Ecology and conservation of the southern woolly lemur (*Avahi meridionalis*) in the Tsitongambarika Protected Area, south-eastern Madagascar

By

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Thesis submitted in partial fulfilment of the requirements of the award of

Doctor of Philosophy

May 2018

Abstract

Recent studies question the assumption that folivorous primates rely on ubiquitous and evenly distributed food resources with a low and uniform nutritional quality. They suggest that folivores experience scramble competition and their resources vary in quality, availability, and spatial distribution. Woolly lemurs, *Avahi* sp., are the only true nocturnal folivorous primates. This study aims to explore whether *A. meridionalis* experiences food constraints in the Tsitongambarika lowland rainforest of south-east Madagascar, a habitat that is expected to have low variation in quality, availability, and spatial distribution of leaves. I collected data from May 2015 to July 2016 at Ampasy, north of the Tsitongambarika Protected Area, on abundance of lemur species, and ranging pattern, sleeping site selection, diet, and activity pattern of *A. meridionalis*. I delivered four lessons to teachers in the municipality that hosts Ampasy to raise awareness on the threats that lemurs and forests are facing, and assessed the effective retention of knowledge after one year. The density of the nocturnal folivore *Lepilemur fleuretae* was very high, suggesting a possible scramble competition with *A. meridionalis*. *Avahi meridionalis* adopted a resource-maximising strategy in terms of annual ranges, suggesting a high-quality habitat, and a time-minimising strategy in terms of daily distances travelled, sleeping site selection, and dietary choices, suggesting a seasonal fluctuation of resources. The competition with *L. fleuretae* may explain the dietary breadth reduction during the lean season and the opportunistic cathemeral activity that I found in *A. meridionalis*. Teachers retained most of the information provided, which can thus be transferred to students. This is the first step to favour a change in attitude by the local community in the area. My results on *A. meridionalis* showed several lines of evidence to support the hypothesis that folivores experience similar food constraints to frugivores.

Acknowledgements

I am very thankful to my advisor, Dr. Giuseppe Donati, for his guidance, support, and motivation throughout this project. Thanks for making my PhD experience productive and stimulating, you have been a tremendous mentor for me.

I am grateful to my advisor, Prof. Anna Nekaris, for her insightful comments and advice that incentivised me to improve my research from various perspectives. Thanks also for giving me the opportunity to be your teaching assistant, it has been a great and formative experience for me.

I wish to express gratitude to Prof. Simon Bearder, Dr. Susan Cheyne, Prof. Kate Hill, Prof. Jeremy McClancy, and Prof. Vincent Nijman, for the help and the opportunities given, your knowledge and dedication are an immense source of inspiration. I thank my external examiner Prof Joerg Ganzhorn and internal examiner Prof Vincent Nijman for feedback and suggestions to improve the dissertation.

My sincere gratitude goes to the foundations for providing the funding to carry on this study: Rufford Foundation, the Mohamed bin Zayed Species Conservation Fund, Primate Conservation Inc., the Conservation International Primate Action Fund, and the Primate Society of Great Britain Conservation Grant.

I would like to express the deepest appreciation to QIT Madagascar Minerals Rio Tinto, specifically the QMM Environmental Team, for the support and the logistical help in Fort Dauphin and at the research station. Special thanks to Laza Andriamandimbiarisoa, Johny Rabenantoandro, Jean-Baptiste Ramanamanjato, and Cedric Tsagnangara.

I am thankful to all the members of Asity Madagascar in Fort Dauphin, with special thanks to Faniry Rakotoarimanana, without your guidance and persistent help in the field this research would not have been possible. I am grateful to the teachers

of the municipalities of Iaboakoho, Mahatalaky, Mandromodromotra, and Ampasy-Nahampoana for giving their time to realise a valuable part of this study. But my deepest heartfelt appreciation goes to every single employee at the research station, to all the collaborators, and to all the villagers in the municipality of Iaboakoho. Laviky, Bergè, Ronaly, Rabiky, Marianah, Nita, Roger, thanks for making me feel at home, literally.

I want to thank Dr. Jacques Rakotondranary and Tolona Andrianasolo for their logistical help and support in Antananarivo, especially for coordinating my research permits/renewals and export permits with the Direction du Système des Aires Protégées, and the Ministère de l’Environnement et Forêts of Madagascar. I am also grateful to Madame Chantal Andrianarivo (Responsable des Recherches au Madagascar National Parks) and Prof. Hanta Razafindraibe (Responsable du Département Biologie Animale de l’Université d’Antananarivo) for approving my research. I would also like to express my gratitude to Irene Tomaschewski for carrying out biochemical analyses on the food items.

I wish to thank the volunteers and the Oxford Brookes Primate Conservation MSc students who spent their time in the field. Thanks to the volunteers Julie Mauguiére, George Selley, and Carina Morris for their help with collecting the data and for the nice time we had together. But I owe my deepest gratitude the MSc students Megan Phelps and Fiona Besnard, you made an enormous contribution to this study and I am truly happy I shared this significant experience with you, we are a great team. Thanks to Toky, Natalie, and Fidél, it was nice to know that you were always there to spend time together during my resting days in Fort-Dauphin. I am grateful to Dr. Sergio Tofanelli and Dr. Tim Eppley for helping me especially during the early stages of my study, their encouragement and suggestions were invaluable.

I owe a very important debt to my closer friends in Italy and the MSc and PhD students I met in Oxford during this journey, you should know that your support and encouragement was worth more than I can express on paper. Special thanks to Jesus Martinéz, Sabrina Reinders, Rachel Sawyer, Aimee Oxley, Hellen Bersacola, Dr. Magdalena Svensson, Katie Reinhardt, Dr. Stephanie Poindexter, and Daniel Bergin.

Words cannot express how grateful I am to my parents and to my sister Monica for their unconditional love and for supporting me emotionally and financially. I dedicate this thesis to you all, thanks for the countless sacrifices and for providing me the opportunity to be where I am today.

Finally, last but by no means least, thanks to Marco for sharing this significant time of our lives together and for pushing me towards my goals.

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List of abbreviations

ADF	Acid Detergent Fibres
AIC	Akaike Information Criterion
ANOVA	Analysis of Variance
B_{sta}	standardised Levin's index
BIC	Bayesian Information Criterion
CDS	Conventional Distance Sampling
DBH	Diameter at Breast Height
EM	Expectation Maximisation
ESW	Effective Strip Width
FAI	Food Availability Index
FK	Fixed Kernel
GLMM	Generalised Linear Mixed Models
GPS	Global Positioning System
HRT	Home-Range Tools
IAA	Incremental Area Analysis
IUCN	International Union for Conservation of Nature
KOMFITA	Community Forest Management in Tsitongambarika
LSD	Fisher's Least Significant Difference
MCP	Minimum Convex Polygon
NDF	Neutral Detergent Fibres
NGO	Non-Governmental Organisation
RM	Repeated Measures
SD	Standard Deviation

SE	Standard Error of mean
SPSS	Statistical Package for the Social Sciences
TGK	Tsitongambarika
UTM	Universal Transverse Mercator
VHF	Very High Frequency
WGS	World Geodetic System

Chapter 1. General Introduction

1.1. The folivore paradox

Socioecological models indicate that diet influences the degree of inter- and intra-specific feeding competition, and consequently group size, ranging patterns, social behaviour, and activity of primates (Wrangham, 1980; van Schaik, 1989; Isbell, 1991; Janson & Goldsmith, 1995). It is thus assumed that folivorous primates, especially in rainforests, experience limited feeding competition due to the low quality, high abundance, and even distribution of leaves (Wrangham, 1980; Isbell, 1991; Sterck et al., 1997). For this reason, on a theoretical level folivorous primates are expected to increase group size to reduce predation risk and to live in cohesive groups with relatively egalitarian social relationships (Wrangham, 1980; Isbell, 1991). Evidence supporting this theory derive from studies that found no relationship between group size and day range or travel cost in folivorous primates (Clutton-Brock & Harvey, 1977; Struhsaker & Leland, 1987; Isbell, 1991; Janson & Goldsmith, 1995; Yeager & Kirkpatrick, 1998; Yeager & Kool, 2000; Fashing, 2001; Korstjens et al., 2002; Robbins et al., 2007). Many of these studies, however, did not control for ecological variations that can determine group size variations, and this might have biased the results (Snaith & Chapman, 2005).

Contrary to expectations, some folivorous primates live in small groups even when they are expected to experience limited feeding competition, and this inconsistency has been named folivore paradox (Steenbeck & van Schaik, 2001; Koenig & Borries, 2002). Living in large groups increases infanticide risk and this may explain the small groups in red howler monkeys *Alouatta seniculus* (Crockett & Janson, 2000) and Thomas's langurs *Presbytis thomasi*

(Steenbeck & van Schaik, 2001). The infanticide hypothesis, however, does not apply to all species, thus other authors recently argued that group size may be limited by feeding competition even in folivorous primates (Snaith & Chapman, 2005, 2007, 2008; Saj et al., 2007; Harris et al., 2010). Moreover, it has been hypothesised that folivorous primates experience scramble competition since their resources vary in quality, availability, and spatial distribution (Snaith & Chapman, 2007). For example, the food intake of ashy red colobus *Piliocolobus tephrosceles* decreases over time despite the increase in daily distance travelled to find food, suggesting that folivorous primates deplete food patches (Snaith & Chapman, 2005, 2008). Food patch depletion was also demonstrated in mantled howler monkeys *Alouatta palliata* (Leighton & Leighton, 1982; Chapman, 1988). Additional evidence comes from the relationship between group size and day range in some folivorous primates, including *Presbytis thomasi* (Steenbeck & van Schaik, 2001), mountain gorilla *Gorilla beringei* (Ganas & Robbins, 2005), and *Piliocolobus tephrosceles* (Snaith & Chapman, 2008). Also, folivorous primates respond to the decrease in food availability by increasing daily distances travelled, number of patches visited per day, percentage of time spent resting, and/or dietary diversity in various species [black colobus *Colobus satanas* (McKey & Waterman, 1982); *G. beringei* (Ganas & Robbins, 2005); guerezas *Colobus guereza* (Harris et al., 2010)]. Furthermore, it has been shown that folivorous primates may exhibit contest competition for food, with consequent aggressive behaviours and dominance hierarchy (Koenig et al., 1998; Koenig, 2000; Fashing, 2001; Harris, 2005, 2006). Other arguments in support of the hypothesis that folivorous primates are limited by food quality, availability, and distribution include: a relationship between group size and habitat quality [*C. guereza* (Dunbar, 1987); *Piliocolobus tephrosceles* (Struhsaker, 2000; Struhsaker et al., 2004); northern plains grey langur *Semnopithecus entellus* (Vasudev et al., 2008)]; fission-fusion, which is typically associated with low food availability, is exhibited by some species [Angolan colobus *Colobus angolensis* (Fimbel et al., 2001); *Piliocolobus tephrosceles* (Struhsaker et al., 2004)]; and the observation that folivorous primates abundance can be predicted by the distribution of mature leaves with a high protein-to-fibre ratio (Chapman et al., 2002, 2004; Ganzhorn et al., 2017).

The aforementioned findings question the assumption that folivores rely on ubiquitous and evenly distributed food resources with a low and uniform nutritional quality. The extent to which folivorous primates are influenced by variation of food quality, distribution, and abundance may vary between species, and cannot be underestimated (Snaith & Chapman, 2007; Tombak et al., 2012). There are several pieces of evidence that folivores select high-quality young leaves that are patchily distributed and vary in nutritional quality and availability (Glander, 1982; Oates, 1994; Harris, 2006; Simmen et al., 2014). Even mature leaves, which are expected to be ubiquitous and evenly distributed, may vary hugely in their nutritional quality and need to be carefully selected by folivorous primates (Koenig et al., 1998; Koenig, 2000). Recent models, however, still consider folivorous primates as not constrained by patch depletion, and suggested funnelling (i.e. physical constraint that reduce group size when travel routes are narrow and food items are sparse) as alternative hypothesis to explain the relationship between group size and day range or travel cost in some species (Isbell, 2012). The question whether and how folivores are constrained by food abundance, quality, and availability is thus open to debate and needs further evidence from other species.

1.2. The woolly lemurs (*Avahi* spp.)

Woolly lemurs are strepsirrhine primates of the genus *Avahi* (Jourdan, 1834), that is the only nocturnal genus of the family Indriidae (Burnett, 1828). The family Indriidae also includes the diurnal genera *Propithecus* and *Indri* (Mittermeier et al., 2010). The common English name of the genus *Avahi* refers to the woolly appearance of the dense fur, while the vernacular Malagasy name "fotsy fe" (i.e. white leg) refers to the characteristic white patches on their thighs (Thalmann, 2003). There are currently nine recognised species of woolly lemurs: the Endangered Betsileo woolly lemur *A. betsileo*, Bemaraha woolly lemur *A. cleesei*, Southern woolly lemur *A. meridionalis*, Masoala woolly lemur *A. moreeorum*, Western woolly lemur *A. occidentali*s, and Sambirano woolly lemur *A. unicolor*; and the Vulnerable Eastern woolly lemur *A. laniger*, Peyrieras's woolly lemur *A. peyrierasi*, and Manombo woolly lemur *A. ramanantsoavanai* [conservation status based on the IUCN red list assessed in 2012 (Andriaholinirina et al., 2014)].This genus reaches the highest diversity in the rainforest along the eastern coast of Madagascar, while only two species are present in the dry deciduous forest (*A. cleesei* and *A. occidentalis*) (Mittermeier et al., 2010) (Figure 1.1).

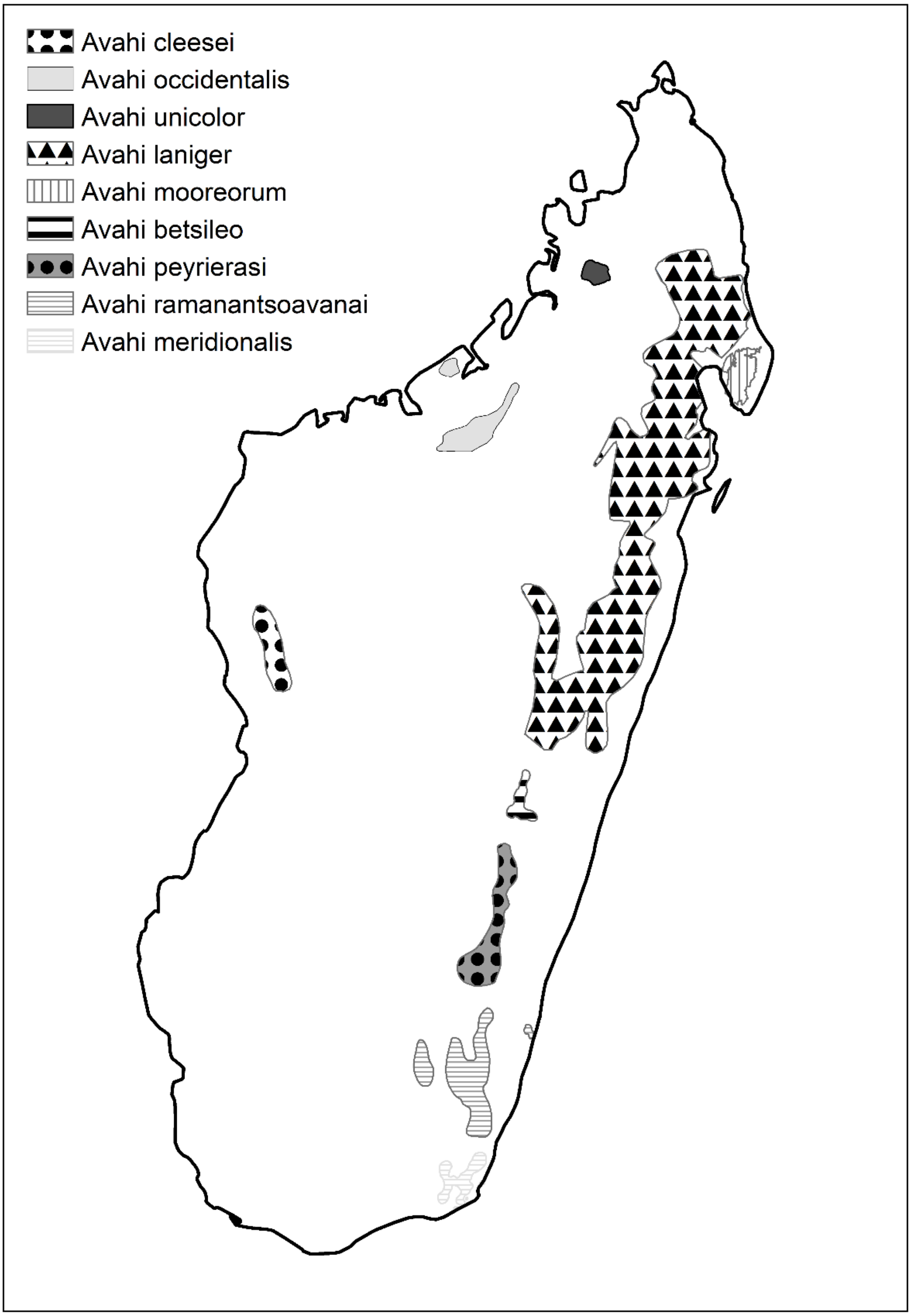

Figure 1.1: Distrubution of the 9 species of sportive lemurs *Avahi* spp. in Madagascar. Geographic ranges were retrieved from the IUCN red list website.

Woolly lemurs are the only true folivorous primates active at night (Ganzhorn, 1985). Weighting between 750 and 1400 g (Lehman, 2007), woolly lemurs are also at the lowest limit of body size for a folivorous diet [700g (Kay, 1984)]. The combination of a folivorous diet, small body size, and nocturnal activity makes this genus peculiar and often compared to the ecologically similar genus *Lepilemur* (Ganzhorn, 1993; Warren & Crompton, 1997a; Thalmann, 2001). Woolly lemurs have anatomical adaptations to allow midgut fermentation such as a sacculated cecum and a looped colon (Chivers & Hladik, 1980; Martin, 1990). Furthermore, the locomotion of this genus is energetically expensive, since woolly lemurs are mainly vertical leapers (Warren & Crompton, 1997b).

Another peculiar trait of the genus *Avahi* is the social structure that is exceptional among nocturnal primates, since woolly lemurs are monogamous, and they feed and move as a cohesive family group containing one adult pair and one to three offspring (Thalmann, 2003). Moreover, they show parental care and females carry their infants during their nocturnal activity, which is rare among nocturnal prosimians (Thalmann, 2003; Kappeler, 2014). For these reasons and for the presence of exclusively diurnal genera within the Indridae with the exception of *Avahi*, woolly lemurs are considered secondarily nocturnal and their social behaviour a retention from a former diurnal activity pattern (Ganzhorn, 1985; Müller & Thalmann, 2000).

The main threats for woolly lemurs are habitat loss and slash and burn agriculture, while opportunistic hunting can occur, but it is not considered a major threat for this cryptic species (Andriaholinirina et al., 2014). Deforestation and logging jeopardise this genus of vertical leapers that require a continuous canopy to move (Norscia, 2008). Since the species of this genus are strictly folivorous and require large patches for their specialised locomotion, they can only be protected *in situ* (Thalmann, 2003). Furthermore, due to the monogamous social behaviour that limits breeding opportunities, woolly lemurs are at risk of demographic extinction (Thalmann, 2003). For all the abovementioned reasons, and for the Endangered conservation status of most of the species, it is important to implement conservation strategies that could include woolly lemurs' protection as a priority.

1.3. Aims of the study

The theoretical aim of this work is to test whether the southern woolly lemur *Avahi meridionalis* inhabiting the Tsitongambarika (TGK) lowland rainforest is constrained by food availability. This species represents an ideal model to test the effect of food availability on folivorous primates since it is a pair living species (i.e. group size is not a factor to be considered) and it occurs in rainforest, a habitat which is expected to have uniform distribution and less differences in the nutritional quality of leaves compared to deciduous forests because leaves have a longer lifespan (Ganzhorn, 1992). Thus, I expect no major influence of seasonal variations on the ecology of this species based on the traditional socioecological models (Wrangham, 1980; Isbell, 1991; Sterck et al., 1997; Isbell, 2012), or *vice versa* seasonal variations on the ecology of this species if *A. meridionalis* is limited by food availability (Snaith & Chapman, 2005, 2007, 2008; Saj et al., 2007; Harris et al., 2010). The other major aim of this work is to present data related to the conservation of the Endangered *Avahi meridionalis* and overall of the TGK Protected Area that is one of the last remnant lowland rainforests in Madagascar. The more specific objectives of this study are:

- To test whether folivorous lemurs inhabiting the eastern rainforest of Madagascar are influenced by altitudinal variations in a similar way than frugivorous and omnivorous lemurs;
- To determine whether the ranging patterns and the sleeping site selection of southern woolly lemurs in TGK are influenced by the availability of young leaves;
- To ascertain whether the dietary choices of southern woolly lemurs in TGK are influenced by the availability of young leaves;
- To investigate the activity patterns of southern woolly lemurs in TGK and determine whether this species shows a cathemeral activity;
- To assess whether teachers from a rural community close to TGK can retain knowledge one year after environmental education lessons were given.

In Chapter 3, I estimated the density of lemurs in the Tsitongambarika Protected Area to explore the influence of elevation on the encounter rates of the local lemur community and to provide important information for their conservation. In Chapter 4, I investigated the influence of food availability on the ranging patterns of this species. In Chapter 5, I explored the influence of food availability on the feeding ecology of the sourthern woolly lemur. In Chapter 6, I illustrated the activity patterns of *A. meridionalis* and highlighted the opportunistic cathemerality of this species. In Chapter 7, I presented the results of a conservation education program meant to raise awareness on environmental issues related to lemur ecology and conservation to local teachers. A synthesis of the topics included in this dissertation and the links between them is illustrated in Figure 1.2.

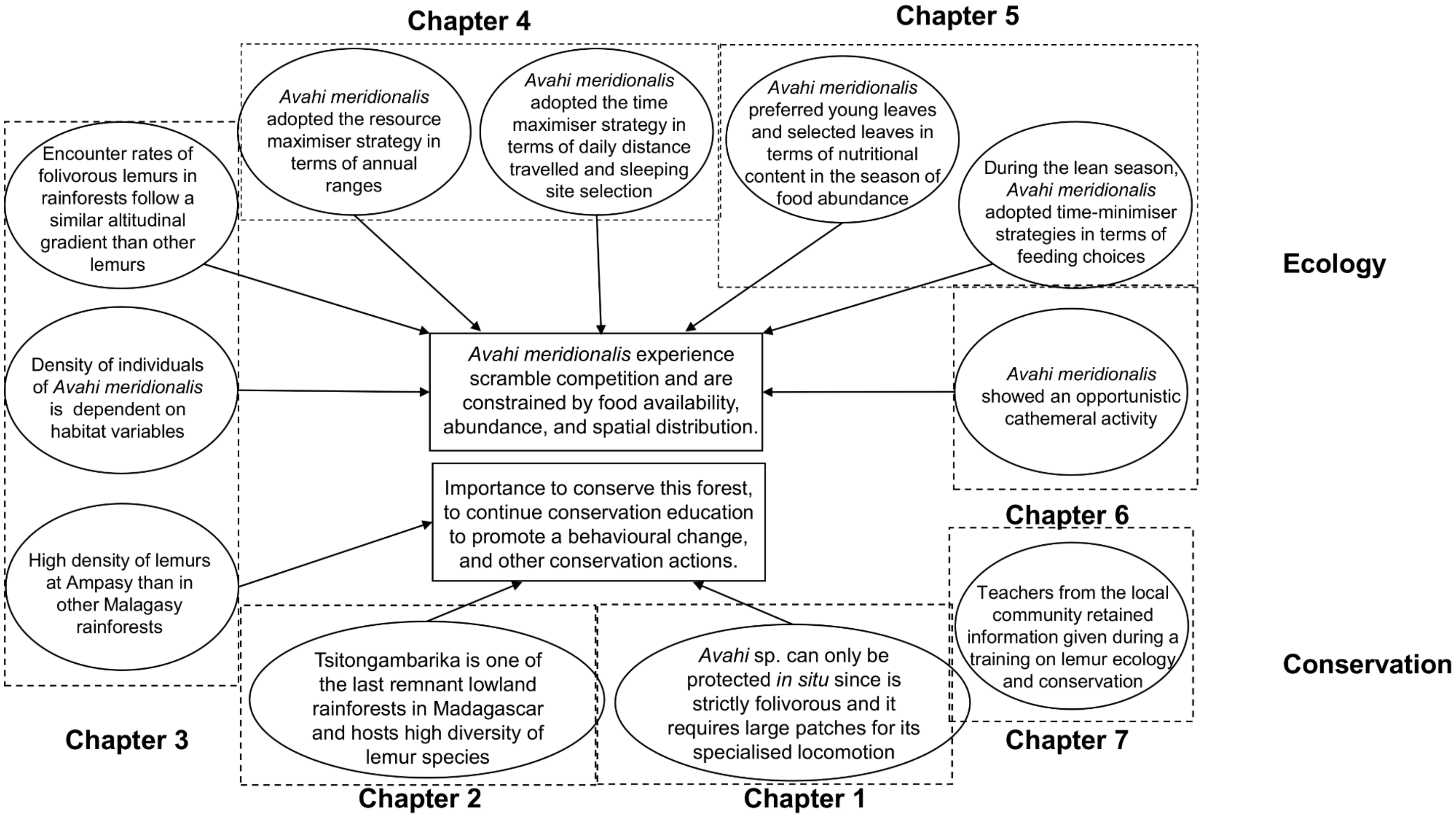

Figure 1.2: Word flowchart representing the topics of this dissertation.

Chapter 2. General methods

2.1. Study area

The study started in May 2015 and finished in July 2016, and was conducted at the newly established research station of Ampasy (S 24° 34’ 58’’, E 47° 09’ 01’’). The Ampasy valley is around 3 km^2 and it is located in the northernmost portion of the Tsitongambarika (TGK) forest (Figure 2.1). The annual rainfall during the study period (July 2015-July 2016) was around 2400 mm, and the only months with less than 100 mm rainfall were July, September, and October 2015 (M. Campera, unpub. data). TGK is a Protected Area connected to the Andohahela National Park, and it is the southernmost lowland rainforest of Madagascar (BirdLife International, 2011). TGK includes an area of around 605 km^2 of rainforests at a maximum altitude of 1,358 m a.s.l. and encompasses large areas of lowland rainforests (0-600 m a.s.l.) (Ganzhorn et al., 1997; BirdLife International, 2011). This forest represents one of the last vast expansion of lowland rainforests on the island (Schwitzer et al., 2013). For this reason, and for the many threatened lemur species in the area, TGK is considered a priority area for lemur conservation (Schwitzer et al., 2013).

The TGK Protected Area was created in 2008 by the ministry of the Environment and Forests and has been co-managed by the NGO Asity Madagascar (BirdLife Madagascar) and KOMFITA (Community Forest Management) since 2013 (Campera et al., 2017). This area provides an important source of products for local people including firewood, charcoal, timber, bushmeat, and medicinal plants (BirdLife International, 2011; Campera et al., 2017). The most significant threat to the TGK forest is slash and burn agriculture and deforestation, especially in areas below 800m a.s.l. (BirdLife International, 2011; Schwitzer et al, 2013).

