Ecological flexibility and conservation of Fleurette's sportive lemur, *Lepilemur fleuretae*, in the lowland rainforest of Ampasy, Tsitongambarika Protected Area

By

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Abstract

Ecological flexibility entails an expansion of niche breadth in response to different environmental conditions. Sportive lemurs *Lepilemur* spp. are known to minimise energetic costs via short distances travelled, small home ranges, increased resting time, and low metabolic rates. Very little information, however, is available in the eastern rainforest, the habitat where this genus has its highest diversity. I investigate whether *L. fleuretae* inhabiting Tsitongambarika (TGK), the southernmost lowland rainforest in Madagascar, shows similar behavioural and ecological adaptations to the sportive lemurs inhabiting dry and deciduous forests. I collected data from July 2015 to July 2016 at Ampasy, northernmost portion of TGK. To understand patterns of resource availability, I collected phenological data on 200 tree species. I explored the ecology of *L. fleuretae* by gathering data on its diet, ranging patterns, and by reconstructing the activity profiles via a novel method, the unsupervised learning algorithm on accelerometer data. I estimated the anthropogenic pressure in the area and I evaluated whether local management and researchers' presence had an effect in decreasing it. *Lepilemur fleuretae* at Ampasy is hyperactive when compared to other species of this genus, with longer distances travelled, larger home ranges, and less time spent resting. The species seems to reduce the competition with the folivorous *A. meridionalis* by including a higher proportion of fruits and flowers in their diet than other sportive lemurs. The activity of *L. fleuretae* is influenced by photoperiod and moon luminosity, indicating the importance of synchronizing activities with the seasonal resource availability. A combination of local management and related development strategies, such as the installation of a research station, can assist in preserving the TGK forest. My results on *L. fleuretae* unveiled the flexibility of the genus *Lepilemur* and its ability to adapt to different habitats. This study showed that the use of automatic loggers such as accelerometers can provide novel information on cryptic species difficul to achieve via direct observations. The use of these devices may shed the light on new behavioural and ecological patterns and lead to a new approach on the study of cryptic animals.

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To the person who is always in my mind and who gives me strength

even though she is not here anymore

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AIC	Akaike Information Criterion
ANOVA	Analysis of Variance
APG	Angiosperm Phylogeny Group
β	Beta coefficient
BIC	Bayesian Information Criterion
BMR	Basal Metabolic Rate
CR	Critically Endangered
DBH	Diameter at Breast Height
DD	Data Deficient
EFH	Energy Frugality Hypothesis
EM	Expectation Maximisation
EN	Endangered
F	Female
FAI	Food Availability Index
FK	Fixed Kernel
FL	Flowers
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
LC	Least Concern
LSD	Fisher's Least Significant Difference
M	Male

MCP	Minimum Convex Polygon
MGA	Malagasy Ariary
ML	Mature Leaves
MR	Metabolic Rate
NA	Not Available (Chapter 4) or Not Assessed (Chapter 7)
ND	Nocturnal vs Diurnal
NGO	Non-Governmental Organisation
NT	Near Threatened
OBDA	Overall Dynamic Body Acceleration
ρ	Sperman's rho
RF	Ripe Fruits
RM	Repeated Measures
RMR	Resting Metabolic Rate
SD	Standard Deviation
SE	Standard Error of mean
SPSS	Statistical Package for the Social Sciences
TGK	Tsitongambarika
USD	United States Dollar
UTM	Universal Transverse Mercator
VHF	Very High Frequency
VU	Vulnerable
WGS	World Geodetic System
YL	Young Leaves
YR	Year Round

Chapter 1. General Introduction

1.1. Ecological flexibility in primates

The behavioural ecology of many primate species, or even genera, has been often assumed based on a few studies and a few study areas. Many species that were previously reported as specialists, however, had been recently found to show differences in their behavioural ecology in different habitats or under different degrees of anthropogenic disturbance (Nowak & Lee, 2013). These differences refer to the term ecological flexibility that can be defined as the ability of a species to adjust to gradual, anthropogenic, and stochastic changes in environmental conditions (Isaac & Cowlishaw, 2004; Nowak & Lee, 2013). Ecological flexibility usually entails an expansion of niche breadth (diet, habitat use, and/or activity) in response to different ecological and anthropogenic conditions (Lee, 2003; Eppley et al., 2017).

Dietary flexibility is determined mainly by anatomical and physiological adaptations (Chivers, 1994), although even animals with anatomical specialisations often exhibit a greater variability in the diet than expected (Chapman & Chapman, 1990). One of the most noteworthy cases of dietary flexibility in primates with anatomical specialisations is the recent finding that primates previously assumed to be bamboo specialists are able to survive in habitats where bamboo is scarce or even absent by shifting towards a diet rich in graminoids [Bale monkey *Chlorocebus djamdjamensis* (Mekonnen et al., 2018); southern bamboo lemur *Hapalemur meridionalis* (Eppley et al., 2015a, 2017)]. Other species that are considered specialist have been recently found to exhibit a certain degree of dietary flexibility, such as including exotic plants in their diet [samango monkey *Cercopithecus albogularis* (Wimberger et al., 2017), southern bamboo lemur (Eppley et al., 2017)] and increasing fallback foods [spider monkey *Ateles geoffroyi* (Chaves et al., 2012), diademed sifaka *Propithecus diadema* (Irwin, 2008a)]. The dietary flexibility of primates can be explained by the fact that their gut morphology is derived from primitive unspecialised forms and do not reach the extreme adaptations found in other mammals (Chivers & Hladik, 1980). As a consequence, no primate species are expected to be fully frugivorous, folivorous, or faunivores (Chivers & Hladik, 1980; Chivers, 1994).

Primates can change their habitat use as a consequence of the variation in food availability and distribution (Hemingway & Bynum, 2005; Boyle et al., 2009). Some species were found to adopt different strategies at different habitat type and food availability. For example, guereza *Colobus guereza*, moustached monkey *Cercopithecus cephus*, lion-tailed macaque *Macaca silenus*, white-thighed colobus *Colobus vellerosus*; mantled howler monkey *Alouatta palliata,* diademed sifaka, and black bearded saki *Chiropotes satanas* are able to persist in forest fragments because of their ability to decrease their home ranges in small fragments (Menon & Poirier, 1996; Tutin, 1999; Onderdonk & Chapman, 2000; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Wong & Sicotte, 2007; Irwin, 2008b; Boyle et al., 2009). Other species can shift their home ranges when fruit availability is low or in periods of water scarcity [Bornean orangutan *Pongo pygmaeus* (Fox et al., 2004); collared brown lemur *Eulemur collaris* (Campera et al., 2014); red-fronted brown lemur *E. rufifrons* (Overdorff, 1993); brown lemur *E. fulvus* (Sato, 2013)]. Different species of the same genus can exhibit different strategies; e.g. the black-and-white snub-nosed monkey *Rhinopithecus bieti* has larger home ranges in the period of fruit abundance (Li et al., 2010), while the golden snub-nosed monkey *R. roxellana* has larger home ranges in the period of fruit scarcity (Tan et al., 2007). Food resources and high food availability usually allow animals to minimise their daily movements to fulfil energy needs, while in habitats where resources are more scattered and/or food availability is low, long travelling paths are necessary (Kaplin, 2001; Boyle et al., 2009). Other species, however, use an opposite strategy, i.e. long travel distances in less degraded habitats and/or in areas with high food availability (Yamagiwa & Mwanza, 1994; Wallace, 2006).

Primates can show flexibility even in the temporal niche since some species are able to expand their activity over the 24 h [i.e. cathemeral activity (Tattersal, 1987)] or to adjust their activity to reduce temporal niche overlap with other sympatric species (Ganzhorn, 1989). Activity patterns are synchronised with photoperiodic variations in habitats where resource availability is predictable (Curtis & Donati, 2013). Shifting activity patterns and expanding the activity over the 24 h are thus flexible behaviours that can be adaptive and bring ecological advantages such as avoiding thermal stress (Curtis et al., 1999), reducing predation risk (Colquhoun, 2006), reducing feeding competition (Curtis et al., 1999), and increasing feeding efficiency related to a fibre-rich diet (Donati et al., 2007, 2009, 2016).

1.2. Energy saving strategies in primates

Primates can exhibit another form of flexibility that is more related to energy saving strategies with both behavioural and physiological adaptations. Animals require energy for their biological processes and activities, and the metabolic rate (MR) is a common measure of their transformation and allocation of energy (Speakman, 1999, Brown et al., 2004). The MR reflects the energetic costs for animals, which are substantial in endotherms, since they produce energy endogenously to regulate their body temperature (Tomlinson et al., 2014). Endotherms require additional energy to maintain a constant body temperature outside the thermoneutral zone, that is the range of ambient temperature in which no additional energy is necessary for thermoregulation apart from the basal metabolic rate (BMR) (Dausmann et al., 2009; Kobbe et al., 2014). Metabolism is shaped by several ecological (e.g. seasonal variations in food, water availability, and in ambient temperature) and physiological (e.g. body size and reproductive state) factors (Speakman, 1999; Brown et al., 2004, Cruz-Neto & Bozinovic, 2004, Seebacher & Franklin, 2012). In particular, body size, ambient temperature, and diet are considered the main factors influencing the MR in endotherms (McNab, 1974; Speakman, 1999; Brown et al., 2004).

Energy balance in small endotherms is particularly expensive due to high heat loss related to the high body surface to volume ratio, and the consequent higher mass-specific MR than large endotherms (McNab, 1999). This is one of the reasons why a low-quality diet coupled with a seasonal environment represents an additional challenge in small endotherms (Kobbe & Dausmann, 2009). A low MR is in fact usually associated with small endotherms living in habitats with limited resources and high daily and seasonal fluctuations in ambient temperature (Lovegrove, 2000, 2003). Also, many small endotherms use behavioural and physiological adaptations to adjust their metabolic rate to variable environmental conditions (Brown et al., 2004; Ruf & Geiser, 2015). Species relying on a low-quality food (i.e. high in indigestible fibre and low in essential nutrients) such as leaves, usually have low MR, especially when tree-dwelling due to the relatively sedentary habits of arboreal species and the need to maintain a low muscle mass (McNab, 1978; Cork and Foley, 1991).

Madagascar is one of the tropical areas with high climatic unpredictability, hypervariable environments, and prolonged periods of fruit scarcity, constraining endothermic species such as the lemurs to rely on various behavioural and physiological adaptations to face harsh environments (Wright, 1999; Dewar & Richard, 2007). On one hand, medium-sized lemur species usually rely on behavioural adaptations such as behavioural thermoregulation [collared brown lemur (Donati et al., 2011b); black-and-white ruffed lemur *Varecia variegata* (Morland, 1993)] and cathemeral activity [mongoose lemur *Eulemur mongoz* (Curtis et al., 1999); Alaotra bamboo lemur *Hapalemur alaotrensis* (Mutschler, 1999); see Curtis & Rasmussen (2006) and Donati & Borgognini-Tarli (2006) for detailed reviews]. On the other hand, small-sized lemur species rely more extensively on physiological adaptations, such as daily and seasonal torpor [i.e. shift in the thermoneutral zone within the day or between seasons; e.g. grey-brown mouse lemur *Microcebus griseorufus* (Kobbe et al., 2014)] and hibernation [i.e. prolonged periods of inactivity with low MR and low thermoneutral zone; e.g. western fat-tailed dwarf lemur *Cheirogaleus medius* (Dausmann et al., 2005)]. Other factors in addition to resource variability and unpredictability have been hypothesised to explain lemur adaptations. For example, the lower protein content of fruits in Madagascar compared to other continents has been recently used to explain the dietary flexibility of lemurs and the overall low degree of frugivory in the island's animal communities (Ganzhorn et al., 2009; Donati et al., 2017).

