe, 1996)
- Quantitative surveys of Javan slow loris in the protected areas of Gunung Gede-Salak-Halimun Complex found them to be at relatively low abundance in the protected area (Nekaris, et al., submitted)
- Qualitative surveys found Javan slow lorises frequently in agroforest, and suggested these areas were vital for their conservation (Winarti, 2009)
- A study on the distribution of Javan slow lorises found 86 % of sightings in forest plantations and agricultural areas located outside of protected areas (Voskamp et al., submitted)
- Our data show that animals seem to cope with the human altered habitat of agricultural area with respect to their behaviour, and even use the ground and artificial substrates like water pipes that lead over the fields

Conclusion

- Our results showed that talun plantation seem to support the Javan slow lorises for their daily activities
- Conservation strategy is needed to ensure the management of the habitat outside protected area

Author affiliations:
[1] Biology Departement University of Indonesia, Departemen Biologi Fakultas MIPA Universitas Indonesia, Indonesia
[2] Nocturnal Primate Research Group, Oxford Brookes University, Oxford, UK
[3] Research Center for Biology-LIPI, Division Zoology, Bogor, Indonesia

*Contact:
- Prof. KAI Nekaris
  anekaris@brookes.ac.uk
- Johanna Rode
  eva.rode-2011@brookes.ac.uk

PLATES

PLATE 1: Sampling of brachial gland exudates and saliva sampling

Sampling saliva with 1 ml syringe

Sampling brachial gland exudates with cotton swab

Animal biting and grabbing hard during examination

Brachial gland in flexor area of elbow

Greater slow loris at IAR in defence position

PLATE 2: Wounds, habitat, habitat use

Missing toes

Mosaic habitat at the study site Cipaganti

Slow lorises using water pipes and pipe support

Slow lorises using the ground

PLATE 3: Infant care, social life

Mother “Tereh” is carrying her already large infant

Mother “Sibau” carrying her small infant “Galaksi“, a few days after the baby was seen for the first time

Male “Guntur” and female “Tereh” in body contact and socialising in a green wattle *Acacia decurrens*, a gum-producing and preferred feeding tree

PLATE 4: Feeding

Slow lorises feeding on the nectar of red calliandra *Calliandra calothyrsus*

Slow lorises gouging and feeding on the gum of green wattle *Acacia decurrens*. Left: Infant “Tahini” at an age of app. 4 months

PLATE 5: Camera trap photos

Common palm civet *Paradoxurus hermaphroditus*

Javan ferret badger *Melogale orientalis*

Leopard cat *Prionailurus bengalensis*

European wild pig *Sus scrofa*