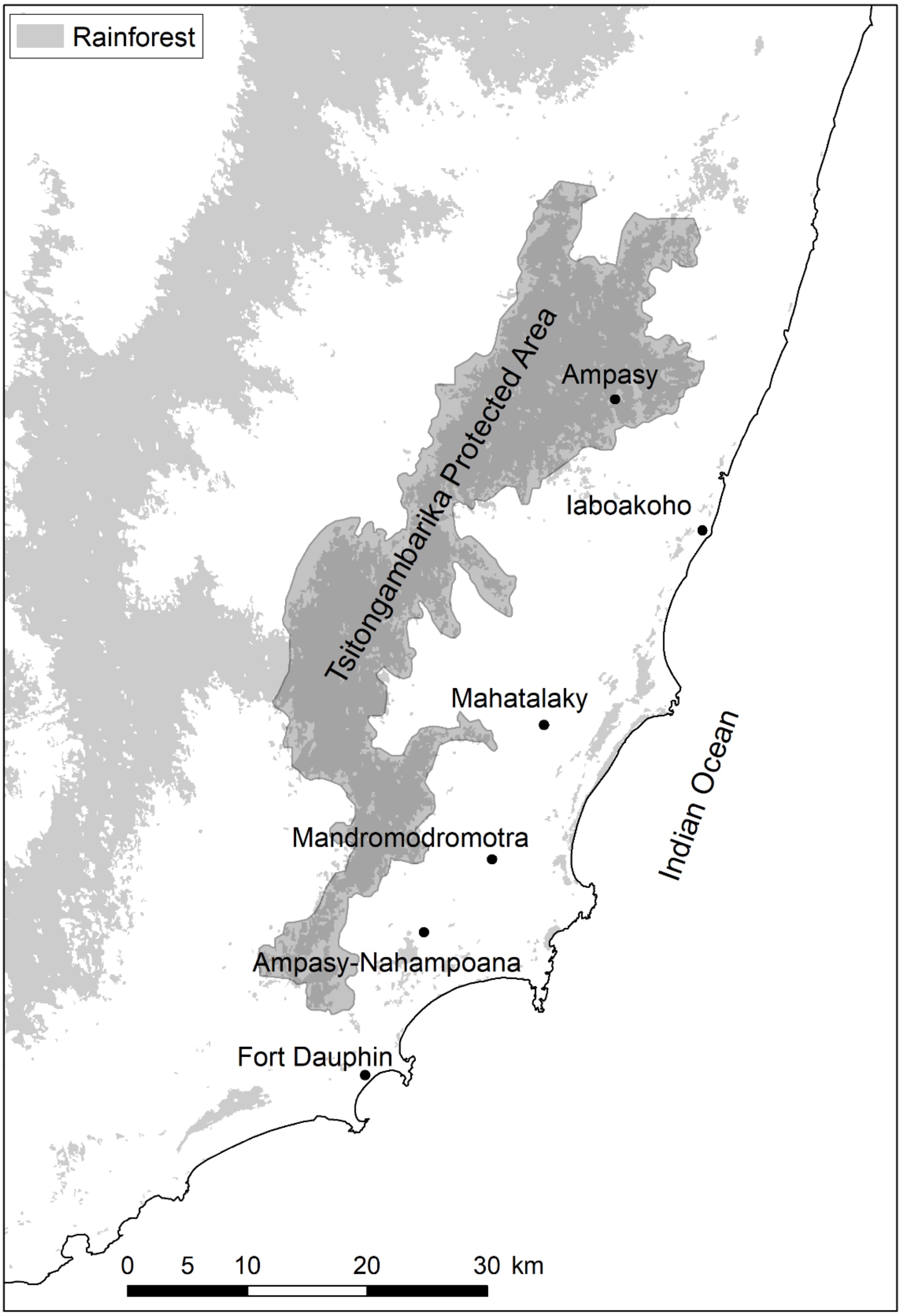

Figure 2.1: **Map of the study site**. Location of the Ampasy research station in the Tsitongambarika Protected Area, in south-east Madagascar.

Asity and KOMFITA offered new job opportunities to local people and limited the impact on the forest. Around 20 people from the municipality of Iaboakoho were hired to patrol the forest and reprimand those carrying out illegal activities. Other people were supported via training in sustainable agriculture (Campera et al., 2017). As part of the local management a buffer zone was created in which local people are allowed to extract timber and firewood, and hunt exotic species (Razafitsalama & Ravoahangy, 2010). Other actions supported by Asity and KOMFITA involved sustainable farming, a tree nursery and reforestation, effective enforcement of the dina (i.e. local law), and environmental education (Razafitsalama & Ravoahangy, 2010; Rakotoarimanana, 2016).

2.2. Context

A preliminary assessment of the lemurs at Ampasy was conducted by Dr Tim Eppley in 2013 (Nguyen et al., 2013). He stayed in the area for around two months looking for the southern bamboo lemur *Hapalemur meridionalis* for his PhD project. Since he did not encounter the species during this period, he decided to rely on a backup plan and study the southern bamboo lemur in the littoral forest of Mandena. I started my PhD project in April 2015 together with Marco Campera, a PhD student from Oxford Brookes University. My original project was about exploring niche partitioning between the ecologically similar Fleurette's sportive lemur *Lepilemur fleuretae* and *Avahi meridionalis* at Ampasy. Marco Campera's project consisted in evaluating the effect of fragmentation on the collared brown lemur *Eulemur collaris*. Similar to what Dr Eppley experienced with southern bamboo lemur, we did not find any individual of collared brown lemur at Ampasy for the first two months, probably due to the high hunting pressure on the two species (Campera et al., 2017). We thus decided, together with our supervisor, Dr Giuseppe Donati, to split my original project in two projects, one focusing on the behavioural ecology and conservation of *A. meridionalis* and one focusing on the ecological flexibility and conservation of *L. fleuretae* (Figure 2.2). The phenological patterns shown in my dissertation (Chapter 2.4) are presented in detail in Chapter 3 of Marco Campera's dissertation. He also shows details of the validation of the unsupervised learning algorithm method to extrapolate activity patterns from accelerometer data. We plan to maintain the original theoretical framework for future publications.

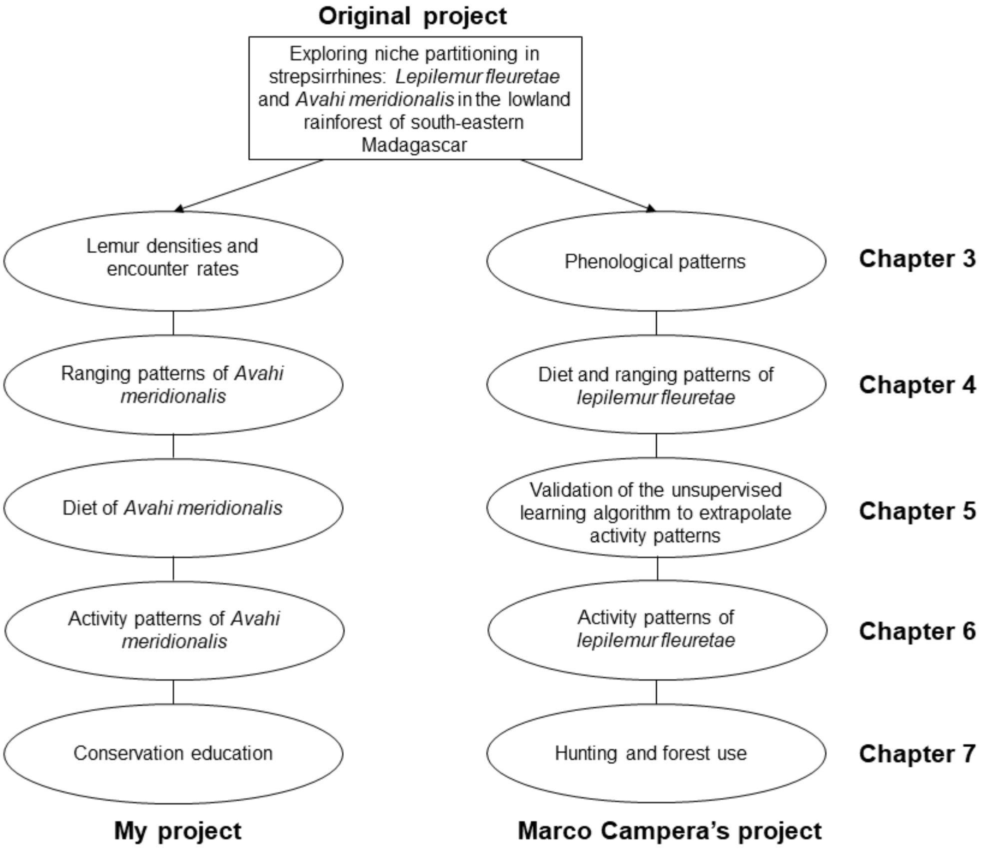

Figure 2.2: Division of the original project into the two new projects.

A temporary research station was firstly built by Dr Eppley in 2012, but nothing was left when we arrived at Ampasy in 2015. Asity asked local people to create a new temporary research station with three shelters for tents, a kitchen, a shower, and a toilet (Figure 2.3).

Figure 2.3: Temporary research station at Ampasy. From April 2015 to February 2016.

In February 2016, QIT Madagascar Minerals (QMM) started the construction of a permanent research station, conluded in April 2016 (Figure 2.4). The Ampasy valley is, in fact, included in the off-set site of QMM, and the mining company planned to build the research station to achieve a net positive impact on biodiversity (Temple et al., 2012).

Figure 2.4: Permanent research station at Ampasy. Since February 2016.

Two MSc students from Oxford Brookes University, Fiona Bensard and Megan Phelps, did their field work at Ampasy during the period I was there. Fiona Besnard investigated the local taboos on the aye aye *Daubentonia madagascariensis*, while Megan Phelps studied the perception of crop raiding of *H. meridionalis* by local people. They both collected data on the habitat structure at Ampasy via vegetation plots. Moreover, three volunteers contributed in the data collection: Julie Maguiere helped with the data collection on lemur densities, George Selley took photographs of study animals, and Carina Morris helped in collecting data on habitat structure and collected preliminary data on the presence of nests of the Tanosy mouse lemur *Microcebus tanosi*. A PhD student, Rachel Sawyer, and a BSc student, Zoe Amieli-Cooper arrived in July 2016 to do their projects (Table 2.1).

Table 2.1: List of students who worked alongside me at Ampasy.

	Apr 2015-Jun 2015	Jul 2015-Sep 2015	Oct 2015-Mar 2016	Apr 2016-Jun 2016	Jul 2016
Marco	X	X	X	X	X
Julie		X			
George		X			
Carina				X	X
Megan				X	X
Fiona				X	X
Rachel					X
Zoe					X

2.3. Study animals

A team, specialised in capturing animals and associated to the Madagascar Biodiversity Partnership, a project leaded by Dr Edward E. Louis Jr., performed the captures of six individuals of *Avahi meridionalis* at Ampasy (Table 2.2). They captured the animals between 6 and 9 July 2015, after I previously selected areas with a higher density of *A. meridionalis*. The team anesthetised the animals with a dose of 10 mg/Kg of Telazol (tiletamine HCl and zolazepam HCl; Zoetis Inc.) by using remote capture rifles. They used rifles since they were the only option for capturing individuals of *A. meridionalis* at Ampasy due to the high canopy height (Nguyen et al., 2013). I equipped the individuals with radio-collars (RI-2D, Holohil System Ltd, 11g) to ensure systematic observations. The animals were supervised until regaining full mobility in trees and there were no injuries as a consequence of the captures. The collars were below the 5 % threshold of the subjects' weight recommended for arboreal animals (Wheater et al., 2011). The team performed the re-captures to remove the collars between 15 and 18 July 2016 with the same procedure.

Table 2.2: **Body measurements of captured animals**. Body parameters of sixindividuals of *Avahi meridionalis* at Ampasy captured between 6 and 9 July 2015.

Parameter	**F1**	**F2**	**F3**	**F4**	**F5**	**M1**
Weight (g)	1000	1290	1160	1325	1260	1050
Body temperature (ºC)	37.1	37.0	38.7	37.1	36.2	36.4
Head Crown (cm)	9.2	9.3	8.7	9.0	8.9	8.1
Body length (cm)	19.3	21.5	21.0	22.6	21.6	19.3
Tail length (cm)	32.3	36.9	32.7	35.4	36.2	34.0
Upper canine length (cm)	3.2	3.0	2.4	3.1	3.2	3.1

F: female; M: male

2.4. Phenology of young leaves

The presence of young leaves was monitored twice a month from July 2015 to June 2016 on a sample of 200 species (769 individuals with up to five individuals per species) included in four phenological trails of 500m each (M. Campera, unpub. data). For each species I calculated the Food Availability Index (FAI) as the product of stem density (trees/ha) and the phenological score for each species [modified from Guo et al. (2007)]. The stem density was calculated based on 33 plots of 10X100 m (M. Campera, unpub. data). To calculate the phenological score, I calculated the proportion of plants with young leaves for each species and multiplied by the mean diameter at breast height (measured in decimetres) for that species. I calculated the highest possible FAI, called total FAI, by adding the maximum FAI for all the species. I calculated a monthly percentage for each phenological phase with the following formula: Σ monthly FAI*i*/total FAI *100, where the monthly FAI*i* is the monthly FAI for the species *i* considering the 200 species (Figure 2.5).

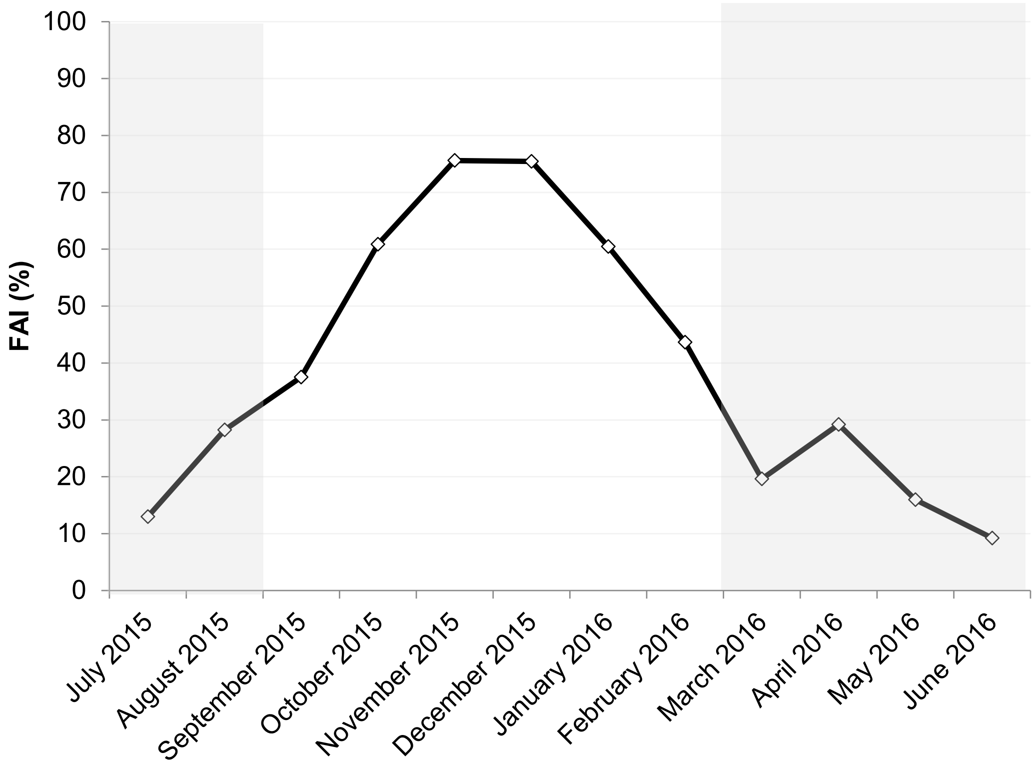

Figure 2.5: Phenology of young leaves at Ampasy. Monthly availability of young leaves in Ampasy from July 2015 to June 2016. Period of abundance is in the white background, lean period in the grey background.

2.5. Behavioural data collection

I followed each individual with radio-collar once a month (from dusk to dawn when possible) from August 2015 to July 2016. In total, I collected 148.2 h of behavioural data via continuous sampling (Altmann, 1974). In the lean season (March-August; Figure 2.5), I collected 83.4 h, while in the season of food abundance (September-February; Figure 2.5) I collected 64.8 h. The data collection was particularly challenging since study areas were inaccessible during periods of heavy rain. September and October 2015 were the only months during the study period in which rainfall was below 100 mm (M. Campera, unpub. data). During behavioural observations, I collected data on: activity (feeding, resting, moving) and food items consumed (Mature Leaves, ML; Young Leaves, YL) (see Appendix I).

2.6. Ethics statement

I obtained ethical approval for animal captures and handling from Oxford Brookes University following the “Guidelines on the observation, handling and care of animals in field research” (Sherwin, 2006). I obtained permission for the field research from the Ministry of Environment and Forest (53/16/MEEMF/SG/DGF/DAPT/SCBT.Re) (Appendix II).

Chapter 3. Lemur abundance in the lowland rainforest of Tsitongambarika and altitudinal comparison of encounter rates within Malagasy rainforests.

3.1. Introduction

Mammal abundance can be shaped by a variety of abiotic and biotic factors. For example, forests with higher structural complexity and dense undergrowth show higher mammal abundance (Emmons, 1984). Also, plant species diversity is known to be positively correlated to animal species richness (Scherber et al., 2010). Climatic variables such as rainfall are indirectly correlated to species richness and abundance (Reed & Fleagle, 1995; Kamilar, 2009) by influencing vegetation type, productivity, and diversity (Peres & Janson, 1999; Dupont et al., 2008). In primates, resource availability and seasonality are recognised predictors of species abundance (Ganzhorn et al., 1997; Janson & Chapman, 1999), especially for small- and medium-sized primates (Stevenson, 2016). Furthermore, having a more generalised diet usually leads to less difference of primate abundance between habitats, while primates with more specialised diets can show higher variation (Moura, 2007).

Even when considering all these factors, altitude has a main impact on primate abundance (Caldecott, 1980). This is because plant species diversity and density usually decrease at higher altitudes (Ganas et al., 2004; Körner, 2007; Kim et al., 2011), and a decrease in tree height and diameter at breast height (DBH) with altitude is expected (Koechlin et al., 1974). Also, the ratio between energy expenditure and nutrient intake is unfavourable at high elevations due to increased costs of thermoregulation and locomotion in cool and harsh habitats (Caldecott, 1980). For these reasons, primates need flexible adaptations to survive at high-altitudes (Hanya et al., 2004; Ganas & Robbins, 2005). Flexible behaviours include reducing group size [Japanese macaque *Macaca fuscata* (Hanya et al., 2004); yellow baboons *Papio cynocephalus ursinus* (Henzi et al., 1990); Nilgiri langur *Trachypithecus johnii* (Kumara & Singh, 2004); Javan lutung *Trachypithecus auratus* (Nijman, 2014)], increasing home range size [silvery gibbon *Hylobates moloch* (Kim et al., 2011)], increasing time spent feeding as a consequence of the reduction of plant species diversity and density [gelada *Theropithecus gelada* (Iwamoto & Dumbar, 1983)], increasing time spent close to the forest edge in response to the higher availability of invertebrates (Grow et al., 2013). These adaptations might lead to lower population densities at higher elevations when comparing the same forest type at lower altitudes as exhibited by several primate species [silvery gibbon (Kim et al., 2011); Javan lutung (Nijman, 2014); Udzungwa red colobus *Procolobus gordonorum*, Angolan colobus *Colobus angolensis palliatus*, blue monkey *Cercopithecus mitis monoides* (Barelli et al., 2015)].

Madagascar shows an elevational asymmetry and a dramatic reduction of the eastern lowland rainforest area since large portions drifted away as a consequence of the break-up of Indo-Madagascar subcontinent between 90 and 80 million years ago (Krause, 2003; Wells, 2003). For this reason, lemurs are expected to show traits of ecological and physiological flexibility to adapt to the biogeographical constraints at mid-elevations (Goodman & Ganzhorn, 2004). In accordance to this hypothesis, the average mid elevation point for lemur species diversity (around 900 m a.s.l.) is higher than that for primates outside Madagascar [around 400 m a.s.l. (Goodman & Ganzhorn, 2004; Lehman, 2014)]. Furthermore, a study on faunal and floral inventories in relation to elevational variation in the Andohahela rainforest, south-east Madagascar, revealed that plant species density and diversity is similar between low- and mid-altitude plots, while plant diversity decreases at high-altitudes (Feistner & Schmid, 1999). Conversely, botanical plots in Costa Rica suggested a more gradual decrease in plant diversity with altitude (Lieberman et al., 1996). More evidence is required to support the hypothesis that lemur species occurring in the eastern rainforest evolved traits to adapt to mid-altitudes. One way to support this hypothesis is to compare lemur encounter rate between low- and mid-altitudes, since species are expected to be more abundant when they are better adapted to a certain habitat (Reed & Fleagle, 1995; Kamilar, 2009). Finding similar encounter rates of primates at low- and mid-elevations in Malagasy rainforests but not in rainforests of other continents may provide support to the hypothesis that lemurs are well adapted to mid-elevations. This comparison has been difficult as most lowland Malagasy rainforests already disappeared on the island or their current size is such that other factors play an overriding role in determining abundance (Goodman and Ganzhorn 2004).

In this study I collected new data on the encounter rates of lemur species inhabiting the lowland rainforest of Ampasy, in the Tsitongambarika Protected Area (TGK). I then compared the lemur encounter rates at TGK with data on the same genera in other low-altitude, mid-altitude, and high-altitude rainforests in Madagascar. I predicted:

1) Encounter rates of lemur species in the lowland rainforest of Ampasy to be similar to the encounter rates of other lemur species of the same genera in mid-altitude rainforests and higher than the encounter rates at high-altitude rainforests.
2) Highly folivorous lemur genera to show a different pattern of encounter rates than frugivorous and omnivorous genera since they are expected to be less constrained by the reduction of plant species diversity (see Chapter 1).
3) Possible trends towards competitive exclusion between ecologically similar species. Since a difference in the use of vegetation strata is considered an important way of differentiation between ecologically similar species (Schreier et al., 2009), I expect the encounter rates of ecologically similar species to be negatively correlated.

In addition to the main aim of this study, I provide important information about the abundance of the species inhabiting the TGK forest.

3.2. Methods

3.2.1. Study site and species

The lowland rainforest of Ampasy is located in the northernmost portion of the TGK Protected Area (see Chapter 2.1). The lemurs confirmed at Ampasy are: Anosy mouse lemur *Microcebus tanosi*, aye-aye *Daubentonia madagascariensis*, collared brown lemur *Eulemur collaris*, Fleurete’s sportive lemur *Lepilemur fleuretae*, greater dwarf lemur *Cheirogaleus cf. major*, southern bamboo lemur *Hapalemur meridionalis*, and southern woolly lemur *Avahi meridionalis* (Campera et al., 2017).

3.2.2. Data collection

I established nine transects of 1 km each along pre-existing trails throughout the forest (Figure 3.1). I established transects with a minimum distance of 200 m in between to maintain independence (Bersacola et al., 2015). I did not cut new transects since it might have had negative effects on primate populations by increasing hunting (Bezanson et al., 2013). Transects encompassed both interior and edge of the forest to cover the habitats of all lemur species, and the altitude of transects ranged from 11 to 346 m a.s.l. In pairs of one researcher and one local assistant, we walked each transect once a month by day and by night from May 2015 until July 2016. I trained the other students who helped with the transects to guarantee inter-observer consistency and the reliability of data.

The team walked the transects at an average speed of about 1–1.5 km/h, in the early morning (between 6:30 and 7:30) or late afternoon (between 15:00 and 16:00) for diurnal transects, and early night (between 19:00 and 21:00) for nocturnal transects. During nocturnal transects I used zoom-in headlamps that allowed to spot animals up to 50 m. I completed the transects in around 1-1.5 h depending on the number of animals observed (average: 1 h 13 m, range: 54 m-1 h 57 m). I did not perform certain transects during the rainy season since some areas of the forest were unreachable. On observing a primate group, I recorded: time, species, number of individuals seen, perpendicular distance from the transect, and height. In case of clusters, I estimated the average distance and height considering all the animals. I extensively trained in estimating perpendicular distance and height before starting the data collection to ensure quick and reliable estimates. I estimated animals’ height to the nearest metre. In total, I walked 125 km by day and 96 km by night. I considered only diurnal transect for cathemeral lemurs (*H. meridionalis* and *E. collaris*) and nocturnal transects for nocturnal lemurs (all the other lemurs present in the area). For *C. major* I excluded months of hibernation [April-September (Blanco et al., 2013)] and so the total effort for this species was 34 km.

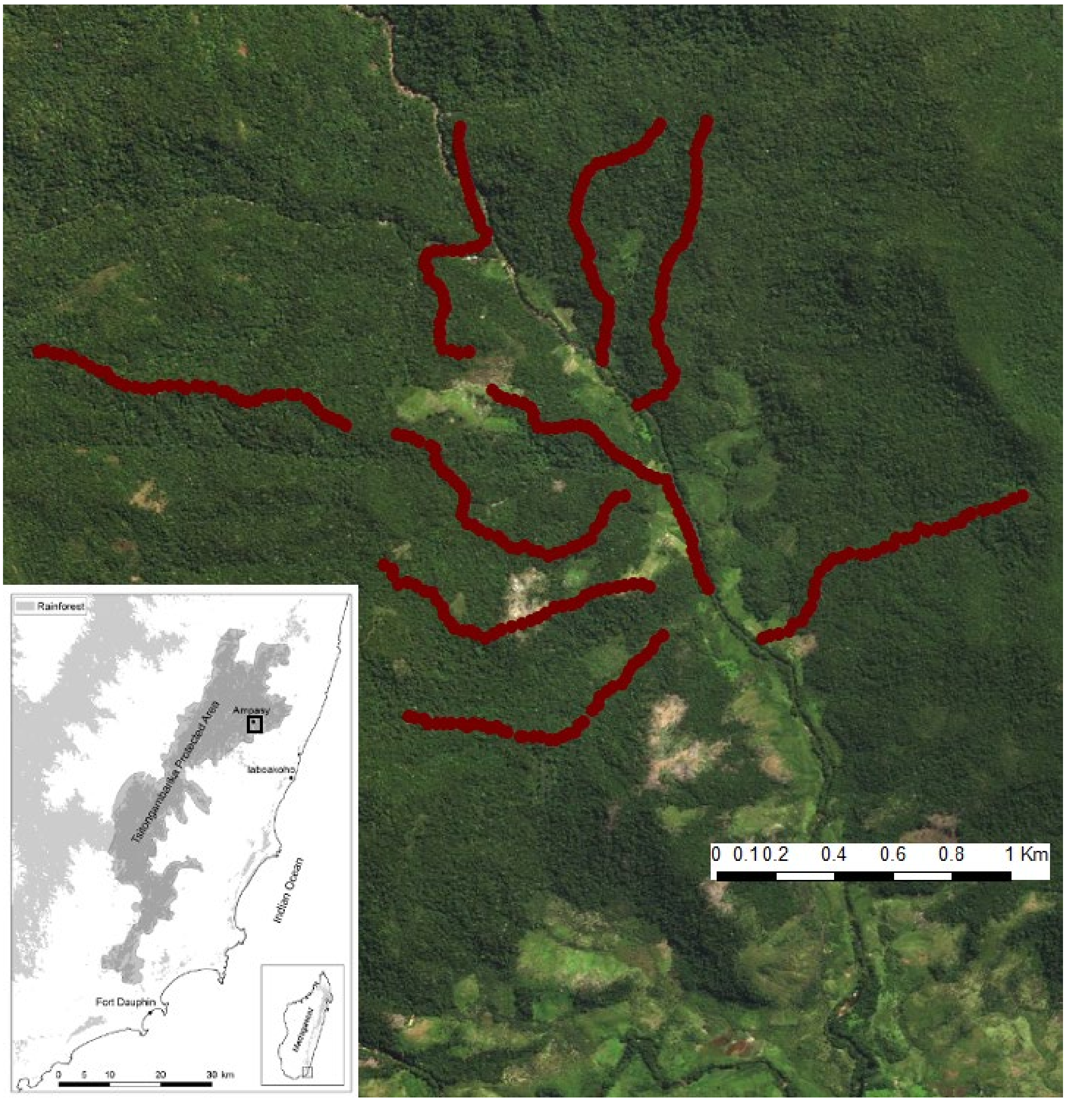

Figure 3.1: Location of the transects. Location of the nine transects used to estimate abundance and encounter rates of lemur species at Ampasy between May 2015 and July 2016.

3.2.3. Data analysis

I analysed the data via the Conventional Distance Sampling (CDS) engine in Distance software (Buckland et al., 2001; Thomas et al., 2010). I estimated animal encounter rates for each species as the number of individuals divided by the distance (km) surveyed. It was not possible to use the CDS engine to calculate densities of *D. madagascariensis* due to the low sightings, thus I only present encounter rate for this species. I firstly explored the untruncated and unbinned data fitted with key functions (half-normal, hazard rate, and uniform) and series adjustments (cosine and simple polynomial) (Murphy et al., 2016). I excluded the negative-exponential key function as suggested by Buckland et al. (2001). Based on histograms, I determined whether and where to right-truncate data and how to bin observations into discrete distance classes to improve key function fit (Murphy et al., 2016). After the potential truncation, I compared models with the three key functions and their respective series adjustments using Akaike's Information Criteria corrected for small sample sizes [AICc (Akaike, 1973)] and selected species-specific models based on the lowest AICc score. All the models I report passed ($P \leq 0.05$) the goodness-of-fit test (Buckland et al., 2001; Thomas et al., 2010).