1.3. The sportive lemurs (*Lepilemur* spp.)

The genus *Lepilemur* is well known for the low metabolism and for the use of energy saving strategies. The sportive lemurs, *Lepilemur* spp., are arboreal and nocturnal prosimians belonging to the family Lepilemuridae (Hoffmann et al., 2009; Mittermeier et al., 2010). This genus includes 26 species of which one Near Threatened (*L. mustelinus*), five Vulnerable (*L. aeeclis*, *L. dorsalis*, *L. petteri*, *L.*

ruficaudatus, *L. seali*), 15 Endangered (*L. ahmansonorum, L. ankaranensis, L. betsileo, L. edwardsi, L. grewcockorum, L. hollandorum, L. hubbardorum, L. leucopus, L. microdon, L. milanoi, L. mittermeieri, L. otto, L. randrianasoloi, L. scottorum, L. wrightae*), and five Critically Endangered (*L. fleuretae, L. jamesorum, L. sahamalazensis, L. septentrionalis, L. tymerlachsoni*) based on the IUCN Red List assessment in 2012 (Andriaholinirina et al., 2014) (Figure 1.1). Tattersall (2007), however, has cautioned that the recent split of most of Malagasy lemurs, including the species in the genus *Lepilemur*, should be further explored since diagnosed exclusively on genetic distance. Despite the large distribution of this genus that is present in all the habitats in Madagascar, only a few species have been studied so far and there is no information on the behavioural ecology of the species inhabiting the eastern rainforest (Table 1.1). This is a serious gap in the knowledge of this phylogenetic group since the eastern rainforests represent the habitat where the majority of the species of this genus occur. In fact, 15 species are present in the eastern rainforest, 11 of which are exclusive of this habitat (Mittermeier et al., 2010; Andriaholinirina et al., 2014). Most of the reports referring to sportive lemurs in the eastern rainforests focus on abundance estimates (Ranaivoarisoa et al., 2013; Sawyer et al., 2017), while little is known about their behavioural and ecological adaptations. A previous study reported short-term information about ranging patterns of *L. mittermeieri* in a mosaic of humid and deciduous forest in the Ampasindava peninsula in northwest Madagascar (Wilmet et al., 2015). Some information is also available on the sleeping site selection and the vocalisation of *L. mustelinus* (Rasoloharijaona, 2001; Rasoloharijaona et al., 2008, 2010).

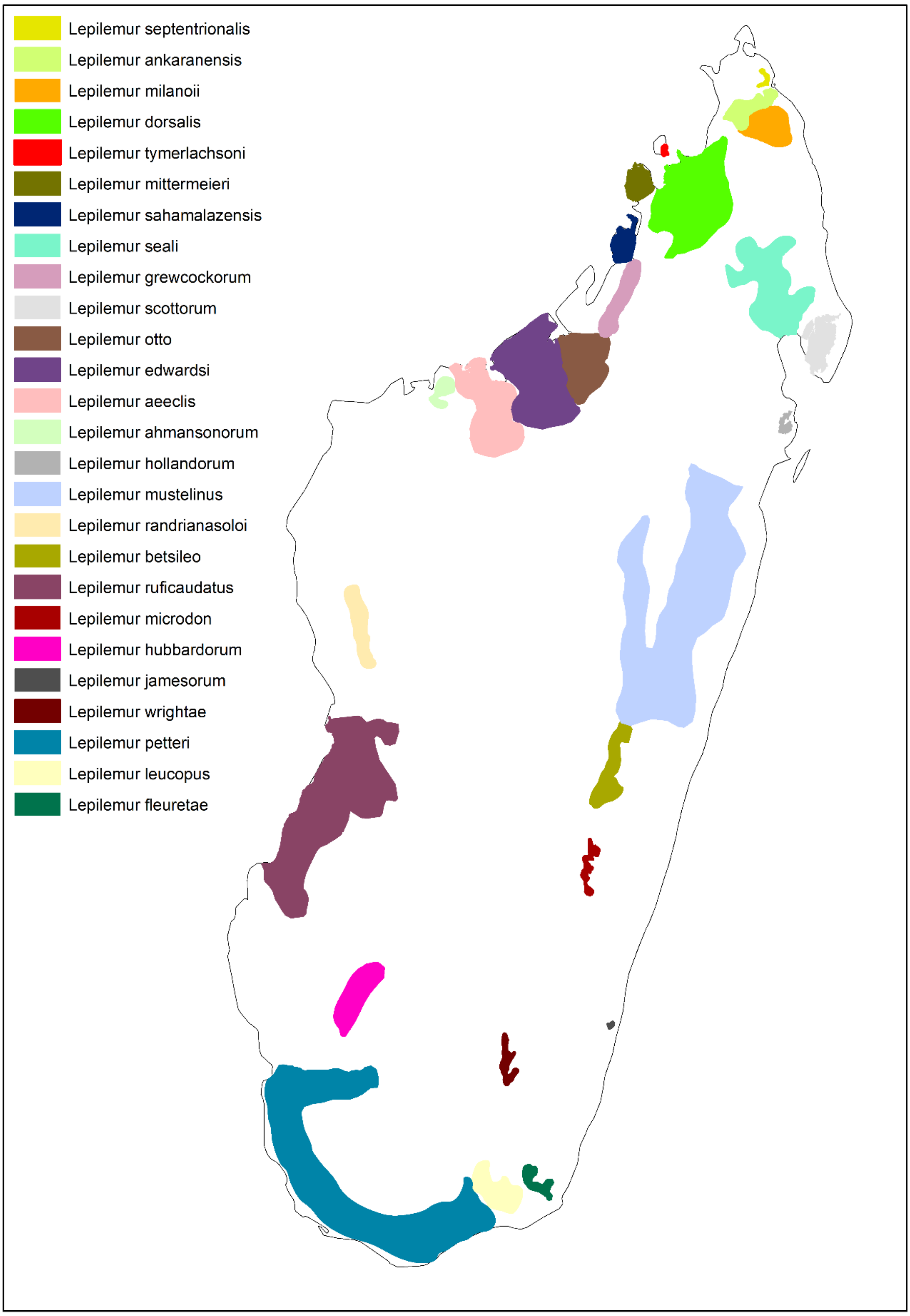

Figure 1.1: Distrubution of the 26 species of sportive lemurs *Lepilemur* spp. in Madagascar. Geographic ranges were retrieved from the IUCN red list website.

Table 1.1: Information available on sportive lemurs *Lepilemur* spp.

Species	IUCN status[a]	Habitat	Activity	Ranging	Diet	Other[b]
L. mustelinus	NT	Humid				SS, VO
L. aeeclis	VU	Deciduous				
L. dorsalis	VU	Semi-humid				
L. petteri	VU	Spiny	X	X	X	
L. ruficaudatus	VU	Deciduous	X	X	X	SS, EN, PD, SO
L. seali	VU	Humid				PD
L. ahmansonorum	EN	Humid				
L. ankaranensis	EN	Semi-humid				
L. betsileo	EN	Humid				
L. edwardsi	EN	Deciduous	X	X	X	SS, VO, SO
L. grewcockorum	EN	Deciduous				PD
L. hollandorum	EN	Humid				PD
L. hubbardorum	EN	Deciduous				
L. leucopus	EN	Spiny	X	X	X	SS, EN, SO
L. microdon	EN	Humid				PD
L. milanoi	EN	Semi-humid				
L. mittermeieri	EN	Semi-humid		X		
L. otto	EN	Deciduous				
L. randrianasoloi	EN	Deciduous				
L. scottorum	EN	Humid				PD
L. wrightae	EN	Humid				PD
L. fleuretae *	CR	Humid	X	X	X	SS, PD
L. jamesorum	CR	Humid				PD
L. sahamalazensis	CR	Deciduous	X	X	X	SS, VO, PD
L. septentrionalis	CR	Deciduous	X	X	X	
L. tymerlachsoni	CR	Humid				

[a]see list of abbreviations (page xiv), [b]SS: Sleeping site selection; VO: Vocalisation; EN: Energetics; PD: Population density; SO: Social Structure. * Present study

The information on the behavioural ecology, social structure, and energetics of sportive lemurs are mainly based on five species inhabiting dry, spiny, and deciduous forests [*L. edwardsi* (Warren & Crompton, 1997a, 1997b, 1998; Rasoloharijaona et al., 2000, 2003, 2006; Thalmann & Ganzhorn, 2003; Thalmann, 2001, 2002, 2006; Méndez-Cárdenas & Zimmermann, 2009); *L. leucopus* (Charles-Dominique & Hladik 1971; Hladik & Charles-Dominique 1974; Dröscher & Kappeler, 2013, 2014; Dröscher et al., 2016; Bethge et al., 2017); *L. petteri* (Nash 1998); *L. ruficaudatus* (Ganzhorn & Kappeler, 1996; Schmid & Ganzhorn, 1996; Ganzhorn, 2002; Zinner et al., 2003; Ganzhorn et al., 2004; Fichtel, 2007; Hilgartner et al., 2008; Fichtel et al., 2011; Hilgartner et al., 2012); *L. sahamalazensis* (Ruperti, 2007; Seiler et al., 2013a, 2013b, 2014, 2015)].

Sportive lemurs are small-sized lemurs with a body mass ranging from 600 to 1000 g and are mainly folivorous (Mittermeier et al., 2010). They are, together with the ecologically similar genus *Avahi*, at the lowest limit of body size for folivory [that is expected to be difficult to sustain below 700g (Kay, 1984)]. Their diet is considered low in nutritional quality and may contain potentially toxic leaf chemicals (Ganzhorn, 1988). Furthermore, sportive lemurs were shown to have a lower quality diet when in sympatry with *Avahi* sp. (Ganzhorn, 1993). Because of the aforementioned constraints, *Lepilemur* spp. evolved physiological adaptations for folivory such as an enlarged caecum, as well as behavioural adaptations for a low-quality diet such as low levels of activity and small home ranges (Hladik & Charles-Dominique, 1974; Hladik, 1975). Moreover, sportive lemurs were reported to rely on caecotrophy [i.e. reingestion of feces for nutritional purposes (Hladik & Charles-Dominique, 1974)], although this peculiar behaviour was never reported again. As for the very low level of energy expenditure of sportive lemurs (*L. petteri*) in the dry forest of Beza Mahafaly, Nash (1998) claimed «*Lepilemur* sits on what it eats and eats what it sits on». Sportive lemurs, however, are expected to show some flexibility in their behaviour and ecology if we consider the extent of their geographical distribution (Seiler et al., 2014).