To explore the first two predictions, I compared the data I extrapolated from species at Ampasy with the data of species from the same genera in other rainforests [excluding the littoral forest on sandy soil that is a different habitat (Bollen & Donati 2005, 2006)]. Since by comparing different habitats it is not possible to isolate altitude from other ecological factors, I only considered rainforests for the comparison. Still, habitat disturbance might be a confounding factor in the analysis although most of the sites considered are undisturbed or lightly disturbed. It was not possible to include this factor in the analysis since most of the studies did not report the disturbance level along transects. I considered low-altitude when below 600 m a.s.l.; mid-altitude when between 600 and 1400 m a.s.l.; and high-altitude when above 1400 m a.s.l (Ganzhorn et al., 1997; Irwin et al., 2005). I only considered studies with a minimum sampling effort (i.e. the total length of transects walked at different altitude categories) of 5 km to avoid including data biased from a low sample size. I calculated the encounter rates for each category of altitude forest when not given directly (i.e. Schmid & Smolker, 1998; Feistner & Schmid, 1999) or when other parameters were given but it was not given directly (i.e. Lehman 2006; Lehman et. al., 2006; Herrera et al. 2011). I ran a comparison between encounter rates since authors reported densities from different methodologies. I compared encounter rates via Generalised Linear Mixed Models using altitude as fixed factor. I fit the dependent variable with different functions and selected the gamma function since it had the lowest AICc score. I selected the distance walked in km as covariate to control for the sampling effort. I selected the genus as the subject to control for the difference of encounter rates within species of the same genus. I selected the genus as a random factor to control for the effect of considering a subset of genera inhabiting the Malagasy rainforest. I ran a sequential Bonferroni post-hoc test to evaluate pairwise differences between altitude categories. Also, I ran the test considering highly folivore genera (*Avahi* sp., *Hapalemur* sp., and *Lepilemur* sp.) and other genera separately to test the second hypothesis.

To test whether there were trends towards competitive exclusion, I ran Spearman correlations between encounter rates of the species in each transect. To test whether animals used different strata as a niche separation strategy, I analysed animals' height via t-tests for independent data using pairwise comparisons between species occupying a similar niche (cathemeral: *H. meridionalis* and *E. collaris*; folivorous nocturnal: *A. meridionalis* and *L. fleuretae*; non-folivorous nocturnal: *C. major* and *M. tanosi*). A statistical comparison was not possible with average heights of *D. madagascariensis* due to the low sightings for this species. I performed statistical tests using IBM SPSS 23 as software and P < 0.05 as threshold for the significance level.

3.3. Results

3.3.1. Abundance and density estimates

During the 125 km of diurnal transects I encountered groups of *E. collaris* 30 times (140 individuals) and groups of *H. meridionalis* 21 times (41 individuals) (Table 3.1). In the 96 km of nocturnal transects the most frequent lemur I observed was *L. fleuretae*, encountered 181 times (197 individuals). I encountered *M. tanosi* 130 times (132 individuals), *A. meridionalis* 66 times (79 individuals), *C. major* ten times (11 individuals), and *D. madagascariensis* two times (two individuals) (Table 3.1). I found a positive correlation between encounter rates of *A. meridionalis* and *M. tanosi* (Spearman correlation: r = 0.72, P = 0.029, N = 9 transects). No other significant results have been found for the other correlations. Estimated average number of individuals in TGK based on my data is: 58,512 (95% CI range: 45,079-75,939) *M. tanosy*; 48,770 (range: 39,149-60,812) *L. fleuretae*; 31,685 (range: 19,441-51,640) *E. collaris*; 17,536 (range: 12,702-24,209) *A. meridionalis*; 14,704 (range: 8,592-25,232) *H. meridionalis*; and 13,006 (range: 6,668-25,368) *C. major* (Table 3.1).

Species	Animal encounter rate (ind/km)	Key function-series expansion adjustment	ESW (95% CI)	Probability of detection (95% CI)	Mean group size (95% CI)	Density of groups (95% CI) Km$^{2-1}$	Density of individuals (95% CI) Km$^{2-1}$	N total in TGK (95% CI)
Avahi meridionalis	0.87	HN-C	13.79±1.13 (11.69-16.22)	0.39±0.03 (0.33-0.46)	1.17±0.05 (1.07-1.28)	27±7 (16-47)	32±8 (19-55)	19,378±4,849 (11,253-33,370)
Cheirogaleus major	0.32	HN-SP	6.85±1.30 (4.47-10.49)	0.57±0.11 (0.37-0.87)	1.03±0.02 (1.00-1.08)	21±7 (11-43)	22±7 (11-45)	13,006±4,352 (6,504-26,007)
Daubentonia madagascariensis	0.02	NA	NA	NA	NA	NA	NA	NA
Eulemur collaris	1.12	HN-SP	10.04±1.57 (7.30-13.78)	0.50±0.08 (0.37-0.69)	4.17±0.42 (3.40-5.11)	13±3 (7-22)	52±15 (29-93)	31,685±8,979 (17,813-56,378)
Hapalemur meridionalis	0.33	HN-SP	8.70±1.29 (6.40-11.84)	0.54±0.08 (0.40-0.74)	1.78±0.22 (1.38-2.31)	10±3 (6-18)	18±5 (10-33)	10,932±3,181 (6,056-19,732)
Lepilemur fleuretae	2.26	HN-C	13.56±1.03 (11.68-15.75)	0.34±0.03 (0.29-0.39)	1.09±0.02 (1.05-1.11)	75±8 (60-93)	81±9 (65-101)	49,259±5,349 (39,505-61,421)
Microcebus tanosi	1.46	HN-SP	7.40±0.39 (6.67-8.22)	0.34±0.02 (0.30-0.37)	1.01±0.01 (1.00-1.03)	96±12 (74-125)	97±12 (74-126)	58,526±7,110 (44,999-76,119)

Table 3.1: Encounter rates, density, and abundance of lemur species at Ampasy. Encounter rates, density, and abundance estimates (mean ± standard error), obtained via the software Distance, of the species present at the Ampasy forest, northernmost portion of Tsitongambarika (TGK). Key functions are HN (Half-Normal). Series expansion adjustment are C (Cosines) and SP (Simple-polynomial). ESW: effective strip width. Densities are individuals or groups per square kilometre.

“NA” = Not Available, number of sightings was not enough to estimate densities.

3.3.2. Effect of altitude

The model explaining the encounter rates with altitude considering sampling effort as a covariate was overall significant (GLMM: $F_{3,54}$ = 20.96, $P < 0.001$). Sampling effort did not have a significant effect on the model (GLMM: $F_{1,54}$ = 2.45, $P = 0.114$). Altitude had a very strong effect in shaping the encounter rates of lemurs in rainforests (Table 3.2; GLMM: $F_{2,54}$ = 16.42, $P < 0.001$). The lemur encounter rate at the high-altitude rainforest (mean: 0.03 ± SE 0.09) was significantly lower than the one at low-altitude (mean: 0.93 ± SE 0.17; sequential Bonferroni post-hoc: $P < 0.001$) and mid-altitude (mean: 0.65 ± SE 0.14; sequential Bonferroni post-hoc: $P = 0.005$) rainforests. There was no significant difference between the lemur encounter rate between low- and mid-altitude rainforest (sequential Bonferroni post-hoc: $P = 0.096$).

The model considering only folivore species was overall significant (GLMM: $F_{3,20}$ = 6.45, $P = 0.011$). Sampling effort did not have a significant effect on the model (GLMM: $F_{1,20}$ = 2.52, $P = 0.112$). Altitude had a significant effect in shaping the encounter rates of folivore lemurs in rainforests (Table 3.2; GLMM: $F_{2,20}$ = 8.22, $P = 0.016$). The sequential Bonferroni post-hoc test, however, did not highlight significant difference encounter rates of folivore species in high-altitude (mean: 0.18 ± SE 0.07), mid-altitude (mean: 0.44 ± SE 0.12), and low-altitude (mean: 0.68 ± SE 0.24), possibly as a consequence to the low sample size for pairwise comparisons (Figure 3.2).

The model excluding folivore species was overall significant (GLMM: $F_{3,30}$ = 18.08, $P < 0.001$). Sampling effort did not have a significant effect on the model (GLMM: $F_{1,30}$ = 3.36, $P = 0.067$). Altitude had a significant effect in shaping the encounter rates (Table 3.2; GLMM: $F_{2,30}$ = 9.76, $P = 0.008$). The lemur encounter rate at the high-altitude rainforest (mean: 0.04 ± SE 0.15) was significantly lower than the one at low-altitude (mean: 1.03 ± SE 0.23; sequential Bonferroni post-hoc: P = 0.008) and mid-altitude (mean: 0.71 ± SE 0.17; sequential Bonferroni post-hoc: P = 0.024) rainforests. There was no significant difference between the lemur encounter rate between low- and mid-altitude rainforest (sequential Bonferroni post-hoc: P = 0.235).

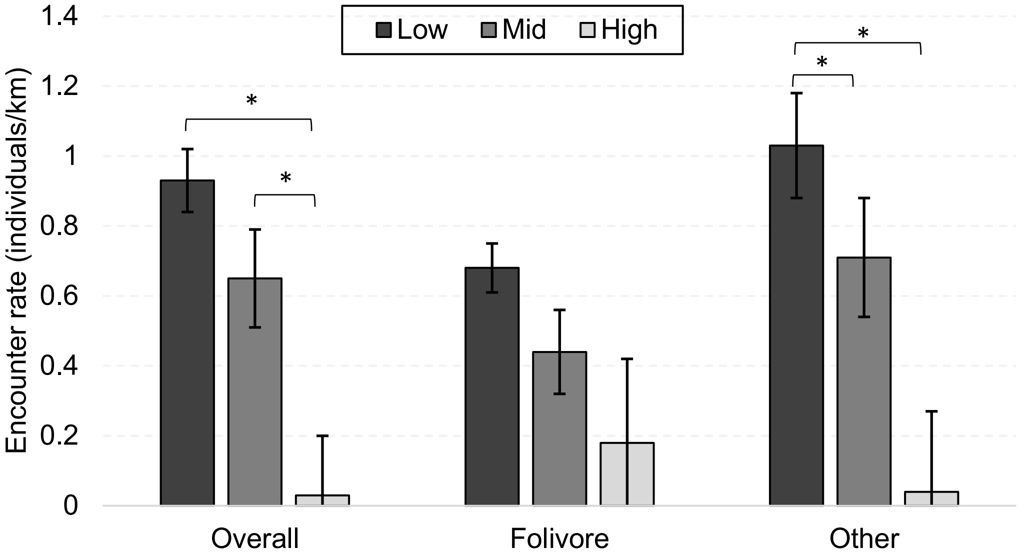

Figure 3.2: Encounter rates of lemur species in low-, mid-, and high-altitude rainforests. Comparison between encounter rates (mean and standard error) of the lemur species present in the lowland rainforest of Ampasy with other species of the same genera within Madagascar (Table 3.2). * P < 0.05

3.3.3. Use of vertical strata

I encountered individuals of *E. collaris* at higher heights (mean: 11.9 ± SE 1.0 metres) when compared to individuals of *H. meridionalis* (8.5 ± SE 0.7) (pairwise t-test: t = 2.43, df = 56, P = 0.018) (Figure 3.3). I found individuals of *L. fleuretae* at significantly higher heights (mean: 14.2 ± SE 0.5) than *A. meridionalis* (12.1 ± SE 0.8) (pairwise t-test: t = 2.21, df = 254, P = 0.028).

Also, *M. tanosi* used significantly lower strata (4.7 ± SE 0.3) than *C. major* (11.4 ± SE 1.9) (pairwise t-test: t = 5.77, df = 146, P < 0.001). The two times I found *D. madagascariensis* it was at around 23 m height.

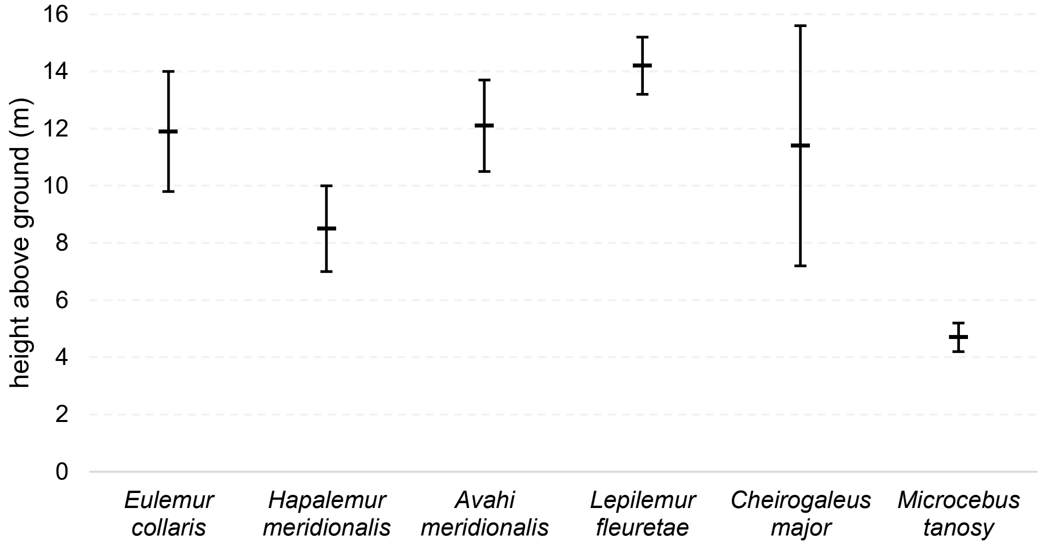

Figure 3.3: Use of vertical strata by lemur species present at Ampasy. Mean and 95% confidence intervals of heights above ground (m) of animals encountered during the transects from May 2015 to July 2016. The average height of adult trees at Ampasy is 15.03 m.

3.4. Discussion

3.4.1. Lemurs and other primates in rainforests at different altitudes

I showed that the encounter rates of lemurs inhabiting low- and mid-altitude rainforests are similar, and they are higher than those of lemurs inhabiting high-altitude rainforests, thus supporting the first prediction. In accordance with previous studies, I provided evidence that altitude is a factor shaping primate encounter rates because at higher altitudes plant species diversity decreases (Ganas et al., 2004; Kim et al., 2011) and the ratio between energy expenditure and nutrient intake is less favourable (Caldecott, 1980). At higher elevations, there is a general increase of ultraviolet radiation (UV) and aridity, as well as a decrease of availability of oxygen and ambient temperature (Sayers, 2014).

Although nonhuman primates are considered shielded from most of the negative effects of UV exposure by the protection of hair, environmental correlates could potentially influence food distribution, and thus primates' foraging strategy (Sayers, 2014).

Since ambient temperature decreases at higher altitudes, individuals living there tend to have larger body sizes compared to closely related species inhabiting lower altitudes (Bergmann, 1847). The Bergmann's rule has been verified on many primate genera (Harcourt & Schreier, 2009) including brown lemurs [*Eulemur* spp. (Gordon et al., 2016)]. It is not valid, however, for some lemur taxa (Kamilar et al., 2012). Malagasy lemurs also cope with high altitudes by exhibiting behavioural and physiological traits to face low temperatures. Some cheirogaleids enter prolonged periods of torpor or hibernation during the cold, dry season when resource availability is low (Dausmann et al., 2005, 2009). Larger lemur species deal with low temperatures by sunbathing and/or huddling in groups (Donati et al., 2011). Other proposed adaptations to the harsh Malagasy environment include low basal metabolic rate (Wright, 1999) and other flexible behaviours related to the energy minimiser strategy (Hixon, 1982; Norscia et al., 2012; Campera et al., 2014).

Lemurs do not seem to reach their diversity maxima in lowland rainforests as for most primate communities and thus probably evolved traits to adapt to mid-altitudes (Goodman & Ganzhorn, 2004). The flexible traits to adapt to mid elevations might have been selected during periods of high climatic variations related to times of glaciation and interglaciation in the Pleistocene (Messmer et al., 2000). During periods of glaciation the vegetation of mid- and high-altitudes descended to lower elevations, thus the extent of the lowland rainforest vegetation was greatly reduced. This change restricted the lowland rainforest habitat and lemurs specialised to this habitat might have suffered compressed ranges. This event in turn may have caused local extinctions since the lowland rainforest cover in Madagascar was already reduced after the break-up of Indo-Madagascar subcontinent (Goodman & Ganzhorn, 2004). As a consequence of this, in Madagascar the mid-altitude rainforest might have been a more stable habitat than the lowland rainforest. This did not happen in other continents since the areas of lowland rainforests were much larger. In fact, data on other primate species outside Madagascar show a clear altitudinal pattern. For instance, the density of the Javan silvery gibbon *Hylobates moloch* at the undisturbed mid-altitude rainforest of Citalahab (Kim et al., 2011) is almost half the density of the same species in the undisturbed lowland rainforest of Turalak (Kappeler, 1984). The density of Bornean white-bearded gibbons *Hylobates albibarbis* in the Gunung Palung National Park, Indonesia is higher in the low-altitude rainforest than in the mid-altitude rainforest (Marshall, 2009). Other studies (e.g. Grow et al., 2013; Nijman, 2014) suggested a lower primate density for species in high-altitude rainforests than for species of the same genus in lowland rainforests, although these studies show no comparison between low- and mid- altitude rainforests. More rarely, in some instance primate abundance is higher along cliffs [e.g. bearded capuchin *Sapajus libidinosus* (Moura, 2007)] and a few primate species are present only in high-altitude rainforests (Lehman, 2014).

The encounter rates of Udzungwa red colobus *Procolobus gordonorum* and Sykes monkey *Cercopithecus mitis monoides* in the Mwanihana forest, Udzungwa Mountains, Tanzania are higher in the lowland semi-deciduous forest than in the mid-altitude rainforest, and higher in the mid-altitude rainforest than in the high-altitude rainforest (Barelli et al., 2014, 2015). The encounter rates of the Angolan colobus *Colobus angolensis palliatus*, however, do not vary significantly between lowland semi-deciduous forest and mid-altitude rainforest, and they occur at lower encounter rates in the high-altitude rainforest, a pattern that might be explained by the species' ability to digest mature instead leaves (Barelli et al., 2014, 2015). Barelli et al. (2014, 2015) suggested that the frugivorous Sykes monkeys were constrained by the low availability of fruits at high elevations, and the folivorous Udzungwa red colobus preferred low elevations due to a higher presence of young leaves in semi-deciduous forests (Lovett, 1993).

From my dataset, the encounter rates of folivorous species in Madagascar did not present a significant difference between low-, mid-, and high-altitude rainforests, while there is a significant difference considering the other genera. This is in line with the prediction that folivorous species are less constrained by habitat structure, thus supporting traditional socioecological models (Wrangham, 1980; Isbell, 1991; Sterck et al., 1997). By looking at the data, however, it emerges that the lack of a significant difference might be due to the encounter rates of bamboo lemurs *Hapalemur* sp. that did not largely differ between sites (Table 3.2). This genus includes species that are highly folivorous [e.g. *H. simus* (Tan 1999, 2000)], but other species integrate more fruits and flowers in their diet [e.g. *H. meridionalis* (Eppley et al., 2011)]. It is thus possible that different species of bamboo lemurs have different constraints, and a comparison may be biased. Another explanation might be the lower sample size related to folivorous species, thus a simple artifact of not having enough data to highlight significant results. At Ampasy, in fact, a correlation between encounter rates and the ecological characteristics of forest plots indicated that the encounter rate of *A. meridionalis* is negatively influenced by mean tree DBH, mean canopy cover, and mean elevation of plots (Phelps, 2016). Furthermore, *A. meridionalis* at Ampasy prefers more degraded areas close to the forest edge, probably to forage on higher-quality leaves (Ganzhorn, 1995). A wider comparison would be necessary to estimate whether folivorous species follow the same pattern of other species or not. From the information available, however, it is evident that encounter rates of *A. meridionalis* are shaped by ecological factors, and significantly decrease with the increase in elevation.

3.4.2. Species-specific trends and conservation implications

The lemur genera were present at very low encounter rates or not present in high-elevation rainforests (Table 3.2). The only exceptions were *C. major* at Anjanaharibe Sud [0.26 ind/km (Schmid & Smolker, 1998)] and at Andohahela [0.48 ind/km (Feistner & Schmid, 1999)], and *M. tanosi* at Andohahela [0.80 ind/km (Feistner & Schmid, 1999)]. The encounter rates of these species were still lower than the average encounter rates of species of the same genera in low- and mid-altitude rainforests. The encounter rates of *A. meridionalis* and *L. fleuretae* at Ampasy are higher than the encounter rate of the same species in the adjacent lowland rainforest of Andohahela (Feistner & Schmid, 1999). I detected individuals of *A. meridionalis* and *L. fleuretae* at a quite high distance from the transect, possibly due to the high visibility in the area and to the rare trees in the understory strata (Nguyen et al., 2013). This fact might explain the higher encounter rate at Ampasy. Also, I cannot exclude a different degree of habitat disturbance between Ampasy and Andohahela where Feistner and Schmid (1999) collected their data. The encounter rates of *A. meridionalis* and *L. fleuretae* at Ampasy are higher than in other rainforests and this may be potentially explained by the lower competition due to the lack of other highly folivorous species such as the diurnal indriidae.

The density of *E. collaris* at Ampasy is higher than the density at Anka, in parcel 1 of the TGK forest (Norscia et al., 2006b). This pattern suggests that the overall population estimate of *E. collaris* in TGK using my density values (31,685) may be overestimated. A more realistic figure is likely to be close to the lower value of the 95% coefficient interval, thus around 20,000 individuals. In fact, hunting pressure at Ampasy forest is low as compared to other areas of TGK, mainly due to the remoteness of the area and the benefits of local management (Campera et al., 2017). For *M. tanosi*, of which the IUCN status was not assessed before, I estimated a total population size of 58,526 in the TGK Protected Area, which are likely to be reliable data since the encounter rate of *M. tanosi* in the adjacent lowland rainforest of Andohahela [1.49 ind/km (Feistner & Schmid, 1999)] is similar to what I found at Ampasy (1.46 ind/km). The encounter rate of *C. major* at Ampasy (0.32 ind/km) is much lower as compared to other low- and mid-altitude rainforests, while it is more similar to high altitude rainforests [0.26 ind/km (Schmid & Smolker, 1998); 0.48 ind/km (Feistner & Schmid, 1999)]. The low encounter rate of *C. major* at Ampasy as compared to other low- and mid-altitude rainforest of Madagascar might be due to the very high density of *L. fleuretae* at Ampasy. Although I do not have direct evidence of a negative correlation between encounter rates of the two species, a low encounter rates of *L. fleuretae* in Andohahela NP (Feistner & Schmid, 1999) and *L. mustelinus* in Anjaharibe Sud SR (Schmid & Smolker, 1998) correspond to high encounter rates of *C. major*. A possible explanation of this is an interspecific resource competition (Tilman, 1982) between *L. fleuretae* and *C. major*. In fact, *C. major* use tree holes for the hibernation period (Blanco et al., 2013) and the high density of *L. fleuretae* at Ampasy might be a limiting factor for finding suitable tree holes.

3.4.3. Conclusions

In conclusion, lemur species seem to occur at similar densities in low- and mid-altitude rainforests as predicted. This might be due to the limited expansion of lowland rainforest in Madagascar and the fact that mid-altitude rainforests were a more stable habitat during lemur evolution (Goodman & Ganzhorn, 2004). Folivorous species do not show a clear pattern, although this might be due to the limited sample analysed in this study. At Ampasy, in fact, *A. meridionalis* showed a preference for edge and degraded areas, and its encounter rate was negatively correlated with altitude (Phelps, 2016). No direct trends for competitive exclusion between ecologically similar species arose from my data. I highlighted a possible interspecific resource competition between *L. fleuretae* and *C. major* since the high density of *Lepilemur* sp. might be a limiting factor for *C. major* to find suitable tree holes for hibernation.

Table 3.2. Density and encounter rates of lemur species at different altitudes in Malagasy rainforests. Densities (ind/ha) and encounter rates (ind/km) of the species of the same genera of lemurs present in the Tsitongambarika PA. For comparisons, I only considered studies in rainforests with a sampling effort >5km. -: not spotted; rare: spotted but not possible to calculate density; NA: Not Available. PA: Protected Area; NP: National Park; SR: Special Reserve. Low-altitude is below 600 m; Mid-altitude is between 600 and 1400 m; High-altitude is above 1400 m (Ganzhorn et al., 1997; Irwin et al., 2005).

Species	**Site**	**Altitude**	**Density (ind/km^2)**	**Encounter rate (ind/km)**	**Reference**
Woolly lemurs (*Avahi* sp.)					
A. laniger	Anjanaharibe Sud SR	Mid	NA	0.24	Schmid & Smolker, 1998.
A. laniger	Anjanaharibe Sud SR	High	NA	-	Schmid & Smolker, 1998.
A. laniger	Makira PA	Low	58	0.90	Murphy et al., 2016.
A. laniger	Vohibola SR-Parcel 3	Mid	24	0.72	Lehman, 2006; Lehman et al., 2006.
A. meridionalis	Andohahela PA-Parcel 1	Low	NA	0.21	Feistner & Schmid, 1999.
A. meridionalis	Andohahela PA-Parcel 1	Mid	NA	0.17	Feistner & Schmid 1999.
A. meridionalis	Andohahela PA-Parcel 1	High	NA	-	Feistner & Schmid 1999.
A. meridionalis	Tsitongambarika PA-Parcel 3	Low	32	0.87	This study
A. peyrierasi	Ranomafana NP-Tala	Mid	19	0.63	Herrera et al., 2011.
A. peyrierasi	Ranomafana NP-Vato	Mid	40	1.47	Herrera et al., 2011.

Species	**Site**	**Altitude**	**Density (ind/km^2)**	**Encounter rate (ind/km)**	**Reference**
Fat-tailed lemurs (*Cheirogaleus* sp.)					
C. major	Andohahela NP-parcel 1	Low	NA	2.87	Feistner & Schmid, 1999.
C. major	Andohahela NP-parcel 1	Mid	NA	0.81	Feistner &Schmid, 1999.
C. major	Andohahela NP-parcel 1	High	NA	0.48	Feistner & Schmid, 1999.
C. major	Anjanaharibe Sud SR	Mid	NA	2.59	Schmid & Smolker, 1998.
C. major	Anjanaharibe Sud SR	High	NA	0.26	Schmid & Smolker, 1998.
C. major	Tsitongambarika PA-Parcel 3	Low	22	0.32	This study
C. major	Vahibola SR- Parcel 3	Mid	70	1.45	Lehman et al., 2006.
Brown lemurs (*Eulemur* sp.)					
E. albifrons	Anjanaharibe Sud SR	Mid	NA	0.09	Schmid & Smolker, 1998.
E. albifrons	Anjanaharibe Sud SR	High	NA	-	Schmid &Smolker, 1998.
E. albifrons	Makira PA	Low	21	0.62	Murphy et al., 2016.
E. albocollaris	Manombo SR	Low	10	NA	Irwin et al., 2005.
E. albocollaris	Manombo SR	Low	14	0.47	Johnson et al., 2011.
E. collaris	Andohahela NP-Parcel 1	Low	NA	0.08	Feistner & Schmid, 1999.

Species	Site	Altitude	Density (ind/km^2)	Encounter rate (ind/km)	Reference
Brown lemurs (*Eulemur* sp.)					
E. collaris	Andohahela NP-Parcel 1	Mid	NA	0.30	Feistner & Schmid, 1999.
E. collaris	Andohahela NP-Parcel 1	High	NA	0.02	Feistner & Schmid, 1999.
E. collaris	Tsitongambarika PA-Parcel 1	Low	15	1.03	Norscia et al., 2006b.
E. collaris	Tsitongambarika PA-Parcel 3	Low	52	1.12	This study
E. collaris	Kalambaditra SR, Midongy du Sud NP	Mid-High	14	NA	Irwin et al., 2005.
E. rubriventer	Anjanaharibe Sud SR	Mid	NA	0.02	Schmid & Smolker, 1998.
E. rubriventer	Anjanaharibe Sud SR	High	NA	0.04	Schmid & Smolker, 1998.
E. rubriventer	Ranomafana NP, Andringitra NP	Mid	5	NA	Irwin et al., 2005.
E. rubriventer	Ranomafana NP-Tala	Mid	8	0.33	Herrera et al., 2011.
E. rubriventer	Ranomafana NP-Vato	Mid	14	0.50	Herrera et al., 2011.
E. rubriventer	Vohibola SR-Parcel 3	Mid	22	0.53	Lehman et al., 2006.
E. rufifrons	Ranomafana NP	Mid	23	NA	Irwin et al., 2005.
E. rufifrons	Ranomafana NP-Tala	Mid	8	0.36	Herrera et al., 2011.
E. rufifrons	Ranomafana NP-Vato	Mid	26	1.39	Herrera et al., 2011.

Species	Site	Altitude	Density (ind/km^2)	Encounter rate (ind/km)	Reference
Brown lemurs (*Eulemur* sp.)					
E. rufifrons	Vohibola SR-Parcel 3	Mid	Rare	0.04	Lehman et al., 2006.
E. rufifrons X albocollaris	Andringitra NP	Mid	57	NA	Irwin et al., 2005.
Bamboo lemurs (*Hapalemur* sp.)					
H. aureus	Ranomafana NP, Andringitra NP	Mid	2	NA	Irwin et al., 2005.
H. griseus griseus	Anjanaharibe Sud SR	Mid	NA	0.40	Schmid & Smolker, 1998.
H. griseus griseus	Anjanaharibe Sud SR	High	NA	0.13	Schmid & Smolker, 1998.
H. griseus griseus	Ranomafana NP-Tala	Mid	27	NA	Grassi, 2006.
H. griseus griseus	Ranomafana NP-Vato	Mid	10	NA	Grassi, 2006.
H. griseus griseus	Vohibola SR-Parcel 3	Mid	5	0.27	Lehman et al., 2006.
H. meridionalis	Andohahela NP-Parcel 1	Low	NA	0.12	Feistner & Schmid, 1999.
H. meridionalis	Andohahela NP-Parcel 1	Mid	NA	0.16	Feistner & Schmid, 1999.
H. meridionalis	Andohahela NP-Parcel 1	High	NA	0.12	Feistner & Schmid, 1999.
H. meridionalis	Tsitongambarika PA-Parcel 3	Low	18	0.33	This study
H. simus	Ranomafana NP, Andringitra NP	Mid	Rare	NA	Irwin et al., 2005.

Species	**Site**	**Altitude**	**Density (ind/km^2)**	**Encounter rate (ind/km)**	**Reference**
Sportive lemurs (*Lepilemur* sp.)					
L. fleuretae	Andohahela NP-Parcel 1	Low	NA	0.42	Feistner & Schmid, 1999.
L. fleuretae	Andohahela NP-Parcel 1	Mid	NA	-	Feistner & Schmid, 1999.
L. fleuretae	Andohahela NP-Parcel 1	High	NA	-	Feistner & Schmid, 1999.
L. fleuretae	Tsitongambarika PA-parcel 3	Low	81	2.26	This study
L. microdon	Vohibola SR-Parcel 3	Mid	Rare	0.16	Lehman, 2006 ; Lehman et al., 2006.
L. mustelinus	Anjanaharibe Sud SR	Mid	NA	0.92	Schmid & Smolker, 1998.
L. mustelinus	Anjanaharibe Sud SR	High	NA	0.13	Schmid & Smolker, 1998.
Mouse lemurs (*Microcebus* sp.)					
M. rufus	Anjanaharibe Sud SR	Mid	NA	0.60	Schmid & Smolker, 1998.
M. rufus	Anjanaharibe Sud SR	High	NA	0.13	Schmid & Smolker 1998
M. rufus	Ranomafana NP-Tala	Mid	16	0.57	Herrera et al., 2011.
M. rufus	Ranomafana NP-Vato	Mid	Rare	0.17	Herrera et al., 2011.
M. rufus	Vohibola SR-Parcel 3	Mid	46	0.82	Lehman et al., 2006.
Microcebus sp.	Makira PA	Low	39	0.47	Murphy et al., 2016.

Species	**Site**	**Altitude**	**Density (ind/km^2)**	**Encounter rate (ind/km)**	**Reference**
Mouse lemurs (*Microcebus* sp.)					
M. tanosi	Andohahela NP-parcel 1	Low	NA	1.49	Feistner & Schmid, 1999.
M. tanosi	Andohahela NP-parcel 1	Mid	NA	0.47	Feistner & Schmid, 1999.
M. tanosi	Andohahela NP-parcel 1	High	NA	0.80	Feistner & Schmid, 1999.
M. tanosi	Tsitongambarika PA-parcel 3	Low	97	1.46	This study

Chapter 4. Effect of resource availability on ranging patterns and sleeping site selection of *Avahi meridionalis* in Tsitongambarika.

4.1. Introduction

Primate ranging patterns are highly dependent on resource availability (Clutton-Brock, 1977; Mitani & Rodman, 1979) that is in turn determined by factors such as seasons, type of habitat and human activities (Chapman & Chapman, 2000; Hemingway & Bynum, 2005). Two different strategies, analogous ofthe optimal foraging theory [energy-maximising and time-minimising strategies (Schoener, 1971; Hixon, 1982)] have been hypothesied to explain the relationship between animal ranging patterns and resource availability: resource-maximising and area-minimising (Mitchell & Powell, 2004, 2012). On one hand, animals using the resource-maximising strategy try to find the optimal balance by maximising the difference between a random and a selective use of the resources within their home ranges, but no variation in home range size is expected (Mitchell & Powell, 2004, 2012). On the other hand, animals may adopt the area-minimising strategy by using the minimum area needed to gather resources to satisfy a minimum resource threshold, thus increasing their home ranges in periods of food scarcity to satisfy energy requirements (Gerber et al., 2012; Campera et al., 2014). Usually, the area-minimising strategy is used when resource availability is low, while the resource-maximising strategy indicates high food availability (Mitchell & Powell, 2004). A high food availability usually allows animals to reduce their daily movements, while in habitats where food availability is low long travelling paths are necessary (Curtis & Zaramody, 1998; Kaplin, 2001; Boyle et al., 2009a; Volampeno et al., 2011). Other studies have found the opposite trend, with shorter travelling paths in areas with low food availability to minimise the energy expenditure (Yamagiwa & Mwanza, 1994; Wallace, 2006; Irwin, 2008). Strategies such as relying on a specific microhabitat within the home ranges (Vedder, 1984; Peres, 1994) and shifting habitats (Wallace, 2006; Sato, 2013) may also be used in periods of food scarcity.

Frugivores often increase their daily distances travelled to access additional, scattered distributed fruit patches (Ganas & Robbins, 2005; Campera et al., 2014), while folivores have been shown to reduce daily distances travelled to conserve energy since edible leaves are supposed to be evenly distributed [(Norscia et al. 2006a); but see Chapter 1]. Different strategies can be adopted by the same species in different conditions and the patterns are not always clear-cut (Gerber et al., 2012; Campera et al., 2014). Folivores are hypothesized to rely on a low-quality diet since leaves are high in structural carbohydrates that are difficult to digest (Milton, 1979). Also, the main adaptation to folivory is an enlarged gastro-intestinal surface that allows a longer digestion time to maximise nutrient absorption (Chivers & Hladik, 1980). For this reason, folivory is rarely observed in small-bodied primates (<1 kg) which usually cope with low-quality diet and a limited nutrient absorption by having a low metabolism and a reduced energy expenditure (Dröscher & Kappeler, 2014).

Sleeping site selection is also influenced by resource availability, although co-dependent by other factors such as protection from predators, microhabitat characteristics, and climate (Anderson, 1998; Albert et al., 2011;

Seiler et al., 2013). Sleeping sites are usually selected in proximity to food resources to reduce energy costs or travel (Chapman et al., 1989; Phoonjampa et al., 2010), although some species do not seem to rely on this strategy [e.g. Lar gibbon *Hylobates lar* (Reichard, 1998); Bornean white-bearded gibbon *Hylobates albibarbis* (Cheyne et al., 2012)]. As a time-minimising strategy, sleeping sites are often located close to core areas (Phoonjampa et al., 2010; Albert et al., 2011) that are the areas with greater availability and abundance of resources where animals are expected to spend more time (Vander Wal & Rodgers, 2012). Animals' core areas tend to be fragmented when preferred food resources are at low availability and clumped (Wallace, 2006; Li et al., 2010; Campera et al., 2014). This is because animals can minimise energy expenditure by having multiple foraging areas and selecting sleeping sites in proximity of them [multiple central place foraging hypothesis (Chapman et al., 1989; Albert et al., 2011)].

Madagascar offers a series of unique environments to investigate the relationship between ranging patterns, sleeping site choice, and food availability. Malagasy environments have a pronounced seasonality and climatic unpredictability that lead to natural fluctuations in food availability and represent a serious challenge to lemur communities (Wright, 1999; Dewar & Richard, 2007). For this reason, lemurs require behavioural adaptations to cope with these conditions (Wright, 1999; Donati et al., 2011) and energy-minimising strategies are usually used during lean seasons (Kelley, 2013; Campera et al., 2014). The strictly folivorous woolly lemurs (*Avahi* spp.) represent interesting models to explore the use of ranging strategies of primates with unfavourable energy balance in habitats with pronounced seasonality since they are at the lower limit of body size for folivory (Kay, 1984), and have an energetically expensive locomotion (Warren & Crompton, 1997). Hence, woolly lemurs are expected to rely on energy saving strategies to balance the low nutrient intake and the high energetic locomotion. The information on ranging patterns of woolly lemurs, however, is scarce, especially in the eastern rainforest that represents the habitat where most species of this genus are present. Harcourt (1991) reported the home range of eastern woolly lemur *A. laniger* in the Ranomafana rainforest based on one-month data collection on one radio-collared individual. Ganzhorn et al. (1985) found that the home ranges of *A. laniger* in the rainforest near Andasibé were 1-2 ha based on two months of data, but no precise estimates were described. Norscia & Borgognini-Tarli (2008) reported the largest data-set for ranging patterns of woolly lemurs in the eastern rainforest, with seven months of data collection on two pairs of *A. meridionalis* in the littoral forest of Ste. Luce. Norscia et al. (2012) suggested that *A. meridionalis* in Ste. Luce adopted a time-minimising feeding strategy. The littoral forest of Ste. Luce, however, is a different habitat compared to the eastern rainforest since it is highly fragmented and characterised by low food availability (Bollen & Donati, 2006; Ganzhorn et al., 2007).

In this chapter I investigated the ranging patterns and sleeping site selection of southern woolly lemurs *A. meridionalis* in the continuous lowland rainforest of Ampasy, in the northernmost portion of the Tsitongambarika Protected Area. In particular, I explored the difference between ranging patterns and sleeping site selection between the season of abundance and scarcity of young leaves, investigating whether *A. meridionalis* in

Tsitongambarika relies on an area-minimising or a resource-maximising strategy, or no clear difference if not influenced by food availability according to the hypothesis that folivores do not face food constraints (see Chapter 1.1). Based on the unfavourable energy balance and on the previous finding that folivorous primates are constrained by food abundance, quality, and availability (see Chapter 1.1), I predicted:

1) seasonal home ranges to be larger during the lean period as an area-minimising strategy;
2) daily path lengths to be shorter during the lean period as a time-minimising strategy;
3) animals to have multiple core areas during the lean season as a time-minimising strategy since young leaves are at lower availability.
4) animals to select more frequently sleeping sites in the core area during the lean season as a time-minimising strategy.

4.2. Methods

4.2.1. Data collection

I collected data on six individuals of southern woolly lemurs via continuous behavioural sampling for a total of 148.2 observation hours (see Chapter 2.4). To ensure systematic observations, I equipped the individuals with radio-collars (RI-2D, Holohil System Ltd, 11g) at the beginning of July and once a month (from dusk to dawn when possible) followed each individual from August 2015 to July 2016 (see Chapter 2.2 and 2.5 for details on animal captures). The animals equipped with radio-collars were all females apart from AVAHI-6. Nevertheless, no large differences between home ranges of males and females were expected since the species is pair-living (Norscia & Borgognini-Tarli, 2008). The data collection on some individuals was shorter since some areas of the forest were not accessible during wet months. An individual (AVAHI-4) was killed by a fossa (*Cryptoprocta ferox*) at the end of August 2015. I collected lemur locations every hour via a handheld GPS (Garmin 60CSx).

Since observations were difficult in the study area, lemur locations were mainly collected via the triangulation method from July 2015 to June 2016 (196 h in total, in addition to the hours of behavioural observation). Firstly, I marked two 500-m forest transects every 25 m and collected the GPS location for each flag. To have a more precise location and minimise the error of the triangulation, I took ten GPS points with an error <6 m for each flag and averaged them. The range of an individual (AVAHI-2) was not recordable from the transects walked for triangulation, thus only locations collected via behavioural observations are available for this individual. Triangulation angles were maintained between 30° and 150° (Gese, 2001) and collected every hour from dusk to dawn to gather independent data. Bearings were plotted using LOAS 4.0 (Ecological Software Solutions) to determine the locations. I set the projected coordinate system of the layers to the related zone (WGS1984-UTM Zone 38S) when imported into ArcMap.

I collected data on sleeping site selection once or twice a month on each animal by locating the animals via radio-telemetry during the day. When spotted, I collected the GPS location.

4.2.2. Data analysis

I calculated home ranges and daily path lengths with home-range tools [HRT 2.0 (Rodgers & Chie, 2011)] for ArcMap 10.2.2 (ESRI, Redlands, CA). I used the 100% Minimum Convex Polygon [MCP (Mohr, 1947)] and the 95% Fixed Kernel [FK (Seaman & Powell, 1996)] methods to determine home range areas. I used the 50% FK method to estimate the core areas. The 100% MCP was used to show annual ranges because it is the most commonly reported method in the literature (Harris et al., 1990), although it is not efficient in detecting small-scale differences of within-species comparisons (Nilsen et al., 2008). Also, the MCP underestimates home ranges at small sample sizes (Downs & Horner, 2008) and overestimates home ranges at large sample sizes because of the inclusion of rarely or never visited areas (Powell, 2000). The FK method has better performances than MCP in simulation trials of home range estimators (Seaman et al., 1999; Downs & Horner, 2008). The minimum sample size to have reliable estimates with the FK method is 30 and possibly 50 locations (Seaman et al., 1999), although it depends on the species (Boyle et al., 2009b). The FK analyses were performed with a bandwidth calculated using least-squares cross-validation that usually performs better than other methods (Powell, 2000; Seaman et al., 1999; Downs & Horner, 2008). Since I had a small sample size, I performed an Incremental Area Analysis (IAA) to determine whether annual ranges estimated via 100% MCP and 95% FK provide evidence of stability. I calculated the Defensibility Index [D (Mitani & Rodman, 1979)] for each individual to assess the feasibility of territorial defense. This was calculated using the formula: $D = d * (4A/\pi)^{0.5}$, where d was the mean daily distance traveled and A was the annual home range obtained via 95 % FK analyses. D ≥ 1 indicates that territoriality is efficient, D < 1 indicates that territoriality is not efficient.

I calculated home range estimates in two different phenological seasons. I distinguished between a lean period (from March to August) and a period of abundance (from September to February) to evaluate the effects of food availability. Since *Avahi meridionalis* is strictly folivorous, I made the distinction based on the availability of young leaves in the forest (Chapter 2.4; Figure 2.5).

I ran a Repeated Measures (RM) ANOVA to evaluate differences in daily distance travelled with seasons (abundance/lean) as intra-subject factor. The monthly average daily distance travelled by each animal, considering only days with a complete dataset from dusk to dawn, was considered as statistical unit. To determine whether southern woolly lemurs selected sleeping sites in the core areas more often during the leans season than the season of food abundance I ran a logistic regression with the presence of sleeping sites in the core area (0: absent, 1: present) as dependent variable and the season as categorical covariate. I performed the test via the software IBM SPSS 23 and considered P < 0.05 as significant level.

4.3. Results

4.3.1. Ranging patterns

The annual home range of southern woolly lemurs at Ampasy varied between 4.53-10.39 ha using the MCP and 4.59-7.86 ha using the FK (Table 4.1). The sample size for AVAHI-2 and AVAHI-4 was too small to assess the annual home range via MCP and did not reach the asymptote via the incremental area analysis for the FK. The seasonal differences in the home ranges of southern woolly lemurs did not show a clear-cut pattern. AVAHI-1 and AVAHI-3 showed a larger range via FK in the season of abundance (AVAHI-1: 5.56 ha, N = 63 locations; AVAHI-3: 6.91 ha, N = 58) than the lean season (AVAHI-1: 4.65 ha, N = 79; AVAHI-3: 6.53 ha, N = 94), while AVAHI-5 and AVAHI-6 showed a larger range via FK in the lean season (AVAHI-5: 4.59 ha, N = 131; AVAHI-6: 4.77 ha, N = 126) than in the season of abundance (AVAHI-5: 4.08 ha, N = 99; AVAHI-6: 4.05 ha, N = 88). All the individuals of *Avahi meridionalis* had a D > 1 (Table 4.1).

The daily distances travelled by southern woolly lemurs were longer during the season of food abundance (640.7 ± SE 27.6 m) than the lean season (498.8 ± SE 36.4 m) (RM ANOVA: $F_{1,22} = 19.47$, $P < 0.001$). In particular, AVAHI-1 travelled a mean daily distance of 711.6 ± SE 86.5 m (N = 5 months) in the season of abundance and 574.4 ± SE 46.6 m (N = 5 months) in the lean season. AVAHI-2 travelled a mean daily distance of 745.8 ± SE 73.8 m (N = 2 months) in the season of abundance and 426.6 ± SE 160.6 m (N = 2 months) in the lean season. AVAHI-3 travelled a mean daily distance of 682.8 ± SE 73.6 m (N = 5 months) in the season of abundance and 608.6 ± SE 45.8 m (N = 5 months) in the lean season. AVAHI-5 travelled a mean daily distance of 569.0 ± SE 24.2 m (N = 6 months) in the season of abundance and 406.6 ± SE 45.8 m (N = 6 months) in the lean season. AVAHI-6 travelled a mean daily distance of 556.2 ± SE 26.1 m (N = 5 months) in the season of abundance and 389.7 ± SE 30.0 m (N = 5 months) in the lean season.

Table 4.1: Home range of *Avahi meridionalis* at Ampasy. Home range comparison between the six individuals of southern woolly lemur at Ampasy. GPS points were collected every hour.

		Annual home range size (ha)				
Individual	**GPS points**	**MCP**	**95%FK[a]**	**50%FK**	**DDT (SE) (m)**	**D***
AVAHI-1	142	6.39	5.77 (102)	0.95	620.2 (35.3)	1.68
AVAHI-2	48	NA	3.11 (>)	0.84	586.3 (121.9)	1.17
AVAHI-3	152	10.39	7.86 (128)	1.76	683.8 (36.1)	2.16
AVAHI-4	36	NA	3.69 (>)	0.96	560.7 (73.0)	1.22
AVAHI-5	230	4.85	4.59 (112)	1.16	486.9 (34.5)	1.18
AVAHI-6	214	4.53	4.67 (116)	0.92	508.9 (32.9)	1.24

Data were collected from July 2015 to July 2016. [a]In parentheses: number of GPS locations needed to obtain a clear stability via the incremental area analysis. (>) indicates that no clear stability was reached via the incremental area analysis. *D: Defensibility Index (Mitani & Rodman, 1979).

4.3.2. Core areas

AVAHI-1 showed a single core area (50%FK: 0.89 ha) during the season of food abundance and a single core area (50%FK: 0.96 ha) during the lean season. AVAHI-3 showed multiple core areas (50%FK: 1.83 ha) during the season of food abundance and multiple core areas (50%FK: 1.63 ha during the lean season. AVAHI-5 showed a single core area (50%FK: 0.90 ha) during the season of food abundance and multiple core areas (50%FK: 1.13 ha) during the lean season. AVAHI-6 showed a single core area (50%FK: 0.77 ha) during the season of food abundance and multiple core areas (50%FK: 1.03 ha) during the lean season (Figure 4.1).

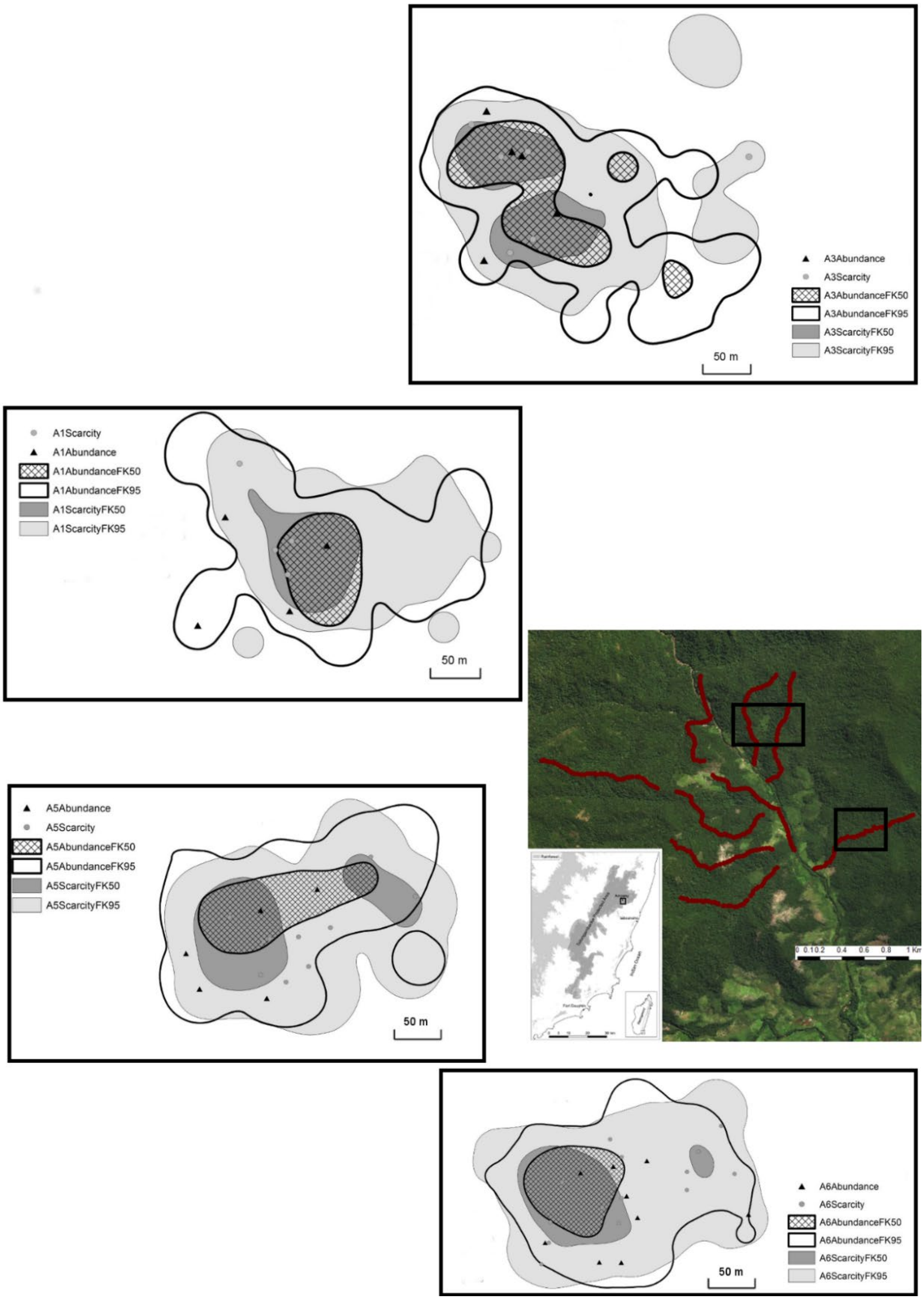

Figure 4.1: Seasonal home ranges and core areas of *Avahi meridionalis* at Ampasy. Seasonal home ranges and core areas calculated via 95% and 50 % Fixed Kernel respectively. Individuals A1 and A3 are two females inhabiting the northern section of the forest, while A5 (female) and A6 (male) inhabit the southern section. Dots and triangles represent sleeping sites in the lean and in the abundance season respectively.

4.3.3. Sleeping site selection

Overall, southern woolly lemurs selected sleeping sites in the core areas more often during the lean season than the season of food abundance (Logistic Regression: Wald χ^2: 4.29, $P = 0.038$, $N = 57$). For AVAHI-1 I recorded 1 sleeping site out of 4 in the core area during the season of food abundance and 3 sleeping sites out of 4 during the lean season. AVAHI-3 selected 3 sleeping sites out of 5 in the core area during the season of food abundance and 5 sleeping sites out of 6 during the lean season. The sleeping sites of AVAHI-5 were selected once out of five times in the core area in the season of food abundance, while six times out of ten during the lean season. AVAHI-6 selected 2 sleeping sites out of 9 in the core area during the season of food abundance and 6 times out of 14 during the lean season.

4.4. Discussion

4.4.1. Home ranges

In contrast with the behaviour of the species in the nearby littoral forest of Ste. Luce (Norscia & Borgognigni 2008), southern woolly lemurs at Ampasy do not seem to rely on the area-minimising strategy since the home ranges during the season of food abundance and the lean season remained similar. This relationship was not expected from my predictions since the area-minimising strategy, analogous ofthe time-minimising strategy, is the pattern that is usually adopted by small-bodied folivorous species such as *Avahi meridionalis* (Hemingway & Bynum, 2005). The increase in home range sizes during lean periods (e.g. Campera et al., 2014) was thus not evident from my data. Strictly folivorous primates may not follow the expected trend because they rely mostly on mature leaves during the season of food scarcity, which has less clumped distribution than young leaves (Norscia et al., 2006a).

Folivores have been shown to prefer leaves with high protein/fibre ratio and to reduce the income of secondary compounds (Chapman et al., 2002; Norscia et al., 2012; Ganzhorn et al. 2017). Moreover, the assumptions that folivores are less constrained by food availability than frugivores and that there is limited within-group scramble competition have been lately questioned [(Steenbeek & van Shaik, 2001; Snaith & Chapman, 2007); see Chapter 1]. In fact, folivores select food resources that vary in availability and spatial distribution, preferring high-quality young leaves in most cases (Koening et al., 1998; Chapman & Chapman, 2002). Even within mature leaves, which are continuously distributed in rainforests, there is a high difference in nutritional content and high-quality mature leaves are actively selected (Koenig et al., 1998). For these reasons, folivores appear to be subjected to similar ecological constraints as frugivores (Snaith & Chapman, 2007) (see Chapter 1.1).

The similar home ranges of *A. meridionalis* between lean and abundance periods may be caused by a low difference in terms of nutritional quality of leaves in the forest, so there may be no advantage to increase the home ranges during the lean season, as previously seen in red-tailed sportive lemur *Lepilemur ruficaudatus* (Ganzhorn, 2002). Another possible explanation for the similar sized home ranges between the two seasons may be related to the higher availability of young leaves (i.e. less months with <10% of young leaves) of the Ampasy rainforests when compared to the littoral rainforest of Ste. Luce (Bollen & Donati, 2005). This is also indirectly confirmed by the Defendibility Index that indicates that all the individuals of *A. meridionalis* can defend their territory. Territoriality, in fact, has been related to high food abundance and distribution (Mitani & Rodman, 1979). At Ampasy, however, I expected high competition due to the high density of Fleurete's sportive lemur *Lepilemur fleuretae* (see Chapter 3). In fact, the resource-maximising strategy is usually employed when preferred food availability is high (Mitchell & Powell, 2004), suggesting that Ampasy may be a high-quality habitat for folivores. This notion is supported by the high densities of *A. meridionalis* and *L. fleuretae* in the study site (see Chapter 3). Also, the home range of *A. meridionalis* in Ste. Luce is around half the size of the home ranges found at Ampasy. This might indicate lower food availability in Ste. Luce than in Ampasy as previously shown for other folivorous primates which have smaller home ranges where food availability is low [white-thighed colobus *Colobus vellerosus* (Wong & Sicotte, 2007); mantled howler monkey *Alouatta palliata* (Cristóbal-Azkarate & Arroyo-Rodríguez, 2007); black bearded saki *Chiropotes satanas* (Boyle et al., 2009a); diademed sifaka *Propithecus diadema* (Irwin, 2008)].