Lepilemur ruficaudatus has the lowest resting metabolic rate (RMR; i.e. the metabolism during inactivity) measured so far in a folivorous mammal (Speakman, 1999). In fact, the RMR of this species was approximately only 50% of the BMR expected from the Kleiber equation for a small-bodied mammal like *L. ruficaudatus* (Schmid & Ganzhorn, 1996). For *L. leucopus*, the dry season in the spiny forest of Berenty appears to be a physiologically demanding season because of high ambient temperatures during the day combined with a lack of water, requiring an increase in MR to enable heat dissipation (Dröscher & Kappeler, 2013). Apart from the increase in MR, *L. leucopus* were found to shift the termoneutral zone from 29-32 °C in the dry season to 25-30 °C in the wet season (Bethge et al., 2017).

The social structure of sportive lemurs ranges from dispersed to cohesive pairs (Kappeler, 2014). Some studies also reported solitary living (Petter et al., 1977; Albignac, 1981) and dispersed one-male multi-female social structures (Warren & Crompton, 1997a), suggesting high variability within the genus. Within sportive lemurs, *L. edwardsi* showed the highest male-female cohesiveness and the largest home range overlap between sexes (Méndez-Cárdenas & Zimmermann, 2009). *Lepilemur ruficaudatus* has also been described as a pair-living based on spatiotemporal overlaps of individual home ranges (Zinner et al., 2003; Hilgartner et al., 2012). *Lepilemur leucopus* is the most asocial of all primates living in dispersed pairs studied to date, with very limited male-female interactions, low spatial cohesiveness, males having a substantially larger home range than females, and a minimal range overlap (Dröscher & Kappeler, 2013).

Sportive lemurs do not show a flight response towards humans, even at sites where hunting occurs (Rabesandratana & Zimmermann, 2005). The absence of a flight response towards humans, as well as the tendency to stay in the interior part of the forest (Lehman, 2007), indicate that sportive lemurs may be strongly threatened by habitat fragmentation and hunting (Craul et al., 2009). Since the geographical ranges of *Lepilemur* spp. are usually small, and the information on density estimates for most of these species is lacking (Andriaholinirina et al., 2014), assessing the level of hunting in an area is important when investigating the ecology of sportive lemurs.

1.4. Aims of the study

The aim of this study was to investigate the ecology of the Critically Endangered Fluerete's sportive lemur *L. fleuretae* in the lowland rainforest of Ampasy, Tsitongabarika Protected Area (TGK). Sportive lemurs in rainforests are expected to be exposed to different ecological pressures than sportive lemurs in other habitats in terms of resource availability, distribution and quality, and to be in competition with ecologically similar species. Exploring the ecology of these lemurs in humid forests may shed light on the full flexibility and the evolution of this genus. I first evaluated resource availability for frugivores and folivores in the lowland rainforest of Ampasy. I then examined whether sportive lemurs inhabiting the Ampasy rainforest show behavioural and ecological patterns similar to the sportive lemurs inhabiting dry and deciduous rainforests of Madagascar. Finally, I aimed to assess the hunting pressure in the area to evaluate the threats faced by this species. The more specific objectives of this study are:

- To investigate the phenological patterns in the TGK Protected Area and to understand why this forest hosts a low proportion of frugivorous species;
- To determine whether the ranging patterns and the feeding choices of Fleurette's sportive lemurs in TGK are different from the ones of the other species of sportive lemurs inhabiting other habitats, and why;
- To evaluate the efficiency of a novel technique, the unsupervised learning algorithm on accelerometer data, to extrapolate the activity patterns of the cryptic *L. fleuretae*;
- To explore the influence of photoperiodic variations and moon phase on the activity patterns of *L. fleuretae* in TGK;
- To assess whether forest management and researchers' presence can assist in significantly reducing forest exploitation by local communities.

In Chapter 3, I explored the phenological profile of a sample of 200 tree species in the TGK rainforest to determine the variation in food availability for the local lemur community, which hosts a low number of frugivorous species and a high density of folivorous species. In Chapter 4, I compared the ranging patterns and the diet of *L. fleuretae* at TGK with the ones of other sportive lemurs inhabiting dry and deciduous forests in Madagascar. In Chapter 5, I validated a new method for estimating the activity patterns in cryptic animals via accelerometer loggers using the time budget of *L. fleuretae* as a model. In Chapter 6, I explored the influence of moon phase and photoperiodic variation in the activity patterns of *L. fleuretae*, comparing the activity levels with other nocturnal and cathemeral lemurs. Finally, in Chapter 7 I investigated the conservation threats in the Ampasy area, evaluating the effect of forest management and researchers' presence to reduce hunting and forest exploitation by local communities. A synthesis of the topics included in this dissertation and the links between them is shown in Figure 1.2.

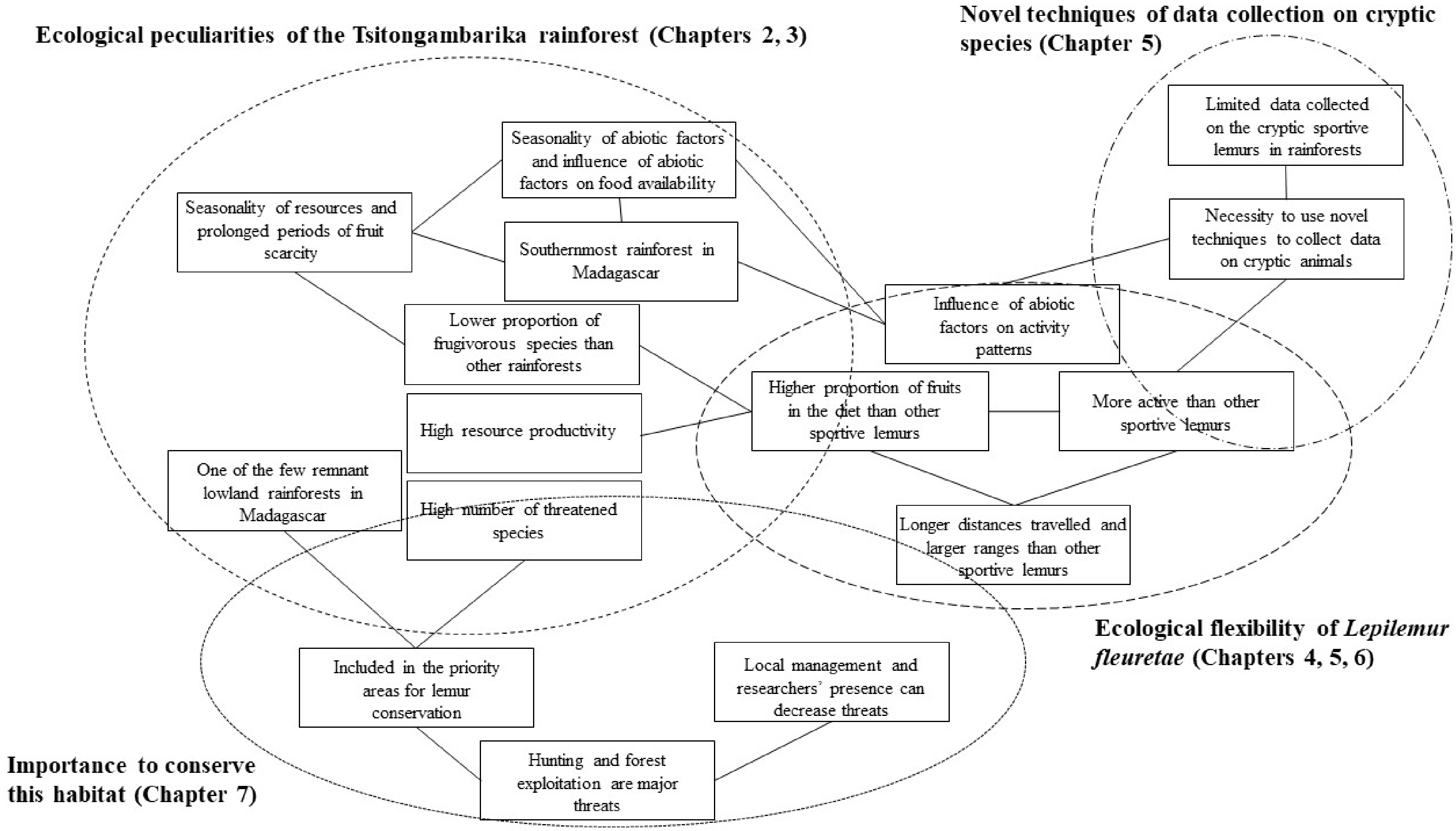

Figure 1.2: Word flowchart representing the topics of this dissertation.

Chapter 2. General methods

2.1. Study area

The study was conducted at the Ampasy research station (S 24° 34’ 58’’, E 47° 09’ 01’’), a valley of around 3 km^2 located in the northernmost portion of the Tsitongambarika Protected Area (TGK) (Figure 2.1). The TGK forest, together with the connected Andohahela National Park, is the southernmost rainforest of Madagascar and one of the last large expansions of lowland rainforests in the island (Schwitzer et al., 2013). TGK includes an area of 605 km^2 of forests that reaches a maximum altitude of 1,358 m and contains vast areas of lowland rainforests (0-600 m) (Ganzhorn et al., 1997; Birdlife International, 2011). This area includes large areas below 400 m (BirdLife International, 2011). For this reason, and for the high number of threatened species in the area, TGK has been included in the 30 priority areas for lemur conservation (Schwitzer et al., 2013). The lemurs confirmed at Ampasy are: Anosy mouse lemur *Microcebus tanosi*, aye-aye *Daubentonia madagascariensis*, collared brown lemur *Eulemur collaris*, Fleurette’s sportive lemur *Lepilemur fleuretae*, greater dwarf lemur *Cheirogaleus major* (although the taxonomic status of this species has not been verified), southern bamboo lemur *Hapalemur meridionalis*, and southern woolly lemur *Avahi meridionalis*.

The TGK Protected Area was created in 2008 by the ministry of the Environment and Forests and provides an important source of products for local people including firewood, charcoal, construction materials, bushmeat, and medicinal plants, other than representing the main source of water in the coastal area of the Fort Dauphin region (BirdLife International, 2011). The most significant threat to the TGK forest is represented by shifting cultivation (slash and burn agriculture), principally manioc and rice (BirdLife International, 2011; Schwitzer et al, 2013).

Deforestation is of particular concern in areas below 800m, which are the very vulnerable areas from a biodiversity conservation perspective due to their easy accessibility (BirdLife International, 2011).