4.4.2. Distances travelled, core areas, and sleeping site selection

In line with the second and the fourth predictions, southern woolly lemurs travelled shorter distances and selected more frequently sleeping sites in the core area during the lean period than during the period of food abundance. Thus, the time-minimising strategy is an important behavioural adaptation to reduce energy consumption as suggested in earlier studies (Schoener, 1971; Hixon, 1982). Other folivores [e.g. Verreaux's sifaka *Propithecus verreauxi* (Norscia et al., 2006a)], as well as frugivorous lemurs [e.g. ring-tailed lemur *Lemur catta* (Kelley 2013); collared brown lemur *Eulemur collaris* (Campera et al., 2014)], have been shown to reduce the daily distance travelled to reduce energy expenses during lean seasons. Energy saving strategies are often used by lemurs since Madagascar is considered a harsh environment with important seasonal variations in terms of food quality but also in terms of ambient temperature (Wright, 1999). Woolly lemurs have an expensive locomotion as vertical climbers and leapers (Warren & Crompton, 1998) and this, coupled with the low-quality strictly folivorous diet, may explain why this genus relies heavily on energy-minimising strategies (Warren & Crompton, 1998; Norscia et al., 2012). The finding that southern woolly lemurs adopt the time-minimiser strategy, however, contrasts with the finding on the use of resource maximiser strategy related to annual home ranges. Other folivores increase their daily ranges in lean periods to reach patches of high-quality resources [e.g. black colobus *Colobus satanas* (McKay & Waterman, 1982); eastern gorilla *Gorilla beringei* (Ganas & Robbins, 2005)]. Conversely, southern woolly lemurs at Ampasy may have adopted the strategy of changing their diet to rely more on evenly distributed leaves during the lean season (Yeager & Kool, 2000). This hypothesis is supported by the fact that *A. meridionalis* selected leaves based on their nutritional content during the season of abundance and not during the lean season (see Chapter 5).

The prediction that individuals of *A. meridionalis* have a fragmented core area during the lean season is supported by the two individuals that had multiple core areas during the lean season and a single core area during the period of food abundance. The other two individuals, however, did not show differences, thus further evidence is required to support this hypothesis. Several studies have shown the relationship between low food availability and increase in core area number and size (Lurz et al., 2000; Pasch & Koprowski, 2011; Richard et al., 2011; Campera et al., 2014), thus this strategy may be adopted by *A. meridionalis*. My observations are also in line with the hypothesis that animals can minimise the energy expenditure by selecting multiple central foraging places and selecting sleeping sites in proximity to them [multiple central place foraging hypothesis (Chapman et al., 1989; Albert et al., 2011)]. The two individuals that showed a fragmented core area in the lean season and a single core area in the season of food abundance were inhabiting a forest area that was the subject of selective logging in the past (Faniry Rakotoarimanana, Asity Madagascar, pers. comm. 2016). Although I do not have data on habitat structure in the home ranges of the four animals, random plots suggested lower density of trees with a DBH>10 cm in the area with selective logging history [tree density area with past selective logging = 1655 ± SE 105 trees/ha; tree density in the more pristine area = 2330 ± SE 250 trees/ha (Phelps, 2016)]. This difference might indicate that the two individuals inhabiting the forest area with selective logging history have a relatively lower availability of resources than the individuals in the more pristine area. Since I have no data on the resource distribution within individuals' home ranges, however, I cannot speculate more on the influence of habitat structure on ranging patterns of southern woolly lemurs at Ampasy.

4.4.3. Conclusions

In conclusion, *A. meridionalis* in Ampasy adopted a resource maximising strategy in terms of annual ranges, while a time-minimising strategy was adopted in terms of daily distance travelled and sleeping site selection. *Avahi* *meridionalis* may be a resource maximiser for annual ranges due to the high food availability at Ampasy or to the low difference between food items consumed (i.e. no advantage to increase the home range during the lean season). The fact that *A. meridioanlis* was a time-minimiser for daily distances travelled and sleeping site selection indicates that energy saving strategies were used as expected due to the low nutrient intake coupled with the high energetic locomotion of this species. The lowland rainforest of Tsitongambarika is highly seasonal in terms of young leaves abundance, and this led individuals to use energy saving strategies during the lean season. Overall, the ranging pattern and sleeping site selection of *A. meridionalis* is influenced by availability of young leaves, supporting the hypothesis that folivorous species face food constraints.

Chapter 5. Effect of seasonality on the feeding behaviour of *Avahi meridionalis* in the lowland rainforest of Tsitongambarika.

5.1. Introduction

The variation of phenological patterns, with the consequent reduction of food availability, determines a complex response in terms of sociality, ranging and feeding behaviours in primates (Van Schaik et al., 1993; Hemingway & Bynum, 2005). In terms of feeding and foraging patterns, primates may face lean periods by increasing time spent foraging (Garber, 1993, Gursky, 2000), reducing their activity to conserve energy (Oates, 1987), increasing dietary breadth (Nagy-Reis & Setz, 2017), and/or switching their diet by including different food items (McConkey et al., 2002) or by relying on keystone species (Terborgh, 1983).

Based on the optimal foraging theory, animals may respond to the reduction of food availability and distribution by either minimising their time spent foraging to reach a fixed energy threshold that depends on food availability (time-minimiser strategy), or spending as much time as possible foraging to maximise their energy intake (resource-maximising strategy) (Schoener, 1971; Hixon, 1982). When resource availability is low, resource-maximisers spend more time foraging, forage on more feeding trees, and spend less time resting than time-minimisers (Schoener, 1971, Hixon & Carpenter, 1988). In terms of responses to seasonal variation of food abundance, resource-maximisers are expected to have similar feeding patterns between seasons of abundance of food resources and lean periods, while time-minimisers spend less time foraging and more time resting in lean periods (Schoener, 1971, Nagy-Reis & Setz, 2017).

The optimal foraging theory has been shown to fit most animal species, however, other complementary models may help to explain feeding behaviours. The diet-breadth model, for example, predicts that when preferred food items (i.e. high-quality food item) become scarce and the available food items have a much lower ratio of energy intake to time, dietary diversity increases (MacArthur & Pianka, 1966; Hemingway & Bynum, 2005). In some cases, the nutrient balancing-strategy (i.e. selecting food items to balance the daily nutrient intake) may explain better dietary patterns than energy-maximiser or time-minimiser strategies (Randolph & Cameron, 2001; Johnson et al., 2013; Dröscher et al., 2016). In particular, protein balance has repeatedly been reported to have a central role in the dietary choices of folivorous primates, although other studies reported no selection on proteins [see Ganzhorn et al. (2017) for a detailed review]. Ganzhorn et al. (2017) showed that primates select for high protein leaves mainly in forests where the average protein content in leaves is low. In fact, primates should be able to satisfy their protein requirements with a diet containing around 6.4-8 % of crude protein (NRC, 2003), so they can potentially feed based on the average availability of protein in the forest (Simmen et al., 2014). Other components such as tannins can reduce protein absorption (Ramachandra et al., 1977), although the role of tannins has been debated and there is no clear evidence whether primates avoid them or whether they have benefits [e.g. self-medication (Huffman, 2001)] from their inclusion in the diet (Norscia et al., 2012; Balestri et al., 2014b).

The woolly lemurs *Avahi* sp. are strictly folivorous and have anatomical specialisations for folivory such as a sacculated cecum and a looped colon that allow midgut fermentation (Chivers & Hladik, 1980; Martin, 1990). The diet of *Avahi* sp. in the habitat where this genus evolved the majority of its species, the Malagasy eastern rainforest, is almost unknown. Only a few studies reported preliminary data on the diet of *Avahi* sp. in this habitat [eastern woolly lemur *A. laniger* (Ganzhorn et al., 1985; Harcourt, 1991; Faulkner & Lehman, 2006)], where the genus was found to be completely folivorous (Harcourt, 1991; Faulkner & Lehman, 2006) or to integrate flowers into the diet in small portions (Ganzhorn et al., 1985). Also, *A. laniger* showed a time-minimiser strategy and a selective diet (Ganzhorn et al., 1985; Harcourt, 1991). These studies included data collected for less than three months and all of them were in the lean season.

In this study, I want to test whether there is an influence of food availability on the feeding strategies employed by the southern woolly lemur *A. meridionalis* in the lowland rainforest of Ampasy, in the Tsitongambarika Protected Area (TGK). Since woolly lemurs are strictly folivorous, seasonality might have a limited effect on their behavioural ecology, assuming that the rainforest is an environment with relatively low variation between seasons in terms of leaf quality (van Schaik & Pfannes, 2005). The assumptions that folivores are less constrained by food availability than frugivores and that there is limited within-group scramble competition, however, have been lately questioned (Steenbeek & van Shaik, 2001, Snaith & Chapman, 2007). In fact, folivores select food resources that vary in availability and spatial distribution, preferring high-quality young leaves in most cases (Koening et al., 1998;

Chapman & Chapman, 2002). Also, folivores may select mature leaves that are highly variable in nutritional quality since they accumulate higher levels of secondary compounds in rainforests as compared to deciduous forests (Hemingway, 1998).

The TGK forest represents an interesting model to test whether a seasonal feeding ecology is present in folivorous primates living in rainforests since, due to its latitude, it has a relatively high seasonal variation with a peak of young leaf production between September and February (see Chapter 2.4; Figure 2.4). The sole previous long-term study on this species suggested that *A. meridionalis* in the littoral rainforest of Ste. Luce, which is located nearby TGK despite being a different habitat, acts as time-minimiser by spending more time resting in the lean season than in the season of food abundance to conserve energy (Norscia et al., 2012). Norscia et al. (2012) reported that *A. meridionalis* has a moderate selectivity on leaves based on nutritional quality and tolerance of secondary compounds. *Avahi occidentalis* in the deciduous forest of Ampijoroa was reported as specialist, relying more on rare resources, and it acted as time-minimiser due to the low food quality associated with the expensive locomotion type (Warren & Crompton, 1998; Thalmann, 2001). At Ampijoroa, the westerns woolly lemur *A. occidentalis* is selective on rare resources probably as a consequence of the competition with the Milne-Edwards' sportive lemur *Lepilemur edwardsi* that occupies a similar niche (Thalmann, 2001).

Based on the unfavourable energy balance and on the previous finding that folivorous primates are constrained by food abundance, quality, and availability (see Chapter 1.1), I predicted that *A. meridionalis* uses a time-minimiser strategy and reduces the time spent foraging during the lean season, where high-quality food items (i.e. young leaves) are rare. The diet-breadth model should also be represented as in other species hypothesising that *A. meridionalis* selects young leaves as preferred food items (see Chapter 1.1). Also, I predicted that nutrient-balance, especially in terms of protein and secondary compounds, is an important strategy for *A. meridionalis* as in other folivores (Ganzhorn et al., 2017). For these reasons, I expected *A. meridionalis* to:

1) have longer feeding bouts and to eat fewer food items per hour in the lean season than in the season of abundance;
2) spend more time resting and less time feeding in the lean season than in the season of abundance;
3) higher diet diversity in the lean season than in the season of abundance;
4) select food items with higher nitrogen and lower secondary compounds during the season of food abundance than in the lean season.

5.2. Methods

5.2.1. Data collection

I collected behavioural data via continuous sampling on five radio-collared individuals of *A. meridionalis* (four females and one male) between August 2015 and July 2016 (see Chapter 2.2 and 2.5 for details on animal captures, and Chapter 2.4 for details on behavioural observations). I initially planned to estimate food intake to calculate nutrient intake and metabolised energy; however, it was only possible to estimate the food intake for 11 out of the 43 food items consumed by *A. meridionalis* during the study period. For this reason, I do not report nutrient intakes here but only the proportion of time spent feeding on the food items.

5.2.2. Analysis of the nutritional content

I collected food samples from the feeding trees when possible, however, most the individuals fed frequently above 15 m high, so most of the food samples were collected the following day on accessible trees of the same species. I air-dried samples under sun warmth until completely dry and sealed them in plastic bags. Biochemical analyses were conducted at the Department of Animal Ecology and Conservation of the University of Hamburg by Irene Tomaschewski). Neutral Detergent Fibres (NDF) and Acid Detergent Fibres (ADF) were obtained via the "Ankom fibre analyser" (Goering & van Soest, 1970; van Soest, 1994), and nitrogen was measured via the Kjeldahl method. Soluble protein content was assessed via Bio-Rad after extraction of the plant material with 0.1 N NaOH for 15 h at room temperature. Sugar content was calculated as the equivalent of galactose after hydrolysation of 50% methanol extract. Condensed tannins were measured as equivalents of quebracho tannin (Oates et al., 1977), and polyphenols were determined following Folin-Ciocalteau (Stolter et al., 2009). The fat content was determined by extraction using petroleum ether, followed by evaporation of the solvent. A detailed review of the procedures and their biological relevance is provided by Ortmann et al. (2006).

Alkaloids were analised qualitatively via triple assays with Mayer's, Dragendorf's, and Wagner's reagents (Cromwell, 1956) and I considered a sample to contain alkaloids when at least two of the reagents showed a positive reaction (Norscia et al., 2012).

5.2.3. Data analysis

Dietary breadth during the two seasons was calculated via the standardised Levin's index (B_{sta}) applied to the proportions of food items consumed via the formula:

$B_{sta} = (B-1)/(B_{max}-1)$

where B is the Levin's niche breadth index [$B=1/\Sigma p_i^2$; where p_i is the proportion of a food item in the diet] and B_{max} is the total number of food items reported in the diet. The standardised Levin's index ranges from 0 (minimal niche breadth) to 1 (maximal niche breadth) (Levins, 1968; Colwell & Futuyma, 1971).

To test whether food items were selected based on their availability or whether there was no correlation between frequency of use and availability of food items within seasons (lean period from March to August and period of abundance from September to February; see Chapter 2.5 and Figure 2.5), I ran a linear regression with the time spent feeding on a food item as dependent variable and the Food Availability Index (see Chapter 2.4) of each food item as independent variable. To examine whether the nutritional content of food items was different between the two seasons, I ran a Mann-Whitney U test. To investigate whether there was a difference in the selection of food items within seasons based on their nutritional content, I ran linear regressions with the nutritional contents of food items as dependent variables and the proportion of time spent feeding on a food item as independent variable. To understand whether *A. meridionalis* used a time-minimiser strategy, I used Wilcoxon tests with average time spent feeding on a food item, number of feeding trees/h, feeding time, and resting time as dependent variables (paired by month), and season as repeated factor. I performed the test via the software IBM SPSS 23 and considered $P < 0.05$ as significant level.

5.3. Results

5.3.1. General diet

Avahi meridionalis during the lean season spent 31.5 % of time feeding on young leaves and 68.5 % of time feeding on mature leaves. Conversely, in the season of abundance *A. meridionalis* spent 64.2 % of time feeding on young leaves and 35.8 % of time feeding on mature leaves (Table 5.1). The dietary niche breadth was higher during the season of food abundance (Levin's index: 0.46) than in the lean season (Levin's index: 0.36). The proportion of time spent feeding on tree species was not related to the Food Availability Index of the food item both in the lean season (linear regression: $F_{1,29} = 0.63$, $\beta = 0.15$, $P = 0.433$) and in the season of food abundance (linear regression: $F_{1,22} = 1.23$, $\beta = -2.24$, $P = 0.269$). This, together with the mid-low Levin's index, are indicators that *A. meridionalis* is moderately specialist and integrates high proportions of uncommon resources in its diet.

Table 5.1: Seasonal food items eaten by *Avahi meridionalis* at Ampasy. Plant species (vernacular and scientific names), food items, and proportion of time spent feeding by *A. meridionalis* between August 2015 and July 2016 in Ampasy in the lean season and in the period of food abundance, and Food Availability Index (FAI) of food items. Only preferred food items (eaten >1 % of feeding time) are shown.

Vernacular name	Family	Scientific name	Food item	% of feeding time	FAI[a]
Lean season					
Hazomamy	Anisophylleaceae	*Anisophyllea phallax*	YL	16.3	1.55
Mafotra	Myristicaceae	*Brochoneura acuminata*	ML	12.0	117.33
Rehiaky	Sapotaceae	*Chrysophyllum boivinianum*	ML	11.8	13.26
Bemahova	Meliaceae	*Neobeguea mahafaliensis*	ML	8.7	2.46
Mendoravy	Fabaceae	*Albizia* sp.	ML	6.6	22.16
Mampay	Fabaceae	*Cynometra* sp.	YL	6.2	4.99
Hafomena	Malvaceae	*Dombeya oblongifolia*	ML	5.7	16.86
Mampay	Fabaceae	*Cynometra* sp.	ML	4.7	25.83
Fandramana	Aphloiaceae	*Aphloia theiformis*	ML	3.3	5.80
Haronga	Hypericaceae	*Harungana madagascariensis*	ML	3.0	2.14
Valimafy	Malvaceae	*Dombeya* sp.	ML	2.3	11.59

Vernacular name	**Family**	**Scientific name**	**Food item**	**% of feeding time**	**FAI**[a]
Lean season					
Rehiaky	Sapotaceae	*Chrysophyllum boivinianum*	YL	2.3	2.92
Vahikarabo	Fabaceae	*Philenoptera madagascariensis*	ML	2.0	NA
Nanto	Sapotaceae	*Capurodendron* sp.	ML	2.0	79.53
Zora	Salicaceae	*Scolopia erythrocarpa*	YL	1.6	3.81
Haziny	Clusiaceae	*Symphonia tanalensis*	YL	1.3	11.09
Voariotry	Fabaceae	*Cynometra cloiselii*	YL	1.3	2.18
Fanstykaitry	Rubiaceae	*Canthium medium*	ML	1.2	21.09
Randrombitro	Buddlejaceae	*Buddleja indica*	ML	1.2	NA
Fotsyvavy	Annonaceae	*Xylopia* sp.	ML	1.1	18.61
Sanira	Sapindaceae	*Tinopsis conjugate*	YL	1.1	7.06
Abundance season					
Mampay	Fabaceae	*Cynometra* sp.	YL	13.4	14.64
Voariotry	Fabaceae	*Cynometra cloiselii*	YL	11.2	8.61
Mendoravy	Fabaceae	*Albizia sp.*	YL	10.2	9.60
Fantsikaitry	Rubiaceae	*Canthium medium*	ML	8.9	21.09

Vernacular name	Family	Scientific name	Food item	% of feeding time	FAI[a]
Abundance season					
Menahihy	Erythroxylaceae	*Erythroxylum sp.*	YL	8.4	30.28
Mendoravy	Fabaceae	*Albizia sp.*	ML	8.3	22.16
Bemavao	Apocynaceae	*Sarcostemma viminale*	YL	6.3	0.30
Rotry	Myrtaceae	*Syzygium emirnensis*	YL	5.5	61.26
Rehiaky	Sapotaceae	*Chrysophyllum boivinianum*	YL	4.5	10.60
Hazongalala	Rubiaceae	*Canephora madagascariensis*	ML	4.1	3.54
Votakala	Phyllanthaceae	*Wielandia leandriana*	ML	3.9	3.97
Sanira	Sapindaceae	*Tinopsis conjugate*	YL	3.1	26.17
Fandramana	Aphloiaceae	*Aphloia theiformis*	ML	2.6	5.80
Mampay	Fabaceae	*Cynometra sp.*	ML	2.2	25.83
Vahifisoroky	Rhamnaceae	*Gouania pannigera*	ML	1.7	NA
Randrombitro	Buddlejaceae	*Buddleja indica*	ML	1.6	NA

[a] Details on the calculation of the Food Availability Index (FAI) are in Chapter 2.3. The FAI is not available (NA) for lianas.

5.3.2. Nutritional content of the diet

The nutrient content was available for 27 food items out of 32 (84.4 %) in the lean season and 23 food items out of 25 (92.0 %) in the season of food abundance. The nutrient content was not different between food items consumed in the two seasons (Figure 5.1).

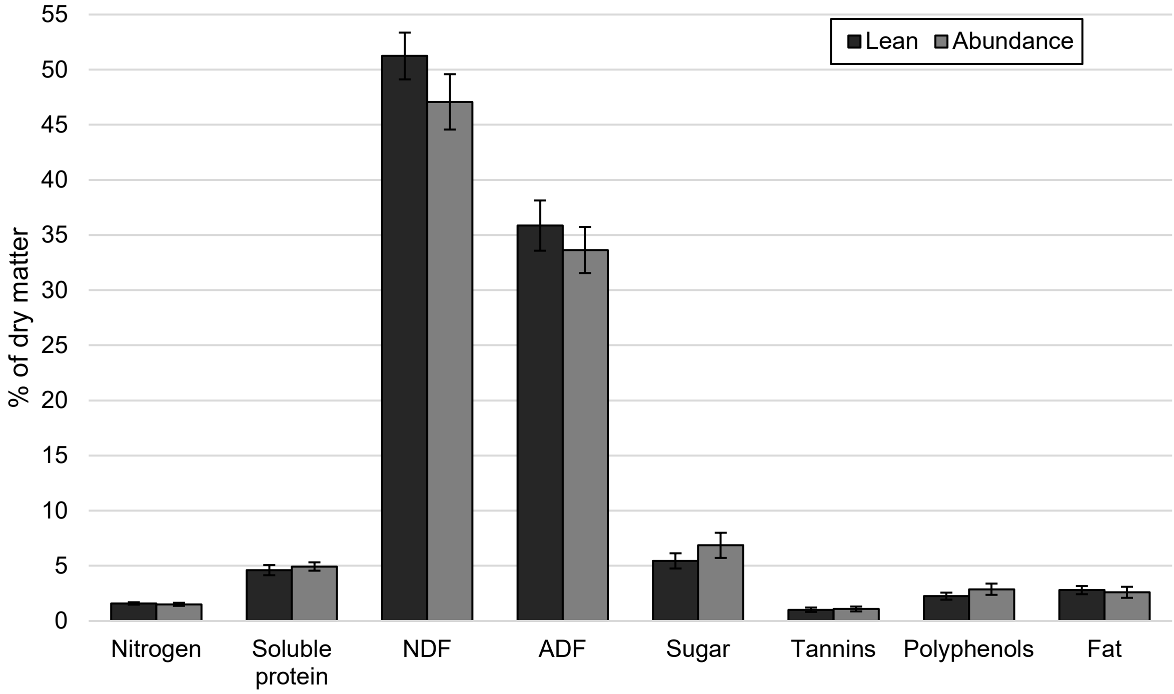

Figure 5.1: Nutritional content of food items. Nutritional content of the food items eaten by *Avahi meridionalis* between August 2015 and July 2016. Means and standard errors are shown. No significant differences were found between seasons with the Mann-Whitney U test.

When the proportion of feeding is considered, however, it emerged that *A. meridionalis* selected more frequently food items higher in nitrogen, NDF, ADF, and lower sugar, tannins, and polyphenols content in the season of abundance (Table 5.2). In the lean season, there was no relationship between nutritional content and percentage on the diet of food items. Alkaloids were reported in only one food item (young leaves of *Sarcostemma viminale*) eaten during the season of food abundance.

Table 5.2: Relationship between nutritional content and feeding time. Model estimated beta and p-value (in brackets) for the linear regression with nutrition content of food items eaten by *Avahi meridionalis* between August 2015 and July 2016 as dependent variable and feeding time in the abundance and lean seasons as independent variables.

Nutritional content	**Feeding time lean (N=23)**	**Feeding time abundance (N=20)**
Nitrogen %	0.01 (0.959)	0.48 (0.021) *
Soluble protein %	-0.25 (0.219)	-0.31 (0.147)
NDF %	0.17 (0.409)	0.58 (0.004) *
ADF %	0.38 (0.055)	0.60 (0.002) *
Sugar %	-0.24 (0.224)	-0.47 (0.025) *
Tannins %	-0.21 (0.285)	-0.44 (0.038) *
Polyphenols %	-0.06 (0.781)	-0.51 (0.013) *
Fat %	-0.02 (0.942)	-0.23 (0.294)

* $P < 0.05$

5.3.3. Frequency and length of feeding bouts

Avahi meridionalis spent on average 997.9 ± SE 140.3 seconds feeding on a tree species during the lean season, and 895.3 ± SE 91.6 s during the season of abundance, with no significant difference between the two seasons (Wilcoxon test: W = 24.0, N = 11 months, P = 0.424). Conversely, the number of feeding trees/h used by *A. meridionalis* were significantly higher during the season of abundance (1.38 ± SE 0.15 trees/h) than during the lean season (1.08 ± SE 0.13 trees/h) (Wilcoxon test: W = 58.0, N = 11, P = 0.026).

The time spent feeding and foraging by *A. meridionalis* was not significantly different between lean (27.2 ± SE 3.8 %) and abundance (34.0 ± SE 3.1 %) seasons, although there is a trend towards significance (Wilcoxon test: W = 13.0, N = 11, P = 0.075). Also, the time spent resting by *A. meridionalis* was not significantly different between lean (67.0 ± SE 4.3 %) and abundance (57.5 ± SE 3.7 %) seasons, again there is a trend towards significance (Wilcoxon test: W = 52.5, N = 11, P = 0.083).

5.4. Discussion

5.4.1. Time-minimising strategy

Avahi meridionalis at Ampasy relied on a time-minimising strategy for its feeding ecology, and the nutrient balance strategy seems to contribute in shaping its dietary patterns in the season of food abundance. The results indicate seasonal difference in terms of feeding strategies and are in line with what was previously found in *A. meridionalis* in the littoral forest of Ste. Luce (Norscia et al., 2012). The trend toward lower feeding and higher resting time, coupled with the lower frequency of trees used for feeding per hour during the lean season as compared to the season of food abundance support the use of a time-minimising strategy (Hixon & Carpenter, 1988; Nagy-Reis & Setz, 2017). This relationship was predicted since the low-quality folivorous diet coupled with the highly energetic locomotion should lead the species to conserve energy (Warren & Crompton, 1997b, 1998; Norscia et al., 2012). Contrary to woolly lemurs, the highly folivorous guerezas *Colobus guereza* at Kibale showed a resource-maximising strategy with an increase of daily distances travelled, time spent feeding, number of feeding patches visited, and dietary breadth during the period of scarcity of the preferred food items (Harris et al., 2009). This difference is probably explained by the fact that *C. guereza* at Kibale is highly specialist (it mainly relies on two food items when available), while *A. meridionalis* at Ampasy is relatively more generalist. The woolly lemurs at Ampasy included several plants at high proportion in their diet, and had a moderate selectivity based on nutritional quality in periods of food abundance. *Avahi meridionalis* spent more time searching for high quality food items when more available, while they preserved energy when young leaves were scarce. This is similar to what found in *A. meridionalis* at Ste. Luce (Norscia et al., 2012). This indicates that the TGK rainforest, that is the southernmost rainforest in Madagascar, is a highly seasonal environment with similar ecological constraints to the neighbouring littoral rainforest of Ste. Luce. Rainforests may thus exhibit seasonal variations and cause similar food constraints than well known seasonal environments such as deciduous forests. Other Indriidae showed similar patterns with no correlation between food availability and time spent feeding, but rather a selection on food quality [western woolly lemur *A. occidentalis* (Thalmann 2001); Indri *Indri indri* (Powzyk & Mowry, 2003); Verreaux's sifaka *Propithecus verreauxi* (Norscia et al., 2006a)]. Other folivorous species showed preference for high-quality leaves such as young leaves [e.g. mantled howler monkey *Alouatta palliata* (Glander, 1981); upper Guinea red colobus *Procolobus badius* (Chapman & Chapman, 2002)] or mature leaves high in protein content [northern plains grey langur *Semnopithecus entellus* (Koenig et al., 1998; Koenig, 2000)]. It appears clear that folivores are highly selective in their diet, mainly depending on nutritional content, and seasonal variations of high-quality food items drive their feeding behaviours (Snaith & Chapman, 2007).

5.4.2. Dietary breadth and nutritional content

The lowland rainforest of Ampasy, showing a great amplitude of leafing seasonality, had a clear lean season and a clear season of abundance in terms of young leaves production (see Chapter 2.4 and Figure 2.5). It is unclear why *A. meridionalis* had a lower dietary breadth during the lean season as compared to the season of food abundance, and do not follow the diet-breadth model (MacArthur & Pianka, 1966). In fact, the increase in diet diversity in lean periods is a behavioural flexibility that may provide some defence to food scarcity (Hemingway & Bynum, 2005). The lower dietary breadth may be explained by the fact that *A. meridionalis* relied more on the few high-quality species present in the lean period, such as *Anisophyllea phallax*. This explanation is supported by the finding that during the lean season there is no significant relationship between time spent feeding on food items and the nutritional content of food items (i.e. only a few food items were at high quality during the lean season and the sample size was too low for having a significant correlation). Conversely, the aforementioned relationship is present for several nutrients in the season of food abundance. This may indicate that, in the season of food abundance, *A. meridionalis* had more possibilities to select food items richer in nitrogen and fibres and lower in tannins and polyphenols. A possible role in the reduction of the dietary niche breadth of *A. meridionalis* during the lean season may potentially be the competition with the other nocturnal folivore *Lepilemur fleuretae*, which occurs at high density in Ampasy (see Chapter 3). Woolly lemurs were found to rely on rare resources when in sympatry with *Lepilemur* sp. to reduce dietary niche competition (Thalmann, 2001). Also, *L. fleuretae* in Ampasy seemed to avoid feeding competition with *A. meridionalis* by including a high proportion of flowers and fruits in its diet when compared to other sportive lemurs (M. Campera, unpub. data). This resulted in a limited dietary niche overlap, measured via the Pianka index, between the two species (0.40 in the lean season and 0.06 in the season of abuncance, considering a scale from 0, no overlap, to 1, complete overlap (Pianka, 1973)].

The food items eaten by *A. meridionalis* at Ampasy had relatively lower content of secondary compounds than the food items eaten in the littoral forest of Ste. Luce (Norscia et al., 2012). This is probably due to the fact that plants growing on sandy soils usually have high concentrations of secondary compounds (Simmen et al., 2003, 2006). Also, alkaloids were present in around half of the food items of *A. meridionalis* in Ste. Luce (Norscia et al., 2012), while only one food item out of 43 had alkaloids at Ampasy. It has been previously suggested that *A. laniger* and *A. occidentalis* avoid food items with alkaloids (Ganzhorn, 1988), although this idea was not supported by *A. meridionalis* in Ste. Luce. Although I only reported one food item with alkaloids; I do not have the nutritional content of non-food items, so I cannot draw clear conclusions on this hypothesis.

The southern woolly lemur in the lowland rainforest of Tsitongambarika is strictly folivorous, with a preference for young leaves when available. The genus *Avahi* sp. has been reported as strictly folivorous by all the previous studies, although there is some evidence of feeding flowers (Ganzhorn et al., 1985; Norscia et al., 2012). I never recorded the study animals feeding flowers, nor I recorded them feeding flowers when encountered while doing other activities. In average, flowers tend to have similar nutritional content as young leaves, with higher protein and lower ADF contents than mature leaves (Norscia et al., 2012). Thus, flowers are also likely to represent a component of the diet of *A. meridionalis* at Ampasy, and further data are necessary to give more insights on the dietary patterns of the species in rainforests.

5.4.3. Conclusions

In conclusion, *A. meridionalis* at Ampasy is a moderate specialist with selectivity based on nutritional quality especially in periods of food abundance. *A. meridionalis* at Ampasy shows a time-minimising strategy as a consequence of the relatively low-quality diet coupled with the highly energetic locomotion. *Avahi meridionalis* showed reduced dietary breadth during the lean season possibly to select the few high-quality food items present and reduce feeding competition with the nocturnal folivore *L. fleuretae* that occur at high density in Ampasy. *Avahi meridionalis* occupied a different dietary niche than *L. fleuretae* despite the similar habits of these two species. The dietary data collected in this study, despite the relatively limited sample size, represents the larger dataset available for woolly lemurs in the eastern rainforest. This highlights the necessity of further studies on *Avahi* sp. in the habitat where this genus has its higher diversity. Being the findings on the diet of *A. meridionalis* at Ampasy similar to the findings in other habitats in Madagascar, however, it seems that the genus *Avahi* relies on a specific niche that is similar in the different habitats in Madagascar and that helps in reducing niche overlap with ecologically similar sympatric species.

Chapter 6. Opportunistic cathemeral activity in the nocturnal Indriidae *Avahi meridionalis*.

6.1. Introduction

In terms of activity patterns, primates were historically classified as diurnal or nocturnal until the discovery that a lemur species of the genus *Eulemur* exhibits activity over 24 h (Tattersal, 1979). This behavioural pattern is defined as cathemerality (Tattersal, 1987) and is now well-documented among four genera of the family Lemuridae [*Prolemur* (Tan, 2000; Grassi, 2001); *Eulemur* (Donati & Borgognini-Tarli, 2006a; Curtis & Rasmussen, 2006); *Lemur* (Donati et al., 2013); *Hapalemur* (Mutschler, 2002; Eppley et al., 2015)]. The other genus of lemurid, *Varecia*, has also anecdotally been reported to exhibit cathemeral behaviour (Donati & Borgognini-Tarli, 2006b), including in captivity (Bray et al., 2017), meaning cathemerality is likely to be present in all lemurids. There remains some debate as to whether the emergence of cathemerality should be dated at the separation node between *Varecia* and the other lemurid genera [between 22.3 and 16.8 Mya (Donati et al., 2013; Markolf & Kappeler, 2013)] or at the split between lemurids and the other families of lemurs (Santini et al., 2015).

Malagasy lemurs are the only monophyletic primate radiation that regularly yields diurnal, nocturnal, and cathemeral genera (Mittermeier et al., 2010), although the reasons for this flexibility are still unclear. The attempts to explain the evolution of cathemerality in lemurs are based on two main hypotheses. The first one considers this trait as a stable adaptation, while the second one considers this trait as a current disequilibrium. Based on the first hypothesis, cathemeral behaviour is expected to provide a number of ecological advantages such as thermoregulatory benefits to avoid thermal stress (Curtis et al., 1999; Mutschler, 2002), reduced predation risk (Donati et al. 1999; Rasmussen, 2005; Colquhoun, 2006), reduced feeding competition (Curtis et al., 1999; Curtis & Rasmussen, 2006), and increased feeding efficiency related to a fibre-rich diet (Engqvist & Richard, 1991; Donati et al., 2007, 2009, 2016). Alternatively, the evolutionary disequilibrium hypothesis suggests that cathemerality represents a transitional state between nocturnal and diurnal activity patterns as a consequence of the extinction of large predators and competitor lemurs upon the arrival of humans to Madagascar (van Schaik & Kappeler, 1993, 1996; Kappeler & Erkert, 2003).

One of the traits studied to understand the evolution of cathemerality in lemurs is their eye morphology (Kirk, 2006; Hall et al., 2012). Evidence for the evolutionary disequilibrium hypothesis in the evolution of cathemerality was mainly related to the presence/absence of the *tapetum lucidum*, the reflective layer behind the retina that enhances available light (Martin, 1990; Kirk, 2004). The presence/absence of the *tapetum lucidum* as a useful trait to reconstruct the evolution of activity pattern has been debated since it may have been retained by cathemeral species to be active at low luminosity conditions (Kirk, 2006; Donati et al., 2013). The adaptive role of a *tapetum lucidum* is supported by the fact that many cathemeral lemurs also possess adaptations to day-light such as a fovea-like *area centralis*, suggesting that their eye morphology is intermediate to favour activity over the 24-h and at different light conditions (Curtis & Rassmussen, 2002; Donati et al., 2013). Also, eye morphometrics in cathemeral species are intermediate between nocturnal and diurnal strepsirrhines (Kay & Kirk, 2000; Kirk, 2006), supporting an adaptive origin of cathemerality.

The genus *Avahi* is considered strictly nocturnal, although its ancestors have been hypothesized to be diurnal and its nocturnality is considered as a secondary trait [(Ganzhorn et al., 1985; Roos et al., 2004); but see Santini et al. (2015)]. Recent findings suggested that the strength of selection to maintain SWS1 opsin gene for colour vision in is similar to what found in diurnal primates (Veilleux et al., 2013, 2014). This is considered a retention from diurnal ancestors and *Avahi* may have experienced consistent selection to retain dichromatic colour vision throughout its evolutionary history (Veilleux et al., 2014). Thus, *Avahi* has some visual adaptations that are somehow intermediate between the nocturnal and diurnal lemurs. Also, *Avahi* was found to be occasionally active during the day in some previous studies (Ganzhorn et al., 1985; Warren & Crompton, 1997a). These observations suggest that *Avahi* might exhibit some diurnal activity in certain conditions, although the extent of this activity needs to be explored in detail.

The lowland rainforest of Tsitongambarika (thereafter TGK) represents an ideal model to test whether *Avahi* evolved the ability to be active over the 24-hour cycle as an adaptive trait since it is the southernmost rainforest of Madagascar and thus an area exposed to the most significant photoperiodic variation that can be found in Madagascar (from 10.6 to 13.7 h). This lowland rainforest is characterized by a large thermal excursion with significant seasonality in terms of young leaf availability (see Chapter 2.4 and Figure 2.5). Also, the TGK rainforest has a high density of *Lepilemur* (see Chapter 3), which occupy a similar niche to *Avahi* and this relationship may entail a certain degree of scramble competition, thus favouring activity shifts as a mechanism for niche separation (Warren & Crompton, 1997a; Thalmann, 2001) (see Chapter 3).

In this study I wanted to investigate whether southern woolly lemur *Avahi meridionalis* in the lowland rainforest of Tsitongambarika evolved cathemerality as an adaptive trait. I predict that:

1) *Avahi meridionalis* shows cathemeral activity since this behaviour may represent an ecological advantage in terms of thermal stress avoidance, reduced feeding competition with *Lepilemur fleuretae*, and increased metabolic efficiency related to a fibre-rich diet;
2) night-length, that shows important variation in TGK due to the southern position of this rainforest, would be a significant predictor of the activity of *A. meridionalis*;
3) moon phase (a proxy of nocturnal luminosity) will be a significant factor influencing nocturnal activity if *Avahi* can discriminate leaves by colours.

6.2. Methods

6.2.1. Data collection.

I collected activity data every second on three individuals (two females and one male) of *Avahi meridionalis* at Ampasy via three-axis accelerometer tags (Axi-3, TechnoSmArt) attached to VHF collars (RI-2D, Holohil Systems Ltd). The weight of the combination of VHF collars and accelerometer tags with batteries was around 15 g, thus below the 5% threshold of the subjects' weight recommended for arboreal animals (Wheater et al., 2011). The data collection lasted from 07/07/2015 to 06/08/2015 (31 days) for female 1, from 09/07/2015 to 23/08/2015 (45 days) for female 2, and from 10/07/2015 to 17/09/2015 (68 days) for the male. Detailed information on animal captures are in Chapter 2.2 and 2.5.

6.2.2. Data analysis

I transformed the raw data collected via accelerometers by using the package “plotrix” for R software in the integrated variables dynamic acceleration over the three axes and amplitude of the dynamic acceleration over the three axes with a smoothing factor of 10 s based on previous recommendations (Chimienti et al., 2016). The integrated variables were analysed via the package “Rmixmod” for R software utilising the Expectation Maximisation (EM) algorithm, which statistically associates each data to a cluster (Biernacki et al., 2003).

To test the efficiency of this method in detecting activity and inactivity, I compared the data obtained via the EM algorithm with the behavioural data obtained simultaneously via 20.6 h of continuous sampling (excluding out of sights) on the three animals (see Chapter 2.4 for more information about collection of behavioural data). The algorithm had a correspondence of 98.6-99.4 % with the inactive behaviour detected via behavioural observations.

I calculated the daily proportion of activity during the day, twilight, and night. As twilight, I considered the time between the beginning of the morning astronomical twilight (when the sun is 18º below the horizon before sunrise) and the sunrise, and between the sunset and the end of evening astronomical twilight (when the sun is 18º below the horizon before sunrise or after sunset) (Donati & Borgognini-Tarli, 2006b). I obtained sunset, sunrise, moon phase, and night-length via Moon v.2.0 software, and beginning and end of astronomical twilights from the U.S. Naval Observatory Astronomical Almanac (http://aa.usno.navy.mil/data) using the coordinates of Ampasy (see Chapter 2.1).

To evaluate the influence of night-length and moon phase on the activity of *Avahi meridionalis*, I used a General Linear Model (normal distribution and identity link function) with proportion of activity (during the day, at twilight, and at night) or the ND ratio [including twilight in the nocturnal activity to compare ratios with previous studies on cathemeral lemurs (Fernandez-Duque & Erkert, 2006; Donati et al., 2013; Eppley et al., 2015)] as dependent variables, night-length and moon phase as covariates, and individuals as random factor. I included the twilight in the nocturnal activity to compare my study with other studies on diurnal animals that included twilight in the daily activity since both diurnal and nocturnal animals are active at this low light condition (Donati & Borgognini-Tarli 2006b; Fernandez-Duque & Erkert, 2006).

To represent the activity profiles over the 24 h, I divided the daily activity into 2-h blocks starting from midnight. I considered two moonlight conditions: high luminosity (more than 50% of illuminated moon surface) and low luminosity (less than 50% of illuminated moon surface) (Donati et al., 2013). I ran a Generalised Linear Mixed Model (normal distribution and identity link function) with the percentage of activity every 2-h interval as dependent variable, the time-block (i.e. 2-h intervals) as repeated factor, moon luminosity (high and low) as fixed factor, and individuals as random factors. I included the interaction effect between time-block and moon luminosity to test whether *A. meridionalis* has different 24-h activity at high and low luminosity conditions. I ran a post hoc test with Sidak adjustment for multiple comparisons to test the difference in activity between the 2-h time-blocks.

6.3. Results

6.3.1. Influence of night-length and moon phase

The three individuals of *Avahi meridionalis* were at their peaks of activity at twilight (65.20 ± SE 0.77 %, N = 145 days), high proportion of activity at night (50.45 ± SE 0.69 %, N = 145), and a low proportion of activity during the day (14.69 ± SE 0.51 %, N = 145 days) (Figure 6.1). The duration of the night negatively influenced the activity of *A. meridionalis*: at twilight (night-length effect: $F_{1,142} = 43.93$, $\beta = -13.35$, $P < 0.001$), at night (night-length effect: $F_{1,142} = 40.33$, $\beta = -11.48$, $P < 0.001$), and during the day (night-length effect: $F_{1,142} = 7.62$, $\beta = -3.99$, $P = 0.007$). Moon phase negatively influenced the activity of *A. meridionalis* during the day (moon phase effect: $F_{1,142} = 3.91$, $\beta = -2.81$, $P = 0.048$), while no influence was present at twilight (moon phase effect: $F_{1,142} = 0.33$, $\beta = -1.12$, $P = 0.567$) and at night (moon phase effect: $F_{1,142} = 2.01$, $\beta = 2.49$, $P = 0.159$). The ND ratio, also known as nocturnality, was 4.38 ± SE 0.18 (range = 1.12-13.09, N = 142 days), and there was a trend toward a positive effect of moon phase (moon phase effect: $F_{1,139} = 3.42$, $\beta = 0.97$, $P = 0.066$) and no effect of night-length (night-length effect: $F_{1,142} = 0.00$, $\beta = -0.03$, $P = 0.957$). Thus, the activity of *A. meridionalis* during the day, at twilight, and at night increased when night-length decreased, so the ND ratio was not influenced overall by seasonality (night-length). Also, the activity of *A. meridionalis* during the day increased and the ND ratio decreased with the decrease of moon luminosity, while there was no effect of moon luminosity on the activity at twilight and at night.

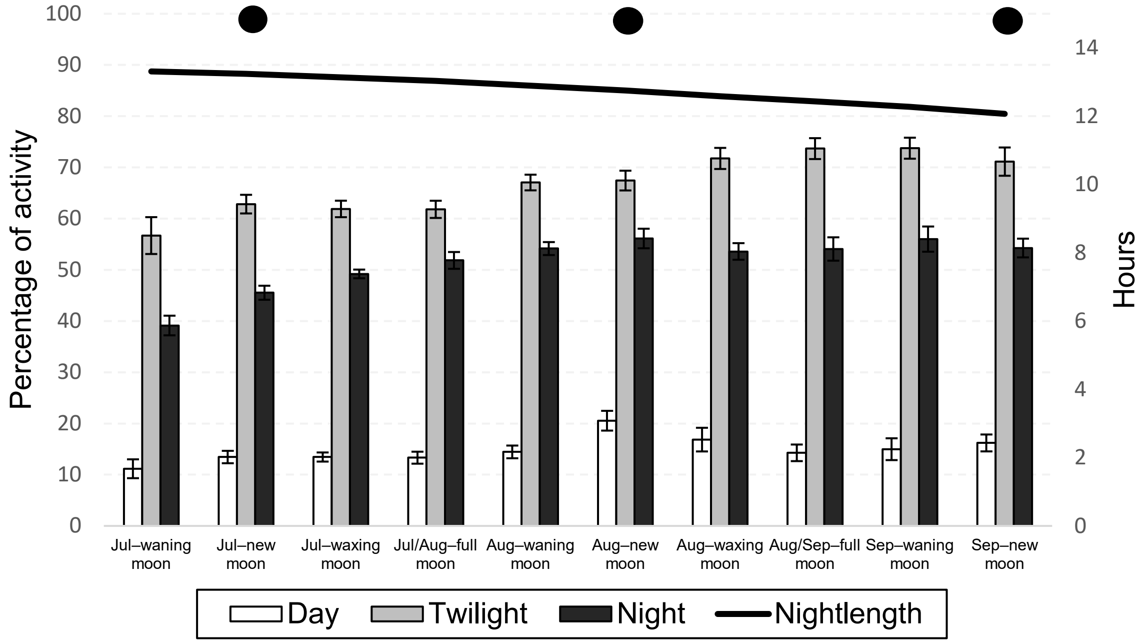

Figure 6.1: Variation of activity of *Avahi meridionalis* at Ampasy during the day, at twilight, and at night. Means and standard errors for successive moon phases from 07/07/2015 to 17/09/2015 are shown. Black circles indicate new moon phases.

6.3.2. Daily activity pattern

The 24-h activity pattern of *Avahi meridionalis* showed two main peaks between 4 am and 6 am and between 6 pm and 8 pm. There is significant variation of the activity in the 24-h (Time-block effect: $F_{11,265.77} = 392.75$, $P < 0.001$) (Figure 6.2). A Sidak post-hoc test revealed a significant difference between all the time-blocks except between 20-22, 22-24, and 0-2 (night blocks), between 4-6 and 18-20 (twiligth blocks), between 6-8, 8-10, and 16-18, and between 8-10, 10-12, and 12-14 (day blocks). *Avahi meridionalis* had a maximum activity of 59.5% during the day (Figure 6.2). The diurnal activity patterns of *A. meridionalis* showed mostly no or low levels of activity with occasional peaks usually lasting 20-30 minutes.

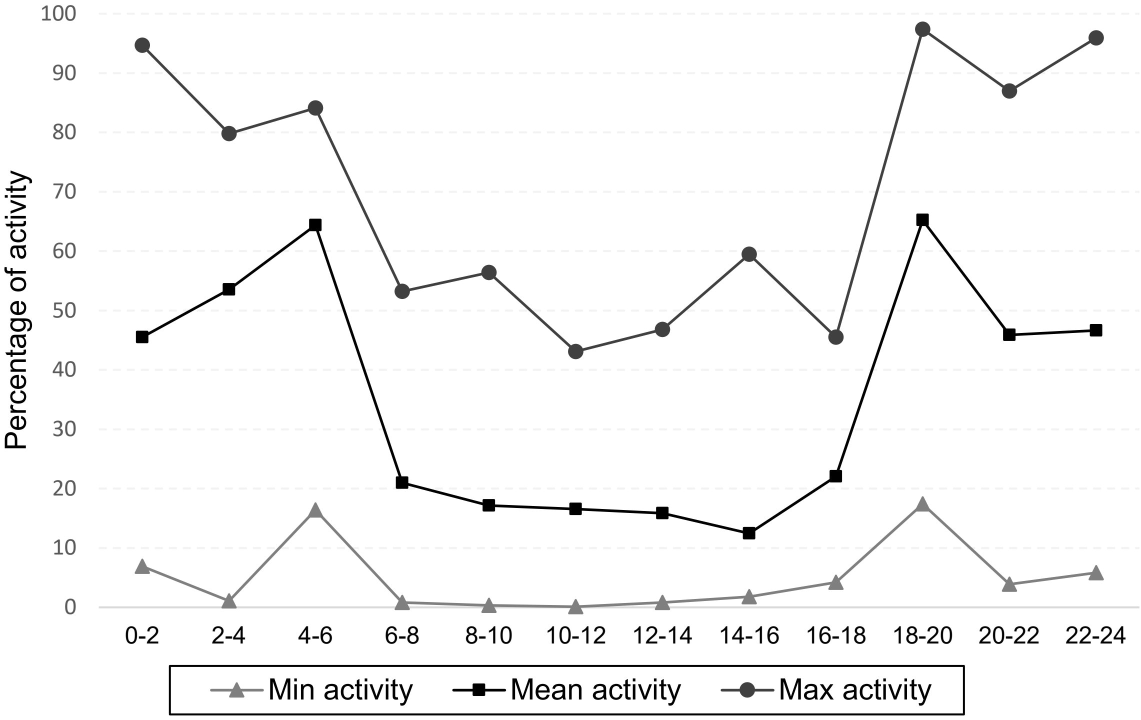

Figure 6.2: Daily activity of *Avahi meridionalis* at Ampasy. Hourly distribution of activity (mean, minimum, and maximum) of three individuals of *A. meridionalis* over the 24-h from 07/07/2015 to 17/09/2015. Sunset: 17:17-17:46; evening astronomical twilight: 18:37-19:02; morning astronomical twilight: 4:32-5:16; sunrise: 5:47-6:36.

The 24-h activity profile of *A. meridionalis* was shaped differently between low and high luminosity conditions (Time-block*moon luminosity effect: $F_{11,265.77}$ = 2.04, P = 0.025) (Figure 6.3). But there is no significant difference in the total activity between high and low luminosity conditions (moon luminosity effect: $F_{1,1417.64}$ = 0.37, P = 0.544).

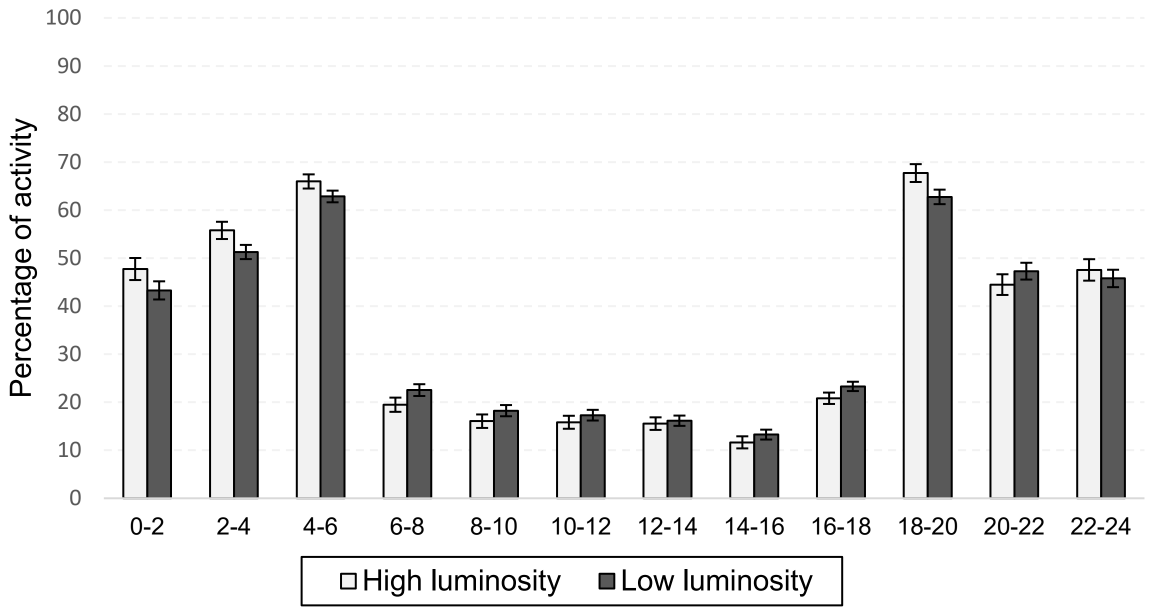

Figure 6.3: Daily activity at high and low luminosity conditions. Hourly distribution of activity (mean and standard error) of three individuals of *Avahi meridionalis* over the 24-h at low and high luminosity conditions from 07/07/2015 to 17/09/2015. Sunset: 17:17-17:46; evening astronomical twilight: 18:37-19:02; morning astronomical twilight: 4:32-5:16; sunrise: 5:47-6:36.

6.4. Discussion

6.4.1. Opportunistic cathemeral activity

Avahi meridionalis in the lowland rainforest of Tsitongambarika showed an opportunistic cathemeral activity, varying from a strict nocturnality (ND ratio of 13.09:1) to a cathemeral activity (ND ratio of 1.12:1). Assuming that I can use nocturnality (ND ratio) as a measure of cathemerality in mainly night active lemurs as I do with diurnality (DN ratio) in mainly diurnal lemurs, *Avahi meridionalis* showed a level of nocturnality of 4.38:1 that is similar to the level of diurnality found in cathemeral species [3.5:1 for collared brown *Eulemur collaris* (Donati et al., 2009); 3.4:1 for red-fronted brown lemur *E. rufifrons* (Kappeler & Erkert, 2003); 3.98:1 for rusty-grey lesser bamboo lemur

Hapalemur meridionalis (Eppley et al., 2015); 4.8:1 for ring-tailed lemur *Lemur catta* (Donati et al., 2013)]. *Avahi meridionalis* seems to show analogous cathemeral behaviour of *H. meridionalis* (Eppley et al., 2015) and *L. catta* (Donati et al., 2013) since they show large variations in diurnal vs nocturnal ratio. This suggests an opportunistic role of cathemerality that can be considered a flexible behaviour. The activity pattern of the southern woolly lemurs is also similar to Azara's night monkey *Aotus azarai azarai* in the Argentinian Chaco, the other nocturnal primate that exhibits cathemeral activity (Fernandez-Duque & Erkert, 2006).

A possible driver that might have determined the flexible cathemerality pattern in *A. meridionalis* is the necessity to maximise the food intake over the 24-h considering its diet rich in fibres (Engqvist & Richard, 1991; Donati et al., 2007, 2009). Despite the adaptation to folivory in *Avahi* [i.e. midgut fermentation via sacculated caecum and looped colon (Chivers & Hladik, 1980; Martin, 1990)], midgut fermentation may still reduce the amount of food that can be processed as well as nutrient intake (Martin, 1990; Campbell et al., 2004). Extra-bouts of feeding activity during the day may maximise nutrient intake in *A. meridionalis*. As a matter of fact, I opportunistically observed individuals of *A. meridionalis* at Ampasy feeding during the day, whilst I was collecting data on sleeping sites. Also, at the beginning of behavioural observations at dusk I frequently found individuals nearby the sleeping site where I left them in the morning, suggesting that they might have had some activity during the day. This limited activity during the day had been also reported in previous research on *Avahi* (Ganzhorn et al., 1985; Warren & Crompton, 1997a).

Competition with Fleurete’s sportive lemur *Lepilemur fleuretae* that occurs at high density at Ampasy might have been another cause for the shift to cathemeral activity rather than strictly nocturnal activity. In fact, *A. meridionalis*, which was more active at twilight and had opportunistic cathemerality, showed a different temporal niche than *L. fleuretae*, which was more active in the central hours of the night (M. Campera, unpub. data). Temporal niche separation is an ecological advantage previously described in cathemeral lemurs (Curtis et al., 1999; Curtis & Rasmussen, 2006; Donati et al., 2013) to reduce feeding competition between species (Ganzhorn, 1989).

6.4.2. Influence of photoperiodic variations and moon phase

The activity of *A. meridionalis* was highly influenced by photoperiodic variations as predicted by the latitude of the Tsitongambarika forest. Photoperiodic variations influenced activity of other cathemeral lemurs (Engqvist & Richard, 1991; Curtis et al., 1999; Donati & Borgognini-Tarli, 2006b; Donati et al., 2009), although other studies did not find a clear relationship (Overdorff & Rasmussen, 1995; Andrews & Birkinshaw, 1998; Colquhoun, 1998; Eppley et al., 2015). The increase in activity with the decrease of night-lengths is probably the consequence of the shorter time to meet energetic requirements Furthermore, this pattern might be further explained by the seasonality characterising Malagasy habitats (Wright, 1999; Ganzhorn et al., 2003; Dewar & Richard, 2007). In fact, photoperiodic variations usually influence the activity of primates when resources are predictable (Curtis & Donati, 2013). Further studies are necessary, however, to highlight the influence of seasonality on the activity patterns of *A. meridionalis* at Ampasy since I do not have data for the entire year.