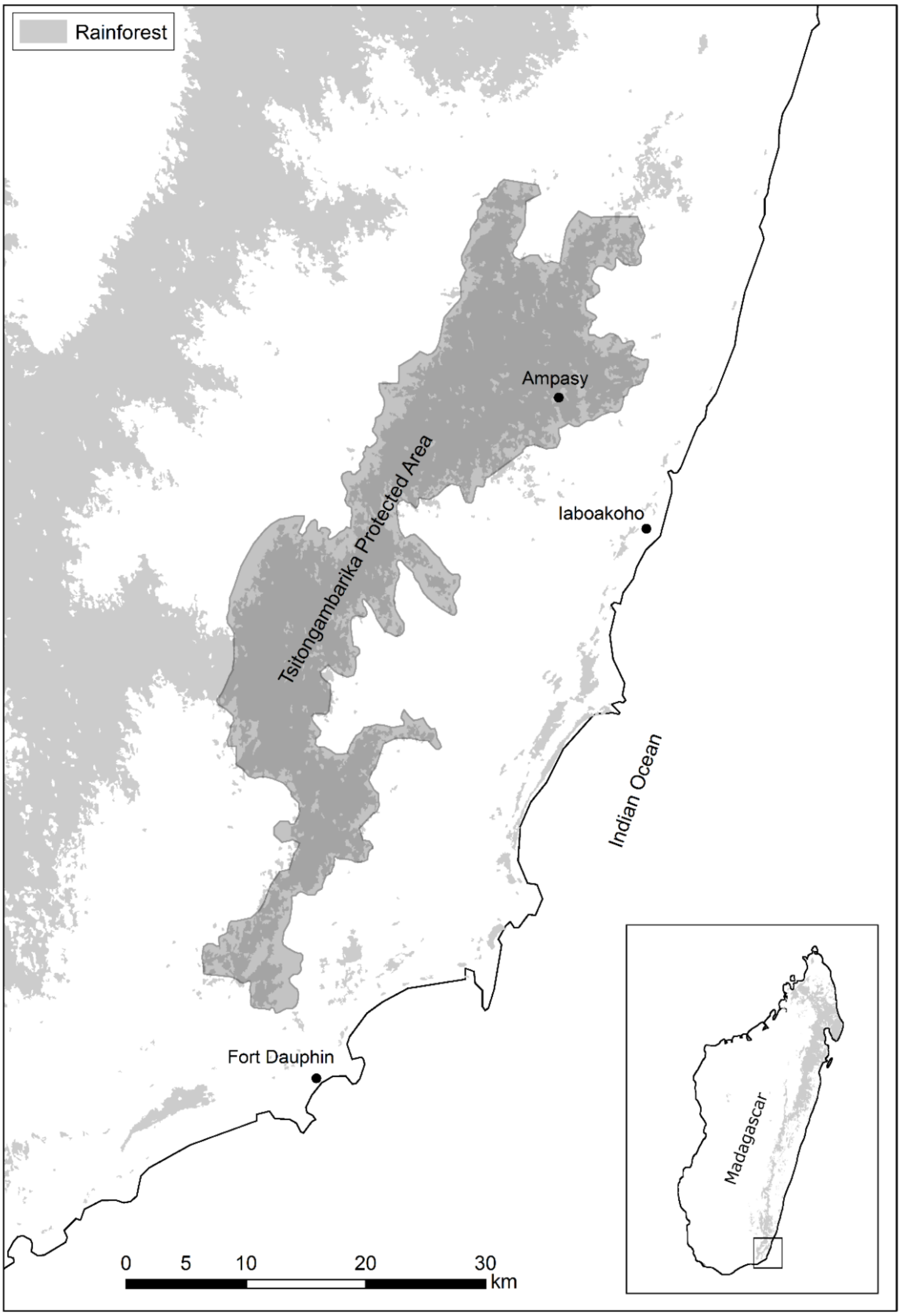

Figure 2.1: **Map of the study site**. Location of the study area in the Tsitongambarika Protected Area, in south-east Madagascar.

2.2. Context

The original project of my PhD was to study the behavioural ecology of collared brown lemur *Eulemur collaris* in the lowland rainforest of TGK. In particular, the project entailed a data collection on the behavioural ecology of collared brown lemurs in the continuous forest of TGK and a comparison of these data with the data previously collected in littoral forest fragments of Mandena and Ste Luce (Campera et al., 2014; Donati et al., 2016). I started the fieldwork in April 2015 together with another PhD student from Oxford Brookes University, Michela Balestri. Her project involved the investigation of niche separation between two ecologically similar species: the Fleurette's sportive lemur *Lepilemur fleuretae* and the Southern woolly lemur *Avahi meridionalis*. In the first two months of the field work, Michela and I mapped (by tagging and taking a GPS point every 25-m) all the pre-existing transects in the Ampasy forest and we walked the transects during the day and at night to find the most suitable areas for capturing lemurs. We selected nine transects that we considered as the most suitable for estimating lemur densities in the area. These transects partly overlapped with the transects used in a pilot study to estimate lemur encounter rates in the area (Nguyen et al., 2013). Another PhD student, Dr Tim Eppley, started his study on the Southern bamboo lemur *Hapalemur meridionalis* at Ampasy. He started surveys to find bamboo lemurs, but he did not manage to complete the study at Ampasy since he did not find any Southern bamboo lemurs during the first two months of his stay. He thus decided to rely on a backup plan and to study the species at Mandena. Similar to what Dr Eppley experienced, we did not encounter a single individual of collared brown lemur during the first two months of our stay at Ampasy. It is likely that the hunting pressure in the area was too high on these two species that are hunted both by snares and opportunistic hunting (see

Chapter 7). We thus agreed, together with Michela and our supervisor Dr Giuseppe Donati, to split Michela's project into two different projects. We decided to expand the project by including an estimate of the hunting pressure in the area for me and a conservation education project for Michela. *A posteriori*, we can say that this was the best decision since Michela's project would have been very difficult for a single researcher considering the difficulties of collecting behavioural data at Ampasy. We plan to maintain the original project of niche partitioning between the two species for publications, also considering the low amount of behavioural observation on the two species.

The transects to estimate lemur abundance were initially done by both of us, while it was a major activity for Michela from July 2015 to July 2016. Details on the data collection for this activity are in Chapter 7. We set up the phenological trails together, while from July 2015 I started the collection of phenological data. Details on the data collection for this activity are in Chapter 3. The data collection on lemurs were mainly done via triangulation and behavioural data collection. For the triangulation, we walked two transects to estimate the locations of lemurs every hour for 12 hours. For the behavioural data collection, I collected data on Fleurette's sportive lemur and Michela collected data on the Southern woolly lemur. More details are in Chapter 4. In April 2016, two MSc students from Oxford Brookes University, Fiona Besnard and Megan Phelps, started their project in the area. We helped them with their projects and with the logistics at the research station. They collected data on vegetation plots at Ampasy (details are in Chapter 3) and they helped me during the interviews with local people on hunting and forest use (details are in Chapter 7). In Table 2.1. there is an overview of the time line of the project and the division of work between Michela and me.

Table 2.1: Time line of the project. Work done at the Ampasy research station by the author and his colleague Michela Balestri between April 2015 and July 2016.

Period	**Research activities**[a]	**Other activities**
April 2015-June 2015	Map the forest (14 days)[AM], lemur transects (20 days)[AM], locate areas with higher density of lemurs, set up phenological trails (14 days)[AM].	Construction of a temporary research station, selection of the personnel for the research station.
July 2015	Capture lemurs (4 days)[AM], triangulation (4 days)[AM], lemur transects (12 days)[M], phenology (12 days)[A].	Tutor two volunteers who arrived at the research station (they stayed two months).
August 2015-October 2015	Behavioural data collection (18 days)[AM], triangulation (12 days)[AM], lemur transects (36 days)[M], phenology (36 days)[A].	Four lessons on the ecology of lemurs given to local teachers, Lemur Day organised for children at local schools.
November 2015-March 2016	Behavioural data collection (18 days)[AM], triangulation (16 days)[AM], lemur transects (36 days) [M], phenology (36 days)[A].	Construction of a permanent research station, 500£ raised (by selling local craftings) for the construction of a school in a village close to Ampasy.
April 2016-June 2016	Behavioural data collection (12 days)[AM], triangulation (12 days)[AM], lemur transects (36 days)[AM], phenology (36 days)[AM], vegetation plots (30 days)[O], interviews with local people on hunting and forest use (20 days)[AO].	Arrival of two MSc students. Selection of two local guides for the two students.
July 2017	Behavioural data collection (4 days)[AM], triangulation (4 days)[AM], lemur transects (9 days)[M], phenology (9 days)[M], re-capture lemurs (3 days)[AM].	Questionnaire to test knowledge on lemur ecology with local teachers.

[a] Research activity done by author (A), Michela (M), and/or other people (O).

An important part of our work at Ampasy was to develop the research station that was initially planned between QIT Madagascar Minerals (QMM) and our supervisor Dr Giuseppe Donati. In April 2015 a temporary research station with three shelters for tents, a kitchen, a shower, and a toilet built by local people selected by Asity (Figure 2.2).

Figure 2.2: Temporary research station at Ampasy.

In February 2016, QMM started the construction of a permanent field station (Figure 2.3). The work lasted around two months considering the difficult weather conditions in the area. Solar panels, financed by Oxford Brookes University, were installed after the end of our study. During our stay, we had a power generator given by QMM. Another activity we did during the research was a conservation education program to local teachers in which we raised awareness on lemur ecology and conservation and we tested the retention of knowledge at the end of our study [details are in Balestri et al. (2017)]. In addition, in December 2015 we raised around 500£ by selling local crafts at the meeting of the Primate Society of Great Britain. This money was devolved to Asity to contribute for the construction of a school in a village close to the research station.

Figure 2.3: Permanent research station at Ampasy.

2.3. Abiotic variables in the study area

Rainfall was measured via a plastic rain gauge at the camp site (annual rainfall: 2382 m). The ambient temperature was measured via HOBO U23 Pro v2 Temperature/Relative Humidity Data Loggers. Daylength was retrieved from MOON software (Curtis et al., 1999) using the latitude and longitude of Ampasy. Moon phase was also retrieved from MOON software as a proxy of moon luminosity (see Chapter 6). Monthly rainfall, mean ambient temperature, and daylength from June 2015 to June 2016 are shown in Figure 2.4.