As predicted, the ND ratio of *A. meridionalis* was influenced by the moon phase with higher ND ratio at higher moon luminosity. Opposite to nocturnal mammals that are usually lunarphobic to reduce predation risk (Bearder et al., 2006; Nash, 2007; Prugh & Golden, 2014), *A. meridionalis* was lunarphilic similar to other cathemeral primates (Erkert, 1989; Donati et al., 2001, 2013; Fernandez-Duque, 2003; Kappeler & Erkert, 2003; Donati & Borgognini-Tarli, 2006b; Schwitzer et al., 2007; Fernández-Duque et al., 2010; Eppley et al., 2015). It has been hypothesised that lunarphilia can be a strategy to reduce predatory risk by increasing vigilance (Gursky, 2003; Prugh & Golden, 2014). This might explain why *A. meridionalis* was lunarphilic since, being usually in pairs, may increase vigilance at high luminosity conditions. The alternative behaviour, i.e. reducing predation risk by camouflaging and reducing activity at high luminosity conditions, may be a better strategy for solitary animals (Starr et al., 2012; Rode-Margono & Nekaris, 2014). Another advantage of being lunarphilic is the higher foraging efficiency at high luminosity conditions (Gursky, 2003; Donati et al., 2006; Prugh & Golden, 2014; Eppley et al., 2015). This may be the main driver for the influence of the moon phase on the nocturnality of *A. meridionalis* since this species was not influenced by moon phase at twilight and at night, while it was negatively influenced during the day. Thus, *A. meridionalis* may spend more time being active during the day as a consequence of the limited visibility to discern young leaves during the new moon phase. This lunarphilia may represent an advantage for *Avahi* sp. since this genus has an adaptation for colour vision and can distinguish young leaves

(Veilleux et al., 2013, 2014). Leaf quality is, in fact, correlated to variation in the green-red and blue-yellow chromatic differences (Dominy & Lucas, 2004). The visual pigments of *Avahi* range from green to red wavelengths and appear optimally adjusted to detect young green leaves (Veilleux et al., 2014).

6.4.3. Conclusions

The finding that *A. meridionalis* is opportunistic cathemeral has wide implications on the evolution of cathemerality. Although the previous finding that routinary cathemerality evolved at the divergence between Lemuridae, Indriidae, Lepilemuridae, and Cheirogaleidae (Donati et al., 2013; Markolf & Kappeler, 2013), considering *Varecia* as cathemeral in the wild (Griffin et al., 2012) may not be questioned with the current data, an opportunistic cathemerality may have emerged even earlier in lemurs. The finding that *A. meridionalis* is cathemeral may suggest that the common ancestor for the Indriidae is likely to be diurnal, thus supporting the hypothesis of a secondary nocturnality for *Avahi* (Ganzhorn et al., 1985; Müller & Thalmann, 2000; Roos et al., 2004). In this scenario, *Avahi* may have evolved an opportunistic cathemerality as an adaptive convergence with the Lemuridae, supporting the idea that cathemerality is a key adaptation to survive lean periods (Donati & Borgognini-Tarli, 2006a). Another possibile scenario [based on the cladogram from Roos et al. (2004)] may be a common cathemeral ancestor between Indriidae and Lemuridae (Donati & Borgognini-Tarli, 2006a).

Chapter 7. Assessment of long-term retention of environmental education lessons given to teachers in rural areas of Madagascar

Chapter published in the Applied Environmental Education & Communication journal

7.1. Introduction

Environmental education programs aim at increasing knowledge, attitude, and behaviour of participants (Kuhar et al., 2010; van der Ploeg et al., 2011). The Bloom's taxonomy of educational objectives (Bloom, 1956) is a well-accepted categorization of learning and is commonly applied in environmental education assessment (Bissels & Lemons, 2006; Jacobson et al., 2006; van der Ploeg et al., 2011). Basic knowledge is the first category of Bloom's taxonomy and includes memorizing facts, figures, and basic processes (Bissels & Lemons, 2006). Assessment of basic knowledge and its increase in the short- and long-term is the first step in environmental education programs (Kuhar et al., 2010). Yet studies investigating the long-term efficiency of environmental education programs in a conservation context are still uncommon (e.g., Kuhar et al., 2010; Rakotomamonjy et al., 2015; Richter et al., 2015; Grúňová et al., 2017), while more studies only evaluated immediate knowledge and attitudes towards these programs (e.g., Dolins et al., 2010; Damerell et al., 2013). Furthermore, information coming from local educators is likely to be more effective than if delivered by foreigners; teacher training is thus pivotal to facilitate a long-term retention of environmental knowledge (Wallis & Lonsdorf, 2010).

Madagascar is a biodiversity hotspot and widely recognized as a conservation priority (Brooks et al., 2006). In fact, habitat exploitation, such as forest fragmentation, logging, and hunting are threatening many lemur species, a unique radiation of primates found only in Madagascar, with extinction (Schwitzer et al., 2014). Madagascar is one of the poorest countries in the world, since more than 92% of Malagasy people live on less than $2 a day (World Bank, 2007). Education level is low in Madagascar, especially in rural villages, and many local people do not have the means (e.g., money and books) to receive an education (Ratsimbazafy, 2003; Dolins et al., 2010). Only 38% of children start at least the first class of schools (UNDP Human Development Report, 2014), hence targeting primary schools for environmental education allows for reaching the largest portion of Malagasy children at school (Richter et al., 2015). This lack of education has been posited as one of the reasons for the dramatic habitat loss over the last 60 years in Madagascar (Green & Sussman, 1990; Dolins et al., 2010). In fact, many local people use traditional cultivation methods (e.g. slash-and-burn agriculture), which have a high impact on the forest and give low profits (Styger et al., 2007). Furthermore, little is taught about endemic lemurs, their ecology, and their protected status, especially in rural areas, despite their use as flagships in many development programs (Ratsimbazafy, 2003; Keane et al., 2011). Despite the integration of environmental education in teaching programs at all levels by the Malagasy government, many teachers have a limited knowledge on this subject and do not receive appropriate training (Dolins et al., 2010). Environmental education is thus crucial in Madagascar to encourage long-term protection of the habitats.

The Protected Area of Tsitongambarika is one of the last remnant lowland rainforests of Madagascar and it is one of the 30 priority areas for conservation on the island in a Lemur Conservation Action Plan (Schwitzer et al., 2013). Unfortunately, the Anosy region, which hosts this forest, is also one of the regions with a lower education level in Madagascar (BirdLife International, 2011), and local people have a high impact on the forest (Bollen & Donati, 2006). In fact, human exploitation such as hunting, slash-and-burn agriculture, logging, and timber harvesting is common in the area (Bollen & Donati, 2006). A program of environmental education in the area is lacking, and launching one has been hindered by high illiteracy in the area (BirdLife International, 2011). In the year 2015, the local Nongovernmental Organization (NGO) Asity linked to BirdLife International started a project on environmental education following international programs for primary schools (UNESCO, 1983).

During the environmental education program promoted by Asity Madagascar, I provided four days of environmental education lessons to teachers of Iaboakoho between July and September 2015. The aim of this study was to test whether the lectures given to the teachers from primary schools of the municipality of Iaboakoho had been retained and the teachers were thus able to provide information on lemurs and their biology to the students. To test this, after one year from the training I gave structured questionnaires to 43 teachers from the primary schools in the municipalities of Iaboakoho, Mahatalaky, Mandromodromotra, and Ampasy-Nahampoana. I selected these four municipalities because they are in the same region (Anosy), along the national road 12A, and all about the same distance from the Tsitongambarika Protected Area. The hypothesis I tested is that the teachers from Iaboakoho retained the information given and have a higher knowledge regarding lemurs and their biology than the teachers from the other municipalities, considered as control groups.

7.2. Methods

7.2.1. Survey design

The Ministry of the Environment and Forests established the Tsitongambarika Protected Area in 2008 and Asity Madagascar manage it with the financial aid of Qit Madagascar Minerals (BirdLife International, 2011). At the end of April 2015, a research station was created in the northernmost portion of Tsitongambarika with the collaboration of Asity Madagascar, Qit Madagascar Minerals, and Oxford Brookes University. The research station was established in a portion of Tsitongambarika included in the municipality of Iaboakoho. I provided training lessons to teachers from the primary school in Iaboakoho and the other primary schools included in the municipality. Not all the teachers attended all the lessons; for this reason, I asked only the teachers who attended all of them to do the test. The three teachers who attended only part of the program were excluded from the test. All the other teachers trained participated in the test. My sessions were organized with the aid of Asity Madagascar that provided training for teachers including environmental education from July to September 2015. No additional environmental education interventions were given in Iaboakoho prior to this training (Faniry Rakotoarimanana, Asity Madagascar, pers. comm. 2016).

Each lesson lasted for about two hours in which I discussed the following subjects: “Generalities on the Tsitongambarika forest and the new research station,” “The lemur species present in Tsitongambarika and their ecology,” “The importance of plant biodiversity for humans and lemurs,” and “Ecosystems equilibrium.” The learning objective of the first lesson was to describe the importance of the Tsitongambarika forest for lemur conservation. I shared information about the research station and the research on lemurs that I was conducting in the area. Also, I highlighted the reasons why I chose this site for the installation of a new research station. The learning objective of the second lesson was to list the lemur species that are present in Tsitongambarika and state information about their scientific names, activity, and diet. The learning objective of the third lesson was to define the concept of “biodiversity,” as well as to recognize threats and ways to preserve biodiversity. Furthermore, in this lesson I provided information about the importance of plant biodiversity for humans and lemurs, with particular focus on the priority species for *Eulemur collaris* that is the biggest frugivore in Southeast Madagascar, and thus the main seed disperser in the area (Bollen et al., 2004). The learning objective of the last lesson was to define the concept of ecosystems and illustrate some examples to make it easier to understand this concept. Also, I explained the trophic chain providing some examples of local species and defining the concepts of primary producers, consumers, and decomposers.

During the training, a member of Asity Madagascar translated the information given into Malagasy. Before starting a new lesson, I asked teachers to participate actively by answering to oral questions concerning the previous subjects treated. After one year from the first lesson, I organised a test to evaluate the efficacy of these trainings. As control groups, I asked teachers from three additional Municipalities (Ampasy-Nahampoana, Mandromodromotra, Mahatalaky) to do the same test. These municipalities are all close to the Tsitongambarika forest and are the only four municipalities (including Iaboakoho), which are located on the East side of this forest (see Chapter 2; Figure 2.1). At the end of the test I provided summarized information to the teachers from the municipalities who did not receive environmental training.

7.2.2. Questionnaire design

The questionnaire consisted of 19 multiple-choice questions (Table 7.1). I grouped questions into four categories: General knowledge about lemurs (G), Conservation knowledge (C), Ecology and behaviour (E), and Identification (I) [modified from Grossberg et al. (2003)]. The questionnaire was originally in English and translated in Malagasy (with terms from the Antanosy dialect) by a student with a degree in Ecology taken at the Libanona Ecological Centre in Fort Dauphin (main city of the Anosy region). The questionnaire was back-translated by a member of Asity Madagascar. The questions were related to topics I previously included during trainings. I asked the participants to write their sex and municipality at the beginning of the test. A total of 43 teachers from the four municipalities participated in the test (Table 7.2).

Table 7.1: Questionnaire. List of questions and answers included in the questionnaires given to teachers. Questions were grouped in: General knowledge about lemurs (G), Conservation knowledge (C), Ecology and behaviour (E), and Identification (I).

	Question	Answers (correct one underlined)
1	How many species of lemurs are present in Madagascar? (G)	A) Less than 10, B) Around 50, C) More than 100
2	Are wild lemurs only present in Madagascar? (G)	A) Yes, B) No
3	Why the Tsitongambarika forest is a priority area for conservation? (C)	A) Because it is important to have trees to build pirogues and houses, B) Because of the high number of endangered species that are present in the area, C) Because it provides bushmeat
4	Why is the "Varika" important for conservation? (C)	A) Because it is good to eat, B) Because it is the biggest frugivorous of the area, C) Because it is gorgeous and attracts tourists
5	Are leaves the main food item for the "Varika"? (E)	A) Yes, B) No
6	Which is the scientific name of "Pondiky"? (G)	A) *Avahi* sp., B) *Eulemur* sp., C) *Lepilemur* sp.
7	Is the "Pondiky" active both by day and by night? (E)	A) Yes, B) No
8	Is the "biodiversity" the number of animals present in an area? (E)	A) Yes, B) No
9	Is the "Tsitsidy" the smallest lemur? (G)	A) Yes, B) No
10	Is it necessary to hunt lemurs to preserve the plant biodiversity? (C)	A) Yes, B) No
11	The "tavy" (slash-and-burn agriculture) is not a threat for biodiversity. (C)	A) True, B) False

	Question	Answers (correct one underlined)
12	The division of the forest in “conservation zone” and “exploitation zone” is a good way to preserve biodiversity. (C)	A) <u>True</u>, B) False
13	The “Voapaky” (*Uapaca* sp.) is very important for the “Varika” especially during the lean season (E)	A) <u>True</u>, B) False
14	Which one of those lemurs is not present in the Tsitongambarika forest? (G)	A) Halo, B) Matavirambo, C) <u>Sifaka</u>, D) Fotsy Fe
15	Which one of the following species is a primary producer? (E)	A) Halo, B) Fossa, C) <u>Voapaky</u>, D) Varika
16	Associate the correct vernacular name to the following picture (I)	A) Tsitsidy, B) <u>Varika</u>, C) Pondiky, D) Fotsy fe
17	Associate the correct vernacular name to the following picture (I)	A) Tsitsidy, B) Varika, C) Pondiky, D) <u>Fotsy fe</u>
18	Associate the correct vernacular name to the following picture (I)	A) Tsitsidy, B) Varika, C) <u>Pondiky</u>, D) Fotsy fe
19	Associate the correct vernacular name to the following picture (I)	A) <u>Tsitsidy</u>, B) Varika, C) Pondiky, D) Fotsy fe

Table 7.2: Participants. Composition of teachers participating to the test meant to evaluate the capacity of the teachers from the municipality of Iaboakoho (Ia) to retain after one year the information given during the four environmental education lessons. The teachers from the municipalities of Mahatalaky (Ma), Mandromodromotra (Md), and Ampasy-Nahampoana (Am) are control groups.

	Ia	**Ma**	**Md**	**Am**
Females	3	5	4	9
Males	7	6	6	3
Total	10	11	10	12

The test encompassed questions about general knowledge on lemurs and questions on activity, ecology, and biology of the lemur species inhabiting the Tsitongambarika forest. Furthermore, I assessed teachers' ability to associate the vernacular name of lemurs to photographs. The lemur species (common and vernacular names in brackets) present in Tsitongambarika are: *Hapalemur meridionalis* (rusty-grey lesser bamboo lemur; halo), *Eulemur collaris* (collared brown lemur; varika), *Daubentonia madagascariensis* (aye-aye; aye-aye), *Avahi meridionalis* (southern woolly lemur; fotsy-fe), *Lepilemur fleuretae* (Fleurete's sportive lemur; pondiky), *Microcebus tanosi* (Anosy mouse lemur; tsitsidy); *Cheirogaleus major* (greater dwarf lemur; matavyrambo). Part of the test included general questions about the Tsitongambarika forest, conservation, biodiversity, and ecosystems.

7.2.3. Ethics statement

The Oxford Brookes University ethics committee approved this research (see Appendix III). I obtained permission from each director of the schools in the four municipalities. Before the test, I met the school directors to explain my project to them and agree upon a day for tests. I explained all the details of the research and that participation was voluntary and that participants had the chance to withdraw at any time during tests.

7.2.4. Data analysis

Questions were marked with a “0” for wrong/not given answers and “1” for correct answers, with a maximum score of 19. I used single teachers as the statistical unit. To test differences between municipalities I used Generalised Linear Model with the score as dependent variable (fitted with a log-linear Poisson distribution for counts) and municipality as fixed factors. I tested whether total score and scores for single categories (G, C, E, I) changed between municipalities. To test differences between municipalities for each question, I used multiple Generalised Linear Models with the answers to questions as dependent variable (fitted with a logistic binary distribution). Fisher’s least significant difference (LSD) has been used as post hoc test for pairwise differences between municipalities. Statistical tests have been performed via IBM SPSS 23 using $P < 0.05$ as level of significance.

7.3. Results

7.3.1. Total score

The total score was significantly different between municipalities (Figure 7.1; Wald $\chi^2 = 13.185$, $P = 0.002$). A LSD post hoc test revealed a significant difference between scores of teachers from the municipality of Iaboakoho (Score: 13.900 ± SE 1.179) and teachers from, Mahatalaky (Score: 9.455 ±

SE 0.927) (P = 0.003), Mandromodromotra (Score: 9.100 ± SE 0.927) (P = 0.002), and Ampasy-Nahampoana (Score: 9.667 ± SE 0.898) (P = 0.004) while I found no other differences between the other municipalities.

The score of General Knowledge about lemurs was significantly different between municipalities (Figure 7.1; Wald $\chi^2 = 8.023$, $P = 0.048$). A LSD post hoc test revealed a significant difference between scores of teachers from the municipality of Iaboakoho (Score: 3.200 ± SE 0.566) and teachers from Mandromodromotra (Score: 1.600 ± SE 0.400) (P = 0.021) and Ampasy-Nahampoana (Score: 1.750 ± SE 0.382) (P = 0.034), but not Mahatalaky (Score: 2.091 ± SE 0.436) (P = 0.120).

The score of Conservation did not differ between municipalities (Figure 7.1; Wald $\chi^2 = 0.676$, $P = 0.879$). Also, I found no significant differences between scores of Ecology and Behaviour between municipalities (Figure 7.1; Wald $\chi^2 = 2.227$, $P = 0.527$).

The score of Identification differed significantly between municipalities (Figure 7.1; Wald $\chi^2 = 20.678$, $P < 0.001$). A LSD post hoc test revealed a significant difference between scores of teachers from the municipality of Iaboakoho (Score: 3.800 ± SE 0.616) and teachers from Mahatalaky (Score: 1.273 ± SE 0.340) (P < 0.001), Mandromodromotra (Score: 1.300 ± SE 0.361) (P < 0.001), and Ampasy-Nahampoana (Score: 1.667 ± SE 0.373) (P = 0.003), while I found no other differences between the other municipalities.

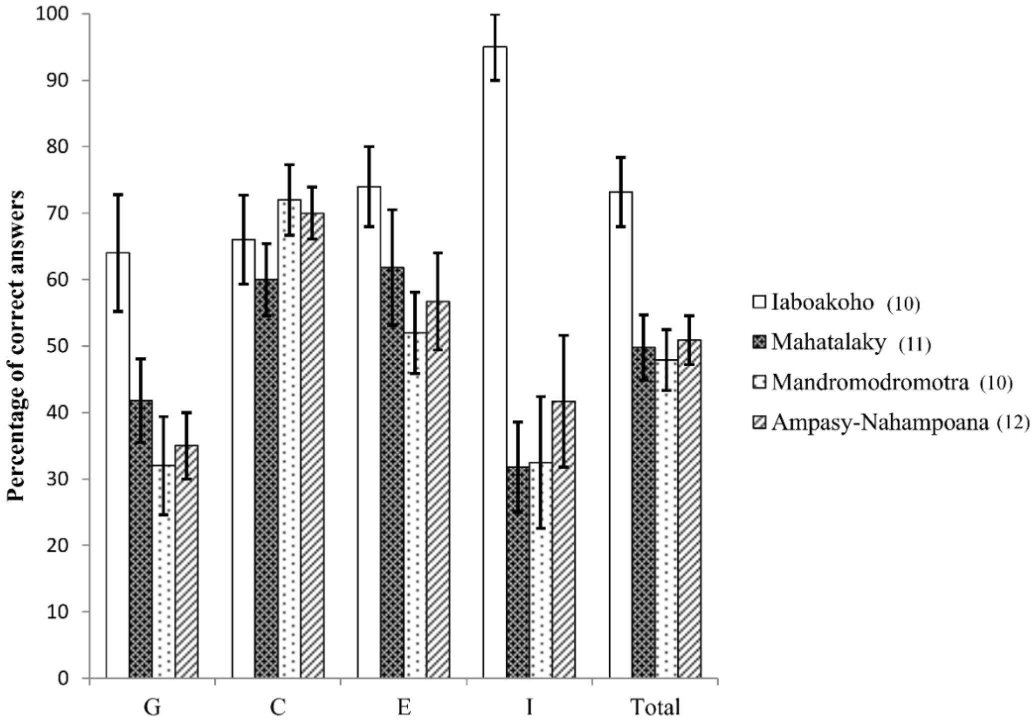

Figure 7.1: Percentage of correct answers by teachers from the four municipalities. Values are means and standard errors. Scores of General knowledge about lemurs (G), Conservation (C), Ecology and behaviour (E), Identification (I), and Total score are shown.

7.3.2. Scores for each question

By analysing the correct answers for single questions (Table 7.3), percentages of correct answers were significantly higher in Iaboakoho as compared to at least one of the other municipalities for nine questions out of 19. Teachers from Ampasy-Nahampoana gave significantly more correct answers than the teachers from Mahatalaky or Mandromodromotra for three questions.

Table 7.3: Questionnaire results. Percentages of correct answers for each question considering teachers from the four municipalities (Ia: Iaboakoho; Ma: Mahatalaky; Md: Mandromodromotra; Am: Ampasy-Nahampoana).

Question	Ia	Ma	Md	Am	Significative differences*
General knowledge about lemurs					
1. How many species of lemurs are present in Madagascar?	70.0	9.1	10.0	8.3	Ia> Ma, Md, Am
2. Are wild lemurs only present in Madagascar?	10.0	36.4	40.0	8.3	
6. Which is the scientific name of “Pondiky”?	70.0	27.3	20.0	58.3	Ia> Ma, Md; Am> Md
9. Is the “Tsitsidy” the smallest lemur?	90.0	81.8	70.0	75.0	
14. Which one of those lemurs is not present in the Tsitongambarika forest?	80.0	54.5	20.0	25.0	Ia> Md, Am
Conservation					
3. Why the Tsitongambarika forest is a priority area for conservation?	70.0	54.5	90.0	91.7	Md, Am> Ma
4. Why is the “Varika” important for conservation?	10.0	0.0	10.0	0.0	
10. Is it necessary to hunt lemurs to preserve the plant biodiversity?	80.0	81.8	80.0	83.3	
11. The “tavy” (slash-and-burn agriculture) is not a threat for biodiversity.	70.0	81.8	90.0	83.3	
12. The division of the forest in “conservation zone” and “exploitation zone” is a good way to preserve biodiversity.	100.0	81.8	90.0	91.7	
Ecology and behaviour					
5. Are leaves the main food item for the “Varika”?	100.0	81.8	70.0	75.0	Ia> Md
7. Is the “Pondiky” active both by day and by night?	90.0	45.5	60.0	58.3	Ia> Ma

Question	Ia	Ma	Md	Am	Significative differences*
Ecology and behaviour					
8. Is the “biodiversity” the number of animals present in an area?	70.0	63.6	40.0	41.7	Ia> Md, Am
13. The “Voapaky” (*Uapaca* sp.) is very important for the “Varika” especially during the lean season.	80.0	72.7	50.0	66.7	
15. Which one of the following species is a primary producer?	30.0	36.4	40.0	41.7	
Identification					
16. Associate the correct vernacular name to the following picture (Varika)	100.0	36.4	60.0	58.3	Ia> Ma, Md, Am
17. Associate the correct vernacular name to the following picture (Fotsy fe)	90.0	36.4	10.0	50.0	Ia> Ma, Md, Am Am> Md
18. Associate the correct vernacular name to the following picture (Pondiky)	100.0	9.1	10.0	16.7	Ia> Ma, Md, Am
19. Associate the correct vernacular name to the following picture (Tsitsidy)	100.0	45.5	50.0	41.7	Ia> Ma, Md, Am

* significative differences ($P < 0.05$) found via LSD post-hoc test.

7.4. Discussion

7.4.1. Long term retention of knowledge

Overall, my results suggested that the teachers retained most of the information provided during the training lessons one year before the test. In fact, the teachers from Iaboahako had significantly higher scores than teachers from the other three municipalities. This supports the finding that people living in rural areas can retain environmental knowledge as tested with children and their parents in Mangabe, eastern Madagascar (Rakotomamonjy et al., 2015). Also, students from primary schools at Lake Alaotra showed higher knowledge one year after the end of an environmental education program (Richter et al., 2015). Further evidence comes from studies in the Kalinzu Forest Reserve, Uganda, (Kuhar et al., 2010) and in the Saloum Biosphere reserve, Senegal, (Grúňová et al., 2017) where students showed long-term knowledge retention about environmental subjects. Furthermore, in this study I showed that teachers, even in rural areas where they are supposed to have lower preparation as compared to teachers from the main town (McEwan, 1999), could retain information. This might lead to the Secondary Comprehension and Application levels of Bloom's taxonomy (Bissels & Lemons, 2006), with the final objective to transfer the information on environmental subjects to students in the area (Wallis & Lonsdorf, 2010). Nevertheless, I cannot exclude the fact that some teachers from Iaboakoho received better education than teachers from the other three municipalities, although this is likely not to be the case from what the members of Asity Madagascar declared. Providing teachers the right means to teach their students is fundamental since they can deliver lessons about environmental education over years to many children (Wallis &

Lonsdorf, 2010). Moreover, several studies (e.g., Damerell et al., 2013; Rakotomamonjy et al., 2015) showed that parents can benefit from education given to their children who may transfer information to them. Thus, giving training to teachers is pivotal to favour the long-term environmental education of an area.

One of the clearest indications from this study is that local people have a limited knowledge on lemurs and their diversity, as suggested in previous studies in Madagascar (Dolins et al., 2010; Keane et al., 2011; Rakotomamonky et al., 2015) and on other primates (Kuhar et al., 2010). In fact, scores of general knowledge about lemurs and their identification were lower than the other scores of teachers from the control municipalities, while they were significantly higher in the municipality of Iaboakoho. This confirms previous findings that knowledge is lacking regarding the many species of lemurs that differ in colour, size, activity patterns, geographical distribution, vocalizations, and other characteristics (Dolins et al., 2010). Also, it has been previously shown that it is difficult to realize that wild lemurs occur only in Madagascar (Dolins et al., 2010; Richter et al., 2015). Even teachers from Iaboakoho had low scores for this question and this result can be explained by the fact that some of them might know that lemurs are present in zoos outside Madagascar. Also, it might have been difficult for them to understand scientific terminologies such as the term “endemic species” that I used during the lessons I gave. For this reason, I strongly suggest to stress the concept of endemic species while planning training in environmental education especially in areas with many endemic species like Madagascar (Brooks et al., 2006). Also, other ecological concepts such as “biodiversity” and “primary producer” should be well explained. In fact, teachers from Iaboakoho had low scores in detecting the primary producer in the question number 15, while they seemed to have retained the concept of “biodiversity.”

The questions related to Conservation had overall high scores in all the four municipalities, confirming that people in Madagascar are aware of local environmental problems and can relate them to human activities (Korhonen & Lappalainen, 2004). However, for question 4 (Why is the “Varika” important for conservation?) even teachers from the municipality of Iaboakoho had low performances, answering mostly “because it is gorgeous and attracts tourists.” Tourism had been considered a good tool for increasing conservation initiatives, although it is mainly ecotourism having this positive role (Schwitzer et al., 2014). It has been also found that a large amount of tourism can actually cause a decrease in lemur populations (Wright et al., 2014), thus tourism can have negative side effects on conservation. For this reason, I considered the answer “because it is the biggest frugivorous in the area” as the only correct one, highlighting the ecological role of this lemur in regenerating the rainforest (Bollen & Donati, 2006). As a consequence of this finding, I recommend to highlight the ecological importance of animal species in environmental conservation lessons. Also, it is pivotal to promote ecotourism with low impact on the forest (Neudert et al., 2016) and regulate tourism that might have deleterious impacts on conservation if not controlled.

7.4.2. Study limitations

The main limitation of this study is the sample size. Although I selected most of the teachers from the four municipalities, I only had data on 43 teachers of which 10 received the training. This effect is something difficult to solve because I considered all the municipalities that are faced to the East part of the Tsitongambarika forest and that are under similar conditions. I considered the Municipalities of Mahatalaky, Mandromodromotra, and Ampasy-Nahampoana as control groups since all are rural areas and are at the same distance from the forest as Iaboakoho. This might compensate for the lack of a pre-training test in Iaboakoho, although I cannot be sure that the level of environmental education in Iaboakoho was the same as in the other three municipalities. Nevertheless, I can assume that it was the same since I found no statistical differences among the other three municipalities. Another limitation of this research is the lack of a post-training assessment of the effectiveness of the environmental education on the participants, as in other studies (Kuhar et al., 2010; Rakotomamonji et al., 2015). I conducted research on hunting pressure in the area after the installation of the research station (Campera et al., 2017), showing that local people had a lower level of forest exploitation after the installation of the research station, especially in villages closer to it. Also, encounter rates of *Eulemur collaris* and *Hapalemur meridionalis*, the most hunted lemurs, were higher at the end of the study as compared at the encounter rates at the beginning of the study (Campera et al., 2017). This difference might be related to the positive effects of the local management by Asity (e.g., forest patrol and favouring sustainable agriculture) and the presence of the research station (e.g., alternative job opportunities available by conserving the forest) to reduce anthropogenic pressure in the area. The conservation education program might lead to pro environmental behaviours, although the effects to reduce anthropogenic pressure on the forest might arise in a few years if the education program continues. Thus, apart from an efficient conservation education program, it is really important to integrate the overall conservation program with other activities, and the collaboration with local NGOs. Other researchers who shared similar experiences also advocate this approach (Kuhar et al., 2010; Padua, 2010; Erhabor & Don, 2016).

7.4.3. Conclusions

In conclusion, the teachers in rural areas of Madagascar retained most of the information provided during training lessons one year before the test. The ultimate goal of environmental education programs is the behavioural change that results in positive changes toward the environment. This goal cannot be achieved until basic knowledge and even empathy towards an environmental issue is established. In the theory of change formula that shows how to achieve the behavioural change (Jenks et al., 2010), knowledge is the first component. The other components are attitudes, interpersonal communication, and barrier removal (Jenks et al., 2010). Thus, knowledge increase from an environmental education program does not necessarily result in participants showing positive attitudes and behaviours (Kuhar et al., 2010; Schultz, 2011). For this reason, other interventions are necessary to reach behavioural change that might lead to threat reduction and, consequently, achieve effective conservation results (Jenks et al., 2010), such as via social marketing campaigns (e.g., Andriamalala et al., 2013; Butler et al., 2013). Thus, this study is the very first step to raise awareness on lemurs in the area, and other tests, lessons, and follow-up controls on attitudes and behaviours are required in order to have effective impacts to reduce environmental exploitation.

Chapter 8. General discussion

The aim of this concluding chapter is to summarise the key findings from the earlier chapters and to discuss them in a broader perspective. The behavioural ecology of *Avahi meridionalis* in the Ampasy lowland rainforest, Tsitongambarika Protected Area (TGK), provided useful insights to explore the main question of my work, i.e. whether a highly folivorous species of strepsirrhine is constrained by food availability.

8.1: Main findings.

Using one-year survey for comparison, in Chapter 3 I showed that the encounter rates of lemurs, as proxy of lemur abundance, were similar between low- and mid-altitude rainforests in Madagascar. This implies that lowland rainforests do not show maxima in species abundance on the island, contrary to what happens in other tropical areas, supporting the idea that lemurs evolved traits to adapt to mid-altitudes (Goodman & Ganzhorn, 2004). The density of folivorous species, excluding the genus *Hapalemur*, had a similar altitudinal pattern than the density of frugivorous and insectivorous species (see Chapter 3). This does not clarify whether folivorous primates are subject to constraints similar to those on frugivorous primates (Snaith & Chapman, 2005, 2007, 2008; Saj et al., 2007; Harris et al., 2010) or whether they are less constrained by food availability and abundance due to the hypothetical low quality, high availability, and even distribution of leaves (Wrangham, 1980; Isbell, 1991; Sterck et al., 1997). At Ampasy the encounter rate of *A. meridionalis* was negatively correlated to mean tree DBH, mean canopy cover, and mean elevation of plots (Phelps, 2016). As a matter of fact, our observations indicate that *A. meridionalis* at Ampasy preferred more the degraded areas close to the forest edge rather than the forest interior. This might be driven by the advantage of foraging on high quality leaves (Ganzhorn, 1995), and this may indicate that sourthern woolly lemurs are constrained by habitat structure and food availability. The potential competition with the ecologically similar species *Lepilemur fleuretae*, which seems to prefer the forest interior (Phelps, 2016), may also explain this finding. In fact, the density of A. *meridionalis* in TGK is much lower than that of *L. fleuretae* (see Chapter 3), suggesting a possible scramble competition between the two species. Scramble competition was previously reported between *A. occidentalis* and *L. edwardsi* in the deciduous forest of Ampijoroa (Warren & Crompton, 1997a; Thalmann, 2001). Considering the ecological similarities between the two species, competition with *L. fleuretae* is thus suggested as a significant driver of the behavioural ecology of *A. meridionalis* at Ampasy.

In Chapters 4 and 5, I showed that *Avahi meridionalis* adopted behavioural strategies to cope with differences in food availability. The southern woolly lemur had area requirements larger than observed in other species of the genus, with annual home range size varying between 4.53 and 10.39 hectares (see Chapter 4). The species ranging patterns indicate that a resource maximising strategy may explain the lack of seasonal variation in the annual ranges, while a time-minimising strategy seems to govern daily path lenghts and sleeping site selection, probably as an energy-saving strategy (see Chapter 4). This double strategy is likely to be linked to the characteristics of the lowland rainforest of Ampasy. In fact, a resource-maximising strategy is expected when preferred food availability is high (Mitchell & Powell, 2004), suggesting that Ampasy may be a high-quality habitat for folivores. This notion is further supported by the high densities of *A. meridionalis* and *L. fleuretae* at the study site compared to other rainforests (see Chapter 3), but also by the relative high proportion of young leaves availability in the Ampasy forest (M. Campera, unpub. data). The rainforest at TGK is, however, highly seasonal (see Chapter 2) in terms of resource availability and phenological phases highly influenced by photoperiodic variations (M. Campera, unpub. data). This resource seasonality may explain why a time-minimising strategy is used in terms of daily distances travelled and sleeping site selection between seasons. Reducing daily distances and selecting sleeping sites in proximity of the core areas [multiple central place foraging hypothesis (Chapman et al., 1989; Albert et al., 2011)] are strategies meant to reduce energy expenditure in periods of food scarcity, suggesting that *A. meriodionalis* was constrained by availability of young leaves.

Avahi meridionalis had a preference for young leaves and selected leaves with a higher nutritional content during the season of food abundance (see Chapter 5). As mentioned in the previous paragraph, the lowland rainforest of Tsitongambarika is highly seasonal in terms of young leaves abundance and this constrained *A. meridionalis* to a time-minimising strategy in its feeding ecology (Schoener, 1971; Hixon, 1982). An indication of this strategy was the reduction of the time spent feeding as well as the number of feeding trees used per hour during the lean season (Hixon & Carpenter, 1988). This indicates that energy saving strategies are used by the species as expected due to the low nutrient intake associated with the high energetic locomotion of woolly lemurs (Warren & Crompton, 1997b, 1998; Norscia et al., 2012). The competition with *L. fleuretae* can also explain the dietary breadth reduction during the lean season (see Chapter 5), supporting the hypothesis that folivorous species face scramble competition (Snaith & Chapman, 2005, 2007). The increase in dietary breadth during the season of food abundance may also be the consequence of the reduced competition with *L. fleuretae* that shifted towards a diet richer in flowers and fruits (M. Campera, unpub. data).

The nutritional quality of food items eaten by *A. meridionalis* was not statistically different between lean and abundance seasons (not considering the proportion of time spent on them), suggesting that food availability at Ampasy did not vary dramatically in terms of quality of resources (see Chapter 5). Higher-quality food items were actively selected during the season of food abundance. This is the time when *A. meridionalis* was more likely to need a more nutritious food intake due to the lactating and weaning periods (M. Balestri, pers. observ.), or simply because they have to store energy to face the following lean period. In the lean season, however, there was no selection based on the nutritional quality. The finding that most of the food items had a similar nutritional quality may further explain the resource maximising strategy adopted by *A. meridionalis* in terms of annual home ranges as no advantage appears evident for increasing the home range area during the lean season (see Chapter 4). This observation partially supports the traditional socioecological models for folivorous primates (Wrangham, 1980; Isbell, 1991; Sterck et al., 1997). In constrast to frugivorous species that usually increase the home ranges in periods of fruit scarcity as an area-minimising strategy (equivalent to the time-minimising strategy for the feeding ecology) (Gerber et al., 2012; Campera et al., 2014), *A. meridionalis* did not show an increase in home range size during the lean season. This strategy seems to be in addition to the use of a time-minimising strategy in terms of daily distances travelled, sleeping site selection, and resting and feeding time. Therefore, the ranging and the feeding ecology of southern woolly lemurs indicate that resources for these folivorous primates vary in quality, availability, and spatial distribution (Snaith & Chapman, 2007) but at a lower extent than for frugivorous primates.

Avahi meridionalis showed an opportunistic cathemeral activity (see Chapter 6), which might be driven by the necessity to maximise the food intake over the 24-h considering a diet rich in fibres and the significant photoperiodic variation (that imposes time constraints) at the latitude of Ampasy (Engqvist & Richard, 1991; Donati et al., 2007, 2009). Competition with *L. fleuretae*, which is mainly active during the central hours of the night (M. Campera, unpub. data), may also have caused the shift to an opportunistic cathemeral activity as a temporal niche separation strategy to reduce feeding competition (Ganzhorn, 1989). This would be a further support to the hypothesis that folivorous primates experience scramble competition. My finding that *A. meridionalis* is an opportunistic cathemeral has important implications in understanding the evolution of cathemerality, supporting the hypothesis that *Avahi* is secondarily nocturnal (Ganzhorn et al., 1985; Müller & Thalmann, 2000; Roos et al., 2004). Cathemerality was suggested to be an adaptation exclusive to the Lemuridae (Curtis & Rasmussen, 2006; Donati & Borgognini-Tarli, 2006a; Bray et al., 2017). The finding that *A. meridionalis* is an opportunistic cathemeral, however, may indicate that the Indriidae and the Lemuridae had a cathemeral common ancestor (Donati & Borgognini-Tarli, 2006a). Considering that cathemerality may have evolved in some species to avoid interspecific competition (Donati & Borgognini-Tarli, 2006a), the fact that *Avahi* may be secondarily nocturnal may indicate that an opportunistic cathemerality is retained more in areas with a high density of competitors (e.g. *Lepilemur*) as a temporal niche separation strategy. Conversely, in areas with lower competition *Avahi* may be more active at night. Further evidence is required to support this hypothesis.

As aforementioned, the Ampasy forest hosts a high density of lemurs (see Chapter 3). For instance, the encounter rates of *A. meridionalis* and *L. fleuretae* at Ampasy are higher than the encounter rate of the same species in the adjacent lowland rainforest of Andohahela (Feistner & Schmid, 1999). Moreover*,* the density of *E. collaris* at Ampasy is higher than the density at Anka, in parcel 1 of the TGK forest (Norscia et al., 2006b). Thus, it is important to improve the conservation management in the area that currently represents one of the most pristine lowland rainforests in Madagascar. Being habitat loss and agriculture the main threats to this species, raising awareness among the population is pivotal to help the conservation of these species. Since education level is low in Madagascar, targeting primary schools for environmental education projects allow for reaching the largest portion of Malagasy children at school (Richter et al., 2015). In Chapter 7, I assessed the long-term retention of environmental education lessons given to teachers in the rural area. This is, however, the very first step in helping the conservation of *A. meridionalis* in the area. In fact, many other steps are necessary to guarantee a behavioural change and help effectively lemur conservation. Together with the conservation education program, we took other actions, in collaboration with the local NGO Asity Madagascar, in order to decrease forest exploitation of local communities by creating alternative job opportunities (Campera et al., 2017). Further studies and assessments are required in the future to monitor and help preserving this species in situ.

8.2: Future directions

In this dissertation, I investigated some aspects of the folivore paradox related to the effects of food availability on the behavioural ecology of a strictly folivorous primate. There are, however, other aspects that can be further investigated to determine whether *Avahi meridionalis* experience scramble competition. Physiological responses to lean periods can be examined to determine whether there is an effect of food availability. For instance, Harris et al. (2010) collected data on parasite loads and urinary C-peptide levels (proxy of net energy gain) on guereza *Colobus guereza* in Kibale National Park, Uganda. They found evidence of physiological costs associated to lean periods in lactating females, with a decrease in urinary C-peptide levels and an increase in parasite loads as top foods became scarce. Guerezas also increased their daily path length, number of feeding patches visited/day, size of individual feeding areas, percentage of time spent feeding, and dietary diversity in lean periods. Physiological stress levels may also be measured between seasons to determine whether there is a stress response in relation to food availability (Balestri et al., 2014a).

Food patch depletion was also considered as an evidence of scramble competition (Snaith & Chapman, 2005; Tombak et al., 2012). The method employed in these two studies involved the data collection on food intake and animal movements in a food patch (i.e. foraging). The collection of this data on

A. meridionalis, however, may be challenging. In fact, I tried to gather data on food intake but only succeded in estimating it for 11 food items out of the 43 food items eaten during the study period. Thus, it would be necessary to focus the study on the animals that are in the more accessible areas at Ampasy.

Another aspect that can be investigated is the inter-individual distance between members of the same pair. Folivorous primates living in groups are known to reduce the group size and to increase group spread to reduce within-group scramble competition (Snaith & Chapman, 2008; Kazahari & Agetsuma, 2010).

The equivalent of this response in pair-living folivorous primates may be the increase of the inter-individual distance in lean periods. It would be necessary to study both members of a pair simultaneously, and to collect data on multiple pairs.

Conservation related projects should be implemented at Ampasy. It is pivotal to continue the collaboration between Asity and Oxford Brookes University. It has been shown, in fact, that a combination of forest management and researchers' presence can assist in significantly decreasing forest use and illegal activities by local people at Ampasy (Campera et al., 2017). Future projects can include a plant nursery to determine germination success and grow rate of trees at Ampasy, similar to what have been done at Kianjavato (Manjaribe et al., 2013).

The conservation education project presented in my dissertation should be expanded to children from all the schools of the municipality of Iaboakoho to raise awareness on lemur ecology and conservation and to increase pro-environmental behaviours in future generations. It would be key to design a children book specific on the lemurs of Ampasy, as previously done for other primates (e.g. Nekaris et al., 2018), to teach children first to have empathy for nature before putting the responsibility on them to tackle hard-hitting problems.

8.3: Conclusions.

In conclusion, this study highlighted the influence of seasonality, food availability, and inter-specific competition on the behavioural ecology of the strictly folivorous *A. meridionalis* in the lowland rainforest of Ampasy, in the TGK Protected Area. All these findings support the hypothesis that folivorous primates experience scramble competition since their resources vary in quality, availability, and spatial distribution (Snaith & Chapman, 2007). Despite the recent evidences of scramble competition in many folivorous primates, other studies found constrasting results. For instance, females of mountain gorilla *Gorilla beringei beringei* at Virunga were more likely to join large groups than to join one-male groups despite a higher risk of infanticide, suggesting a limited scramble competition (Robbins et al., 2009). This finding is related to the social structure as well as the other evidence of no scramble competition in folivororous primates; i.e. no relationship between group size and day range or travel cost (Clutton-Brock & Harvey, 1977; Struhsaker & Leland, 1987; Isbell, 1991; Janson & Goldsmith, 1995; Yeager & Kirkpatrick, 1998; Yeager & Kool, 2000; Fashing, 2001; Korstjens et al., 2002; Robbins et al., 2007). Other factors may thus have interfered in determining group size and emigration. It is important to consider multiple ecological variables while investigating the possible scramble competition in folivorous primates.

Woolly lemurs seem to have a very specialised niche in the different habitats of Madagascar, being the only strictly folivorous nocturnal primate. Further studies will help to clarify some of the novel aspects that emerged from my work. For example, the presence of cathemeral behaviour in *Avahi* sp. in other areas of Madagascar needs to be studied to clarify whether the flexible activity shown at Ampasy is caused by peculiarities of this rainforest (i.e. high density of folivorous competitors and strong seasonality with prolonged bottle-necks of food scarcity) or it is a trait shared by other species in this genus.

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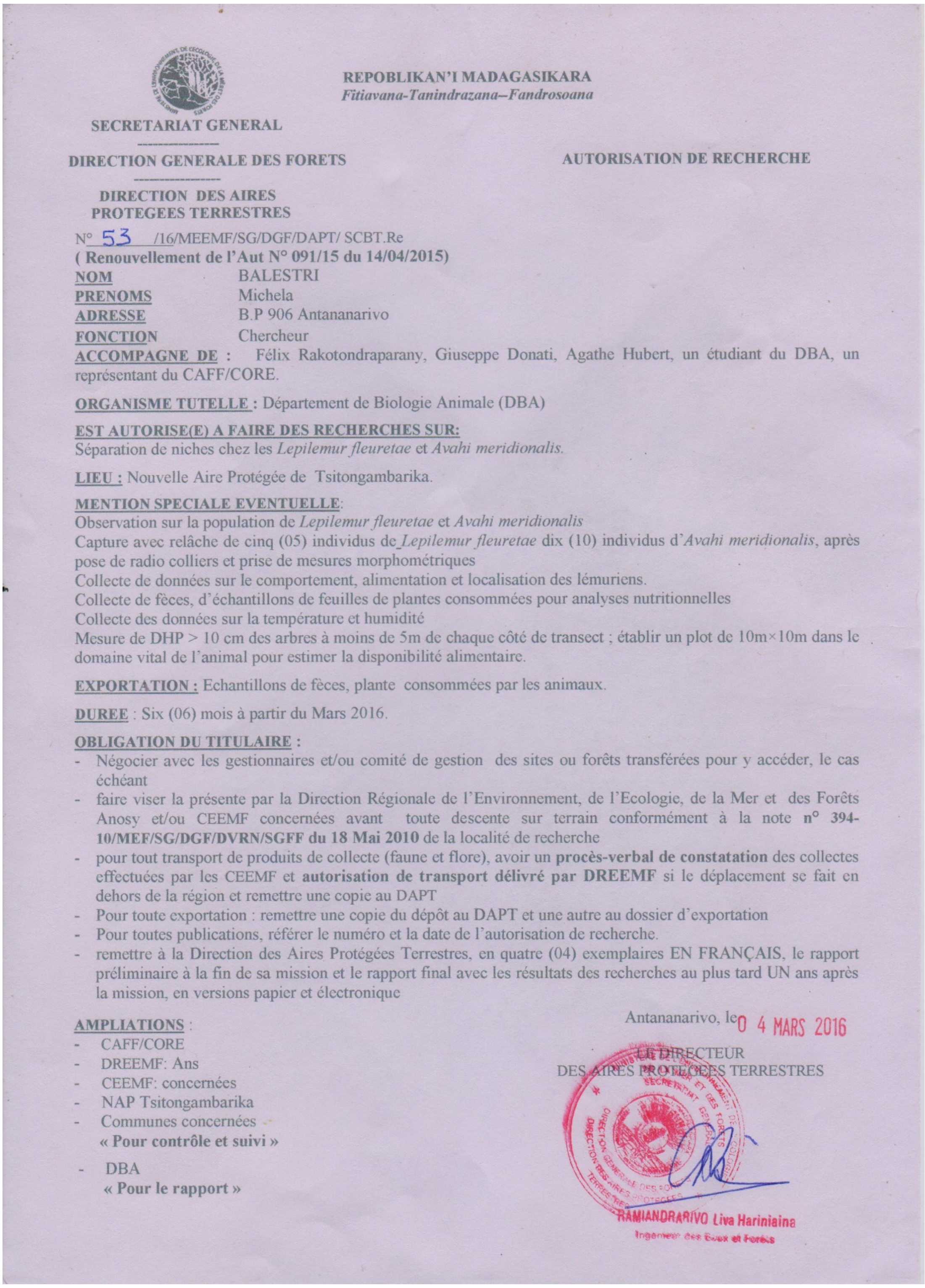
Appendix I: Ethogram used for the behavioural data collection on *Avahi meridionalis* at Ampasy

BEHAVIOURS	
Resting	Remain inactive and motionless; no contact with conspecifics
Huddling	Remain inactive in close body contact with one or more conspecifics
Self-grooming	Smoothing repeatedly own hair using the toothcomb or the tongue
Allo-grooming	Smoothing repeatedly conspecific's hair using the toothcomb or the tongue
Lactating	Female nursing an infant
Feeding	Searching for/manipulating/ingesting food
Moving	Locomotor activities
Vocalisation	Focus animal vocalise
Out of sight	Focus animal cannot be seen
OTHER	
Resting/feeding support orientation	vertical (81–90°); angle (46–80°); oblique (11–45°); horizontal (0–10°); fork (two or more large supports)
Resting/feeding support diameter	small (<5 cm); medium (5–15 cm); large (>15 cm)
Food item	YL (Young Leaves); ML (Mature Leaves)
Proximity during resting/feeding	in contact (<1 m); close (1-5 m); visible (5-25 m); not visible
Feeding/resting/moving height	Estimated at the nearest metre

Appendix II: Research Permits



REPOBLIKAN'I MADAGASIKARA
Fitiavana-Tanindrazana–Fandrosoana

SECRETARIAT GENERAL
DIRECTION GENERALE DES FORETS
DIRECTION DES AIRES PROTEGEES TERRESTRES

AUTORISATION DE RECHERCHE

N° 53 /16/MEEMF/SG/DGF/DAPT/ SCBT.Re
(Renouvellement de l'Aut N° 091/15 du 14/04/2015)
NOM BALESTRI
PRENOMS Michela
ADRESSE B.P 906 Antananarivo
FONCTION Chercheur
ACCOMPAGNE DE : Félix Rakotondraparany, Giuseppe Donati, Agathe Hubert, un étudiant du DBA, un représentant du CAFF/CORE.

ORGANISME TUTELLE : Département de Biologie Animale (DBA)

EST AUTORISE(E) A FAIRE DES RECHERCHES SUR:
Séparation de niches chez les *Lepilemur fleuretae* et *Avahi meridionalis*.

LIEU : Nouvelle Aire Protégée de Tsitongambarika.

MENTION SPECIALE EVENTUELLE:
Observation sur la population de *Lepilemur fleuretae* et *Avahi meridionalis*
Capture avec relâche de cinq (05) individus de *Lepilemur fleuretae* dix (10) individus d'*Avahi meridionalis*, après pose de radio colliers et prise de mesures morphométriques
Collecte de données sur le comportement, alimentation et localisation des lémuriens.
Collecte de fèces, d'échantillons de feuilles de plantes consommées pour analyses nutritionnelles
Collecte des données sur la température et humidité
Mesure de DHP > 10 cm des arbres à moins de 5m de chaque côté de transect ; établir un plot de 10m×10m dans le domaine vital de l'animal pour estimer la disponibilité alimentaire.

EXPORTATION : Echantillons de fèces, plante consommées par les animaux.

DUREE : Six (06) mois à partir du Mars 2016.

OBLIGATION DU TITULAIRE :

- Négocier avec les gestionnaires et/ou comité de gestion des sites ou forêts transférées pour y accéder, le cas échéant
- faire viser la présente par la Direction Régionale de l'Environnement, de l'Ecologie, de la Mer et des Forêts Anosy et/ou CEEMF concernées avant toute descente sur terrain conformément à la note **n° 394-10/MEF/SG/DGF/DVRN/SGFF du 18 Mai 2010** de la localité de recherche
- pour tout transport de produits de collecte (faune et flore), avoir un **procès-verbal de constatation** des collectes effectuées par les CEEMF et **autorisation de transport délivré par DREEMF** si le déplacement se fait en dehors de la région et remettre une copie au DAPT
- Pour toute exportation : remettre une copie du dépôt au DAPT et une autre au dossier d'exportation
- Pour toutes publications, référer le numéro et la date de l'autorisation de recherche.
- remettre à la Direction des Aires Protégées Terrestres, en quatre (04) exemplaires EN FRANÇAIS, le rapport préliminaire à la fin de sa mission et le rapport final avec les résultats des recherches au plus tard UN ans après la mission, en versions papier et électronique

Antananarivo, le 0 4 MARS 2016

LE DIRECTEUR
DES AIRES PROTEGEES TERRESTRES

RAMIANDRARIVO Liva Hariniaina
Ingenieur des Eaux et Forêts

AMPLIATIONS :

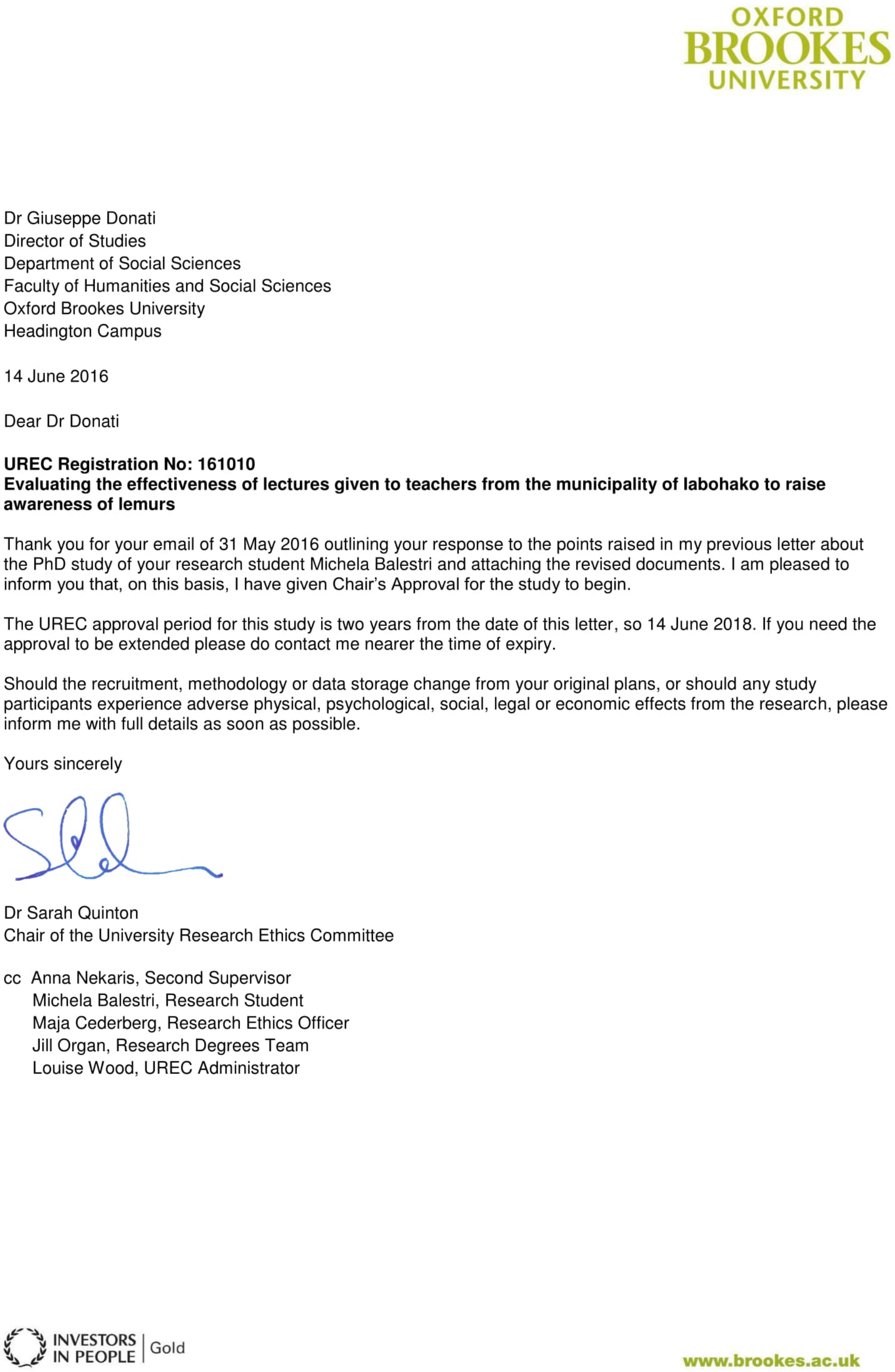
- CAFF/CORE
- DREEMF: Ans
- CEEMF: concernées
- NAP Tsitongambarika
- Communes concernées

« Pour contrôle et suivi »

- DBA

« Pour le rapport »

Appendix III: Ethical approval for the questionnaire



Dr Giuseppe Donati
Director of Studies
Department of Social Sciences
Faculty of Humanities and Social Sciences
Oxford Brookes University
Headington Campus

14 June 2016

Dear Dr Donati

UREC Registration No: 161010
Evaluating the effectiveness of lectures given to teachers from the municipality of labohako to raise awareness of lemurs

Thank you for your email of 31 May 2016 outlining your response to the points raised in my previous letter about the PhD study of your research student Michela Balestri and attaching the revised documents. I am pleased to inform you that, on this basis, I have given Chair's Approval for the study to begin.

The UREC approval period for this study is two years from the date of this letter, so 14 June 2018. If you need the approval to be extended please do contact me nearer the time of expiry.

Should the recruitment, methodology or data storage change from your original plans, or should any study participants experience adverse physical, psychological, social, legal or economic effects from the research, please inform me with full details as soon as possible.

Yours sincerely

Dr Sarah Quinton
Chair of the University Research Ethics Committee

cc Anna Nekaris, Second Supervisor
Michela Balestri, Research Student
Maja Cederberg, Research Ethics Officer
Jill Organ, Research Degrees Team
Louise Wood, UREC Administrator

www.brookes.ac.uk