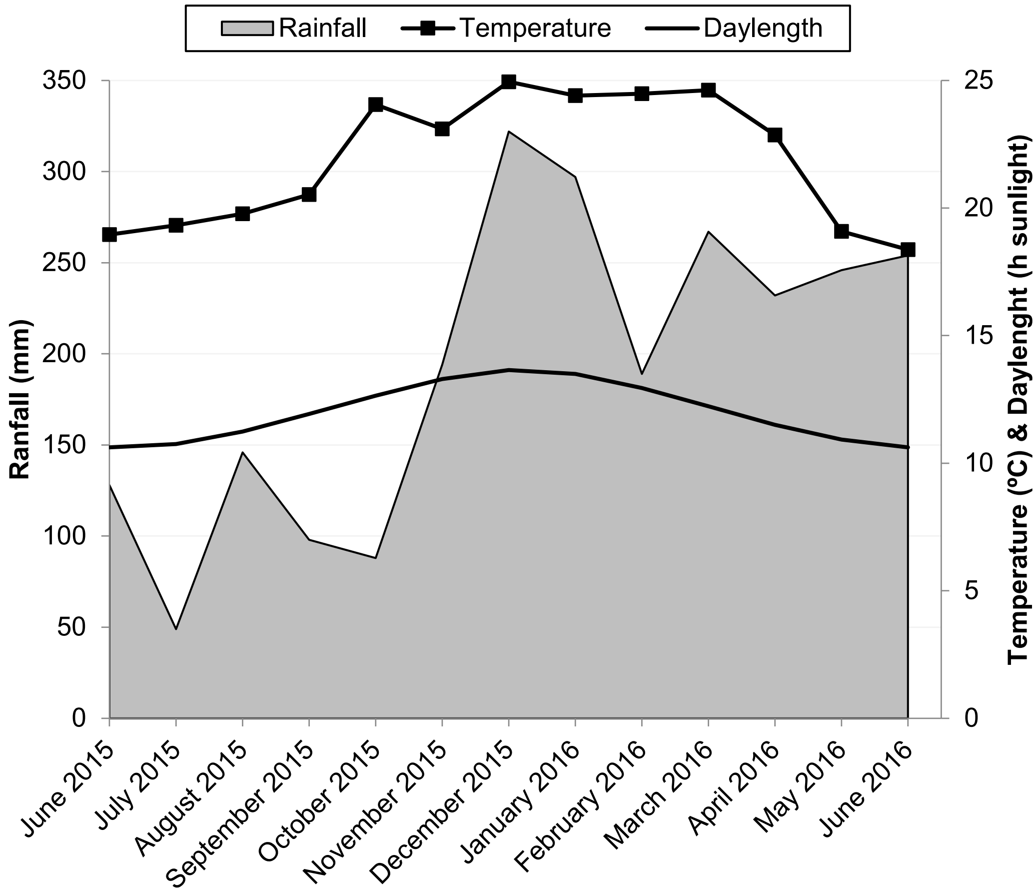

Figure 2.4: Abiotic factors at the lowland rainforest of Ampasy. Data are monthly rainfall, mean ambient temperature, and daylength.

2.4. Study animals

Between 6 and 9 July 2015, an expert team from Kianjavato (operating the Madagascar Biodiversity Partnership, a long-term project on lemur conservation led by Dr Edward E. Louis Jr.) conducted the animal captures on eight individuals of *L. fleuretae* (Table 2.2). Michela and I previously selected areas of the forest most suitable for captures by mapping all the existing paths and performing preliminary transects to estimate encounter rates. Michela and I created a map of the forest by flagging all the pre-existing trails and taking a GPS point every 25 m. The team used a dose of 15 ml of Telazol 100mg/ml (tiletamine HCl and zolazepam HCl; Zoetis Inc.) as anaesthetic using remote capture rifles. Rifles were the only option for capturing sportive lemurs at Ampasy due to the high canopy height (Nguyen et al., 2013). As a standard procedure of the capture team from Kianjavato, captured animals were brought to the camp at the end of the session and they took body measurements the day after. Before taking body measurements the capture team injected a dose of 5 ml Telazol. Animals took around 1 h to fully recover from the 15 ml dose and 0.5 h to fully recover from the 5 ml dose. After taking body measurements, I equipped the individuals with radio-transmitters (RI-2C installed to a backpack, RI-2D installed to a collar, Holohil System Ltd, 11g) to ensure systematic observations. We asked Holohil to manufacture custom brass strip collars (Figure 2.5).

Figure 2.5: Custom brass collar with RI-2D transmitter from Holohil System Ltd.

The night after, before starting a new capture session, we released the animals in the same location where we captured them. A member of the capture team or a local assistant supervised the animals until regaining full mobility in trees. There were no injuries as a consequence of the captures. Sportive lemurs have a small difference in neck and head widths, and this created problems when collaring individuals of other species. This is because collars cannot be too large since animals can easily remove them, or too tight since animals can choke. That is why I also tried to equip two animals with RI-2C transmitters attached to a backpack. The two individuals equipped with RI-2C transmitters, however, removed their backpacks after a few weeks. There was no problem for the animals equipped with the radio-collars RI-2D. Re-captures to remove radio-collars were performed between 15 and 18 July 2016 by the same team and with the same procedure.

I attached three-axis accelerometer tags (Axi-3, TechnoSmart) to three VHF collars (RI-2D, Holohil Systems Ltd). The weight of the combination of VHF collars and accelerometer tags with batteries (around 4 g) was around 15 g, thus below the 5% threshold of the subjects' weight recommended for arboreal animals (Wheater et al., 2011). I collected accelerometer data every second on three individuals (two females and one male) of *Lepilemur fleuretae* at Ampasy. The data collection lasted from 07/07/2015 to 13/09/2015 (69 days) for female 1, from 07/07/2015 to 02/10/2015 (89 days) for female 2, and from 09/07/2015 to 29/09/2015 (83 days) for the male (Table 2.2). The accelerometers were set to last one year, while they only lasted up to three months. This was probably due to a problem of isolation from rain and humidity that limited the battery use. These devices were, in fact, never tested in rainforests before. Nevertheless, the amount of data collected with these accelerometers is difficult to achieve with other devices. Since the accelerometers are installed to VHF collars by TechnoSmart, it is advisable to ensure a particular care to isolate the battery from humidity and rain. The data analysis (details are in Chapter 5) is not user-friendly, and knowledge on specific packages in R software is required.

Table 2.2: **Body measurements of captured animals**. Body parameters of eight individuals of *Lepilemur fleuretae* at Ampasy captured between 6 and 9 July 2015.

Parameter	**F1**	**F2**	**F3**	**F4**	**F5**	**M1**	**M2**	**M3**
Weight (g)	1100	1100	1150	1300	1250	900	1075	1000
Temperature (ºC)	37.4	37.0	40.3	35.8	38.5	35.8	37.0	37.7
Head Crown (cm)	8.5	8.6	9.1	9.1	9.6	9.6	9.9	9.1
Body length (cm)	23.5	23.3	22.5	23.6	25.1	22.6	21.9	22.6
Tail length (cm)	32.0	29.4	28.0	32.6	32.6	28.9	32.6	31.3
Upper canine length (cm)	6.8	6.3	6.2	6.8	5.2	6.8	8.1	6.2
Notes[a]	A, K, R	A, K, R	R	B	R	A	B	R

F: female; M: male. [a]A: animal with accelerometer tags, K: animal killed by fossa (F1 was killed in November 2015; F2 was killed in September 2015), B: animal with backpack (removed in July 2015), R: animal with radio-collar.

The mean body weight of *L. fleuretae* at Ampasy (1.11 ± SD 0.13 kg, N = 8) is slightly higher than the body weight of the type specimen from Andohahela [0.98 ± SD 0.16 kg (Louis Jr. et al., 2006)], although females were at the early gestation stage when captured at Ampasy. The head crown is also larger in *L. fleuretae* from Ampasy (9.2 ± SD 0.5 cm) than the type specimen [7.4 ± SD 0.3 cm (Louis Jr. et al., 2006)]; while the body length is smaller for the *L. fleuretae* from Ampasy (23.1 ± SD 1.0 cm) than the type specimen [25.5 ± SD 2.2 cm (Louis Jr. et al., 2006)]. These phenotypical differences, as well as a slightly different fur colour, initially suggested that this sportive lemur was a new species. However, later genetic tests confirmed that the sportive lemur at Ampasy is *L. fleuretae* (E. E. Louis Jr., unpub. data).

2.5. Ethics statements

I obtained the 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 (54/16/MEEMF/SG/DGF/DAPT/SCBT.Re) (Appendix I).

Research involving questionnaires with local people (Chapter 7) was approved by the Oxford Brookes University Ethics Committee (see Appendix II). In conformity with local customs, I asked for consent from the mayor of the Iaboakoho municipality before commencing interviews. Before each interview I explained all research details to participants, avoiding revealing my main target (i.e. lemur hunting) to favour honest responses (Nuno & St John, 2015), stating that participation was voluntary, with the opportunity to withdraw at any time. Village names are not provided here, to ensure anonymity of participants.

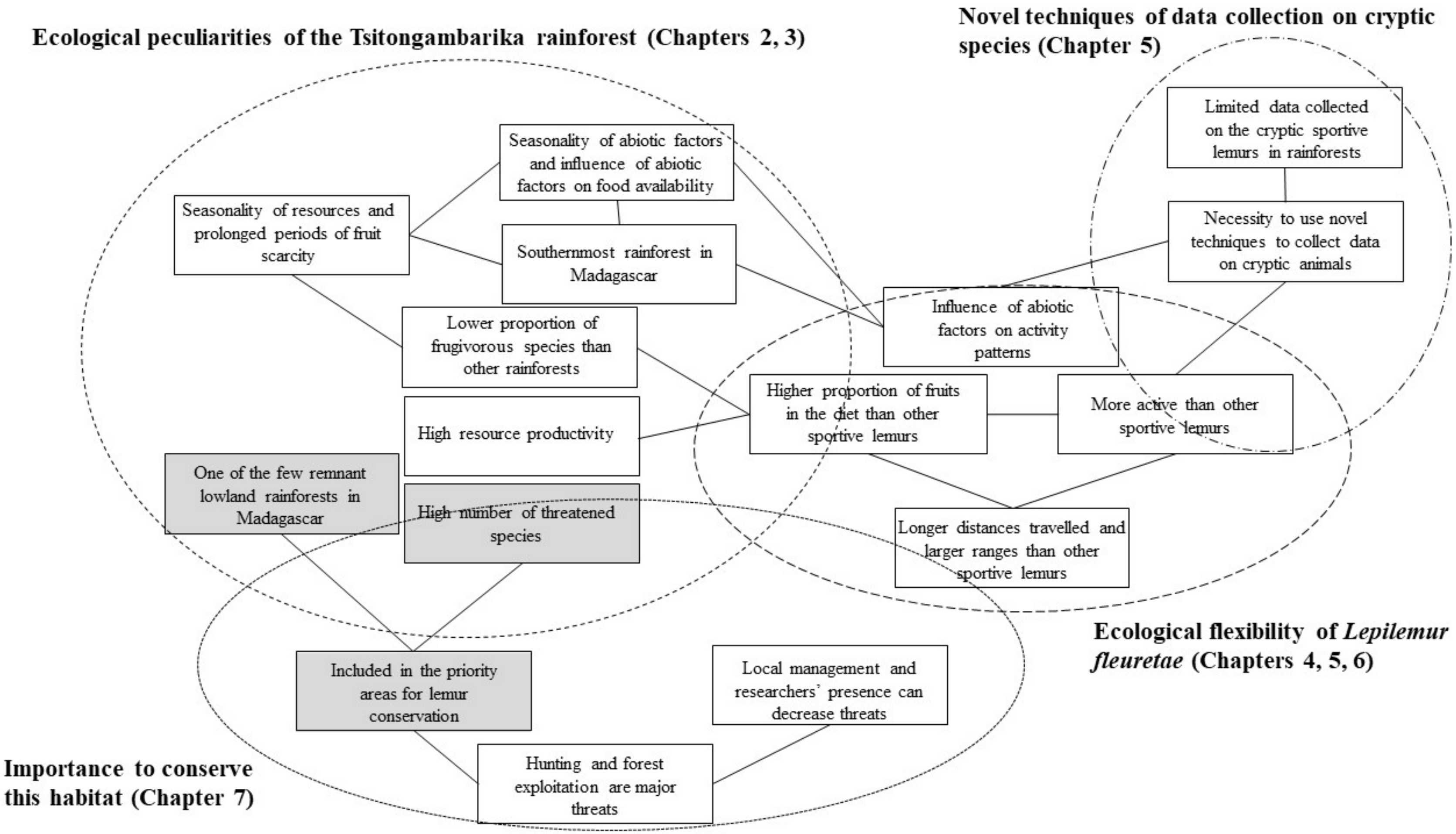

Figure 2.6: Word flowchart representing the topics of Chapter 2. Topics highlighted in grey.

Chapter 3. Phenology of the lowland rainforest of Tsitongambarika: prolonged periods of fruit scarcity may explain low diversity of frugivorous lemurs.

In this chapter, I explore the reasons why the Tsitongambarika forest hosts a low diversity of frugivorous lemurs compared to most of the Malagasy rainforests. This peculiarity may concur to explain the behavioural flexibility in terms of dietary choices, ranging patterns, and activity patterns of Fleurette's sportive lemurs at Ampasy. The low diversity of frugivorous lemurs may, in fact, determine a larger proportion of fruits in the diet of Fleurette's sportive lemurs, with consequent changes in ranging and activity patterns, in the season of fruit abundance. Furthermore, in this chapter I show the availability of young leaves that are expected to be the main food item of Fleurette's sportive lemurs. This information will be used in the next chapter to determine the responses to seasonality of young leaves in terms of diet and ranging patterns.

3.1. Introduction

Phenological patterns of leaf flushing, flowering, and fruiting in tropical rainforests are always characterized by seasonal variations (van Schaik et al., 1993; Chapman et al., 1999; Anderson et al., 2005). However, many tree species show irregular flowering and fruiting patterns (Chapman et al., 1999) and there are substantial differences between years (Bollen & Donati, 2005), with supra-annual patterns often present (Sakai et al., 1999; Brearley et al., 2007). Semi-annual (twice per year) peaks in phenological phases are possible in the tropics because the sun passes at the zenith twice each year, influencing insolation rates and weather patterns (Anderson et al., 2005). Phenological patterns are shaped by both biotic [e.g. temporal abundance of pollinators, seed dispersers and herbivores (Murah & Sukumar, 1993; van Schaik et al., 1993)] and abiotic factors [e.g. rainfall, temperature, irradiance, and water stress (van Schaik et al., 1993; Wright, 1996; Chapman et al., 1999)]. The interaction effect of irradiance, rainfall, and temperature is thought to be one of the main factors driving tree reproductive phases (Anderson et al., 2005). Flowering and leaf flushing usually coincide with periods of high irradiance to take advantage of a high photosynthetic activity (van Schaik, 1986; Wright & van Schaik, 1994: Rivera et al., 2002). Rainfall has been shown to be a limiting factor for flowering and leaf flushing as water stress is constraining plant production (Borchert, 1983; Lieberman & Lieberman, 1984; van Schaik et al., 1993). High water availability increases fleshy fruit production (Lieberman, 1982; Rathcke & Lacey, 1985) and germination success (van Schaik et al., 1993; Justiniano & Fredericksen, 2000). Temperature has also been shown to have an influence on flowering and fruiting (Tutin & Fernandez, 1993; Newbery et al., 1998; Chapman et al., 1999), and it has been hypothesised as the main cue that induces community-wide flowering events (Ashton et al., 1988; Sakai et al., 1999).

From what it is known so far, Malagasy rainforests, when compared to other rainforests, are characterized by prolonged periods of fruit scarcity, up to six months [(Wright, 1999); but see Wright et al. (2005)]. Furthermore, the nutritional quality of fruits, measured as nitrogen content, in Madagascar is lower than the other continents (Donati et al., 2017). This is reflected in a low number of frugivorous animals as compared to the other rainforests outside Madagascar (Ganzhorn et al., 2009). The low number of frugivores in Madagascar has been explained by the Energy Frugality Hypothesis (EFH) that suggests that Madagascar has an unpredictable climate, causing unreliability in fruiting patterns and resulting in few obligate frugivores

(Wright, 1999; Dewar & Richard, 2007). However, this hypothesis has been recently questioned since a comparison of fruiting patterns between the rainforests of Betampona (Madagascar) and Kibale (Uganda) showed more predictable fruiting patterns in Betampona (Federman et al., 2017). The study of Federman et al. (2017) proposed that the paucity of frugivores in Madagascar needs to be referred to the low fruit availability compared to African forests. However, a comparison of phenological profiles is somehow difficult due to the different method used. Phenological profiles have been measured using different approaches, including the number of tree species (White, 1994), the percentage of trees (e.g. Sakai et al., 1999), the percentage of species (e.g. White, 1994; Bollen & Donati, 2005; Breadley et al., 2007), and the density of trees (e.g. Chapman et al., 1999; Brugiere et al., 2002) in each phenological phase. Other profiles have been based on food availability indexes that included an average phenological score and species biomass (e.g. Fashing, 2001), crown volume (e.g. Overdorff, 1996), or stem density (e.g. Nkurunungi et al., 2004; Anderson et al., 2005; Guo et al., 2007). On top of this, since phenological data are not available for most of the rainforests in Madagascar (Federman et al., 2017), a comparison is difficult until further data is provided.

Madagascar's rainforests range from low, tropical latitudes in the North of the country to relatively high latitudes beyond the Capricorn tropic in the South. The Tsitongambarika Protected Area (TGK), together with a portion of the connected Andohahela National Park, is at the southernmost limit of the rainforest distribution in Madagascar and one of the remnant lowland rainforest in the island (Schwitzer et al., 2013). This forest is characterised by the presence of only two frugivorous species: collared brown lemur *Eulemur collaris* and greater dwarf lemur *Cheirogaleus major* (see Chapter 2.1). Thus, TGK represents one of the rainforests with the lowest number of frugivorous lemur species in eastern Madagascar. This area does not host the genera *Varecia* [the largest frugivore in Madagascar (Balko, 1998)] and *Propithecus* [that is an opportunistic frugivore with up to 40% of fruits in their diet (Sato et al., 2016)] that are present in most of the other rainforests on the island. Also, only one species of the genera *Eulemur* and *Cheirogaleus* is present, contrary to other Malagasy rainforests where more than one species of these two genera are present (Figure 3.1).

The low species diversity has been hypothesized to result from contrains in species distribution due to the geometry of the rainforest area in Madagascar (Goodman & Ganzhorn, 2004). According to this idea, species diversity is shaped in a parabolic distribution showing its maxima in the centre and its minima in more peripheral areas due to bounded range overlaps (Lees et al., 1999; Goodman & Ganzhorn, 2004). However, habitat analyses in the Malagasy southern rainforest indicate structural similarity but lower diversity compared to other rainforests in Madagascar (Rakotomalaza & Messmer, 1999). The question thus arises as to whether environmental factors such as resource availability and quality play a role in determining the low diversity of frugivores.

Here I provide the first phenological data from the lowland rainforest of TGK. Based on the above considerations, I hypothesised that TGK hosts a low diversity of frugivores due to large periods of fruit scarcity. In particular, I predicted:

1) the lowland rainforest of TGK to be characterised by a prolonged season with low ripe fruits as compared to other Malagasy rainforests. Thus, I expected a low temporal availability of ripe fruits. Also, I expected lower maximum fruit availability as compared to other rainforests outside Madagascar based on the hypothesis from Federman et al. (2017);

2) daylength to have a strong influence on phenological patterns since TGK is the southernmost rainforest in Madagascar and seasonal photoperiodic variations should affect plants more significantly than in other forests.

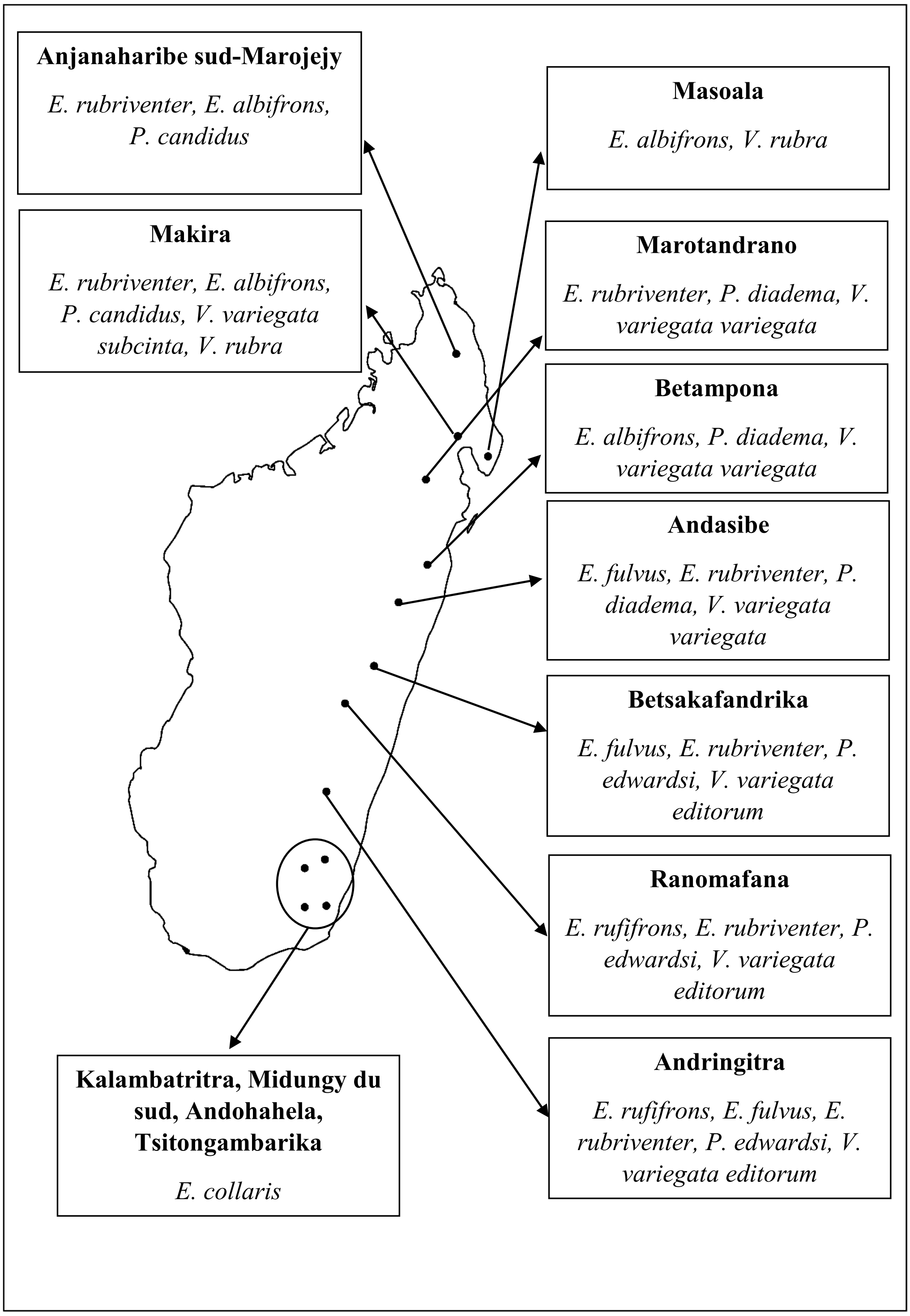

Figure 3.1: Distribution of frugivorous species in Malagasy rainforests.

3.2. Methods

3.2.1. Phenological data collection

I tagged individual plants with the diameter at breast height (DBH) larger than 10 cm within 5 m each side of four trails (Chapman et al., 1994). The phenological trails were 500 m each, covering a total area of 2 ha. Since the number of trees along the trails varied dramatically between species, I considered up to five individuals per species. In total, I tagged 769 individuals corresponding to 200 different species. For most of the species (58.5 percent) I tagged five individuals. Seven trees died during the sampling period.

Phenological data were recorded twice a month from July 2015 to June 2016. However, from December 2015 to March 2016 it was only possible to do it once a month since the forest was inaccessible for long periods. I considered the following phenological phases: leaf flushing (presence of leaf buds or young leaves), flowering (presence of flower buds or open flowers), and ripe fruiting (presence of ripe or fallen fruits). I was always assisted by a field assistant who is an expert on vernacular names of plants in the area. He also assisted in fieldworks with botanists from Asity Madagascar (an NGO associated with BirdLife International) and Missouri Botanical Garden, the only institutions that performed botanical studies in the area. Tree identification was made in the field using vernacular names obtained from the field assistant and associated to the list compiled by botanists from Asity Madagascar (Ravoahangy et al., 2013, 2014). I collected herbarium specimens when the vernacular name was not present in the list. In total, 63 species assessed via vernacular names were not present in the list. Scientific names of these specimens were identified by a botanist from the Biological Department of the University of Antananarivo, Madagascar. It was not possible to identify six of these species.

3.2.2. Botanical data collection

I established 33 plots of 10 X 100 m in the Ampasy area to estimate density and mean size of the species present in the phenological trails. Plots were at a minimum distance of 200m to minimise the spatial autocorrelation. Eight plots were overlapping with the phenological trails. I only sampled adult trees with a minimum DBH of 10 cm (Chapman et al., 1994). A total of 165 species out of 200 (82.5 percent) was present both in the plots and in the phenological trails. For the other species, all rare species with less than five individuals, I estimated the density and DBH based only on the phenological trails. In the case of plants only present in phenological trails, I considered the sum of the total area covered during plots (3.3 ha) and the area covered via the phenological trails and not overlapping with the plots (1.1 ha) as the total area to calculate the tree density.

3.2.3. Data analysis

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)]. To obtain the phenological score I calculated the proportion of plants with young leaves, flowers, or ripe fruits for each species and multiplied by the mean DBH (measured in decimetres, dm) for that species. I considered the DBH in decimetres and not in centimetres since it would have unbalanced the calculation of FAI towards DBH instead of density. I did not estimate a score for the quantity of leaves, flowers, and ripe fruits since these measures were highly unreliable in the study area due to the low visibility of canopy and emergent trees. Also, the number and weight of fruits on trees were largely variable between species, thus adding unreliability to a fine-grained quantitative score. For this reason, I preferred to include the mean DBH for each species in the formula as a proxy of tree productivity (Chapman et al., 1994). The density of trees varied from 0.22 to 60.61 ind/ha (mean: 4.74 ± SE 0.65 ind/ha) and mean DBH varied from 1.06 to 5.19 dm (mean: 1.87 ± SE 0.04 dm). Thus, DBH measured in decimetres could substitute the phenological score in the formula to calculate FAI since also the phenological score usually varies between 1 and 5 (e.g. Fashing, 2001). I reported tree species with a total FAI above 10 and available during the periods of low production as possible “keystone plant resources” (van Schaik et al., 1993). The value is the first integer above the mean value. Forty tree species (20 percent) at Ampasy had a total FAI > 10.

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. This way, it is possible to directly compare the estimates via FAI with the estimates based on the percentage of species in the phenological phase.

To check for differences between the percentages of monthly FAI with the percentages of species, I used a Repeated Measures ANOVA using the individual species as unit of analysis with the monthly percentages as within-subject factor and the phenological phase as fixed factor. I considered the interaction factor monthly percentage*phenological phase to see the differences within the two methods between phenological phases. Overall, the profiles obtained via the percentage of species and the percentage over the total FAI were not different (monthly percentage*phenological phase effect: $F_{2,33} = 0.189$, $P = 0.829$). Thus, I am confident that a comparison between phenological profiles obtained via the two different methods is reliable and that I can compare my data with data collected from the other sites.

To control for abiotic factors influencing phenological phases, I ran three Generalised Linear Mixed Models (normal distribution and identity as link function) with the monthly FAI for the phenological phase for each species as dependent variable and the abiotic factors as covariates. As abiotic factors, I considered mean temperature, rainfall, and daylength in the same month when the phenological phase was recorded and in the two preceding months. I considered the species as subject and random factor in the models, and month as repeated measures. I checked for the violation of the assumption of multicollinearity via Spearman correlations, and no correlations between factors were significant after a Bonferroni correction. I performed the tests via SPSS v23 (IBM, Armonk, USA) considering $P < 0.05$ as level of significance.

3.3. Results

3.3.1. Phenological patterns

The lowland rainforest of Ampasy exhibited a seasonal pattern for the three phenological phases (Figure 3.2). The peak of leaf flushing occurred between October and January for most of the species (60.5-75.5 percent of the total FAI), while the season of low leaf flushing lasts from May to July (less than 14.4 percent of the total FAI). The tree species with max FAI higher than 10 that produced young leaves during the season of low leaf flushing were *Canthium medium*, *Dombeya* sp., *Eugenia cloiselii*, *Eugenia* sp., *Homalium microphyllum*, *Pandanus* sp., *Quassia indica*, *Symphonia tanalensis*, *Syzygium emirnensis*, *Tinopsis conjugata*, and *Uapaca thouarsii* (Appendix III).

The peak of flowering occurred in November-December for most of the species (59.2-62.9 percent of the total FAI), while the season of low flowering lasted from February to September (7.6-10.7 percent of the total FAI) with a peak in May (14.4 percent of the total FAI). The tree species with max FAI higher than 10 that produced flowers during the season of low flowering were *Albizia* sp., *Anthostema madagascariensis*, *Canthium medium*, *Dilobeia thouarsii*, *Eugenia cloiselii*, *Eugenia* sp., *Humbertia madagascariensis*, *Pandanus* sp., *Symphonia tanalensis*, *Syzygium emirnensis*, *Tinopsis conjugata*, and *Uapaca thouarsii* (Appendix III).

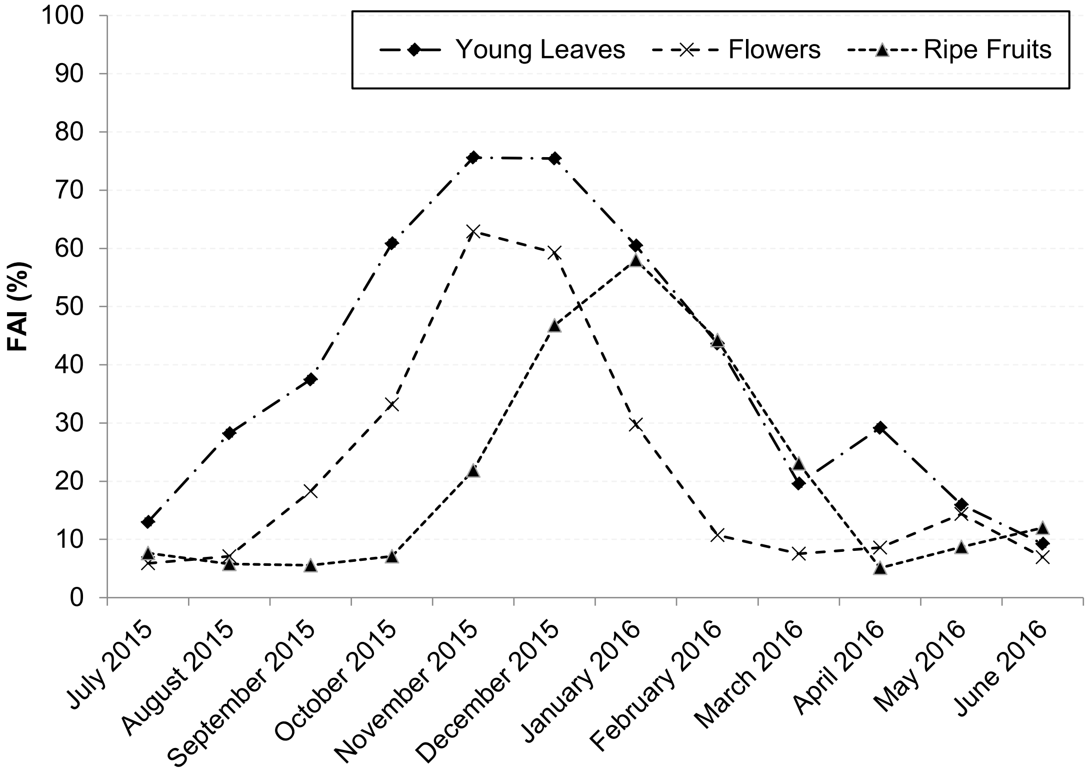

Figure 3.2: Phenological profiles obtained via Food Availability Index (FAI) at Ampasy. Data are monthly percentages over the total FAI. The FAI for each species is the product of stem density (trees/ha), mean diameter at breast height, and proportion of trees in the phenological phase.

The peak of ripe fruiting occurred from December to February (44.2-58.0 percent of the total FAI) with the highest percentage in January. The season of low ripe fruiting lasted from April to October (5.1-12.0 percent of the total FAI). The tree species with max FAI higher than 10 that produced fruits during the season of low ripe fruiting were *Albizia* sp., *Canthium medium*, *Eugenia cloiselii*, *Eugenia* sp., *Pandanus* sp., *Symphonia tanalensis*, *Syzygium emirnensis*, *Tinopsis conjugata*, and *Uapaca thouarsii* (Appendix III).

3.3.2. Influence of abiotic factors on phenological patterns

Leaf flushing of tree species at Ampasy was positively influenced by the temperature in the same month and in the preceding month (Table 3.1).

Table 3.1: Effect of abiotic factors on phenological phases. Parameter estimates of generalised linear mixed models with monthly food availability index for each species as dependent variable and abiotic factors as covariates.

Parameter	**Beta coefficient (SE)**		
	Leaf flushing	Flowering	Ripe fruiting
Rainfall	0.00 (0.00)	0.01 (0.00)	0.02 (0.00) **
Temperature	0.52 (0.20) *	1.34 (0.38) **	0.37 (0.17) *
Daylength	6.09 (7.67)	36.86 (8.12) **	-0.08 (8.84)
Rainfall-1	0.01 (0.01)	0.04 (0.01) **	0.01 (0.01)
Temperature-1	0.78 (0.21) **	1.23 (0.28) **	0.82 (0.22) **
Daylength-1	-7.24 (13.00)	-61.81 (13.70) **	2.96 (14.99)
Rainfall-2	0.01 (0.01)	0.03 (0.01) *	0.01 (0.00) *
Temperature-2	0.37 (0.20)	0.32 (0.16) *	0.22 (0.24)
Daylength-2	-0.77 (6.77)	25.34 (6.86) **	-6.51 (7.77)

-1 and -2 indicates the preceding months

*P < 0.05, **P < 0.001

Flowering was positively influenced by temperature in the same month, in the preceding month, and two months before. Also, flowering was positively influenced by rainfall in the preceding month and two months before, but not influenced by the rainfall in the same month. The daylength in the same month and two months before positively influenced flowering, while the daylength in the preceding month had a negative influence on flowering. Ripe fruiting was positively influenced by rainfall and temperature in the same month, and by rainfall two months before.

3.4. Discussion

3.4.1. Phenological patterns

The phenological profiles indicate a seasonal pattern in the Ampasy lowland rainforest with peaks of productivity of young leaves in October-January, of flowers in November-December, and of ripe fruits in December-February. These profiles are similar to the ones of the adjacent littoral rainforest of Sainte Luce where the peak of leaf flushing was November-January, the peak of flowering was November, and the peak of ripe fruiting was November-January (Bollen & Donati, 2005). The mid-altitude rainforest of Ranomafana also has a similar pattern for ripe fruits with a peak in December-February (Wright et al., 2005). Similar phenological patterns were reported in the lowland rainforest of Nosy Mangabe with peaks of ripe fruiting in November-February (Andrianisa, 1989). Other studies in Madagascar reported peaks of ripe fruiting in different periods [March-June in the lowland rainforest of Lokobe (Andrews & Birkinshaw, 1998), October-November in the mid-altitude rainforest of Ambatonakolahy (Rigamonti, 1993)]. Overdorff (1996) and Federman et al. (2017) reported a large variation in the temporal location of peaks between years (Overdorff, 1996; Federman et al., 2017), although they sampled 26-27 species and the low sample size might have biased the pattern. As a consequence of this inter-annual variation of phenological patterns, it will be important to collect data on multiple years in TGK. However, previous studies showing data on multiple years in Madagascar (Bollen & Donati, 2005; Wright et al., 2005) reported that the peak of fruit production is usually in the same period. Since the TGK forest is adjacent to the forest of Sainte Luce where Bollen & Donati (2005) worked, and both forests have similar variations in abiotic factors, I may reasonably hypothesise that the peak of ripe fruit production might be usually between December and February in the study area. Further studies, however, are necessary to confirm this hypothesis.

In the lowland rainforest of Ampasy I found a larger percentage of tree species with ripe fruits and flowers when compared to the nearby littoral forest of Sainte Luce during the season of abundance (around 60 percent of species of flower at Ampasy and 40 percent in Sainte Luce; around 50 percent of species with ripe fruits in Ampasy and 25 percent in Sainte Luce). This might be due to a higher productivity in the lowland rainforest than in the littoral rainforest on sandy soil (Bollen & Donati, 2005). In fact, a fruit production similar to the one in Sainte Luce has been reported in the other littoral rainforest in the Fort Dauphin region, Mandena [20 percent of species (Campera et al., 2014)]. Similar to the findings at Ampasy, Wright et al. (2005) reported around 45 percent of species with ripe fruits in the mid-altitude rainforest of Ranomafana during the season of fruit abundance. Outside Madagascar, Brearley et al. (2007) also reported peaks of flowering and ripe fruiting on around 40-50 percent of dipterocarp species with prolonged periods of low flowering and ripe fruiting in the lowland rainforest of Barito Ulu, Indonesia. Anderson et al. (2005) reported a peak of fruit production of around 50-60 percent of species in Taï, Ivory Coast. White (1994) reported a peak of ripe fruiting of 35 percent of species in the Lopé Reserve, Gabon. Remis et al. (2001) reported a peak of ripe fruits of around 35 percent of species in Bai Hokou, Central African Republic, although in one isolated year there was a peak of more than 50 percent of species with ripe fruits. Since the peaks reported for Ampasy are similar to the findings in other rainforests, my data do not support the hypothesis that the low number of frugivores at Ampasy is related to lower maximum fruit availability. It is important to note that a proportion of species in a phenophase might not completely reflect the productivity of a forest, while food availability indexes can provide more precise estimations. A comparison of food availability based on different approaches may be biased, although I tested the validity of this comparison at Ampasy (see Methods section 3.2.4). Further evidence is necessary to test the hypothesis that the low number of frugivores in Malagasy rainforests is dependent on the lower fruit availability than in other continents (Federman et al., 2017).

The hypothesis that seems to be better supported to explain the lower number of frugivorous lemurs in TGK is the one related to the prolonged period of fruit scarcity. In fact, TGK appears to be the site with the longest relative period of fruit scarcity [measured as the average number of months per year with less than 25 percent of the maximum fruit productivity reported in the study (Federman et al., 2017)] in Madagascar and in the other continents (Table 3.2). Also, when looking at the absolute period of fruit scarcity (defined here as the average number of months per year with less than 10 percent of species with ripe fruits), TGK is comparable to the degraded littoral rainforest on sandy soil of Mandena, that is a habitat with low productivity (Campera et al., 2014). However, as previously seen, these long periods of fruit scarcity are coupled with the peak of ripe fruiting comparable to other rainforests. Since TGK is the southernmost rainforest in Madagascar and one of the southernmost in the world, daylength should play a pivotal role in shaping phenological phases (Wright, 1996; Chapman et al., 1999). This might explain the similarity with the phenological profiles of Sainte Luce (Bollen & Donati, 2005) and Mandena (Campera et al., 2014). Collecting data in other rainforests that host other frugivorous lemur genera, such as *Propithecus*, *Varecia* and other species of the genera *Cheirogaleus* and *Eulemur,* is necessary to provide further insight on the reasons why TGK host a low number of frugivorous lemurs.

Table 3.2: Number of frugivores and periods of fruit scarcity in rainforests. Comparison between rainforests in terms of number of frugivores and periods of fruit scarcity.

Site	Sampling period (months)	N of tree species	N of frugivores [a]	Relative fruit scarcity [b]	Absolute fruit scarcity [c]	Source
Madagascar						
Betampona	24	27	3	1.5	NA	Federman et al., 2017
Mandena	12	46	3	3.0	6.0	Campera et al., 2014
Ranomafana	27	98	4	0.4	0	Wright et al., 2005
Sainte Luce	36	95	3	3.3	4.3	Bollen & Donati, 2005
Tsitongambarika	12	200	2	7.0	6.0	This study
Other						
Bai Hokou	61	152	8	2.2	2.2	Remis e al., 2001
Barro Colorado Island	180	39	3	2.0	NA	Milton et al., 2005
Bwindi	12	25	5	0.0	NA	Nkurunungi et al., 2004
Kakamega	12	13	5	0.0	NA	Fashing, 2001
Kibale-Kanyawara	78	67	5	0.9	NA	Chapman et al., 2005
Kibale-Ngogo	70	92	5	1.5	NA	Chapman et al., 2005
Lopé	12	195	7	3.0	3.0	White, 1994

Site	**Sampling period (months)**	**N of tree species**	**N of frugivores** [a]	**Relative fruit scarcity** [b]	**Absolute fruit scarcity** [c]	**Source**
Other						
Makandé	22	NA	4	6.0	NA	Brugiere et al., 2002
Taï	35	38	5	1.4	0.0	Anderson et al., 2005
Tinigua	36	75	4	4.0	NA	Stevenson, 2005

[a] number of primate frugivores [i.e. with more than 50% of fruits in their diet (Terborgh, 1986)] reported in the cited paper or obtained from Donati et al. (2017).

[b] average number of months per year with <25% of the maximum fruit productivity reported in the study.

[c] absolute fruit scarcity: average number of months per year with <10% of species with ripe fruits.

The nine tree species with high productivity (FAI > 10) with a fruiting peak during the period of scarcity of resources should be considered as “keystone plant resources” (van Schaik et al., 1993). It has been shown that in tropical rainforests there are only a dozen plant species that are vital for herbivores during the period of scarcity of resources (Terborgh, 1986). For example, flowers of *Albizia* sp. and *Humbertia madagascariensis* were two of the main food items of Fleurette’s sportive lemur during the study period (see Table 4.1). Fruits of *Eugenia* sp., *Pandanus* sp., *Syzygium emirnensis,* and *Uapaca* sp. are known to be the main food items in the diet of collared brown lemur (Donati et al., 2011a), the main seed disperser in the area (Bollen et al., 2005). Although there is a paucity of information on the diet of frugivores in TGK, I may argue that the tree species I reported flowering or fruiting during the period of scarcity of resources might be crucial resources in the area. Further evidence on other frugivores in the area is necessary to support this conclusion.

3.4.2. Influence of abiotic factors on phenological patterns

At Ampasy, daylength did not have the main influence on phenological patterns contrary to my expectations based on the latitude of this site and the high photoperiodic variations. In fact, only flowering was highly influenced by daylength, contrary to the findings of Bollen & Donati (2005) who concluded that, being the littoral rainforest of Sainte Luce one of the southernmost rainforests, irradiance [correlated to daylength (van Schaik et al., 1993)] is the main abiotic factor determining phenological phases. Peaks of leaf flushing and flowering are usually subsequent to peak periods of irradiance in seasonal rainforests (van Schaik et al., 1993; Wright & van Schaik, 1994). Fruiting at Ampasy was not influenced by daylength and this might be explained by the irradiance being not coincident with daylength due to confounding factors such as rainfall and cloud density (Wright & van Schaik, 1994). The insulation-limitation hypothesis (van Schaik et al., 1993) also predicts that leaf flushing should coincide with periods of high solar irradiance and thus influenced by daylength. This is not supported by this study since there is no influence of daylength on leaf flushing and the peak of leaf flushing begins two months before the solar zenith. An anticipated leaf flushing was also reported at Taï National Park, Ivory Coast (Anderson et al., 2005), and it has been related to the need of minimising herbivory on young leaves before the increase in insect biomass that coincides with the wet season (Murah & Sukumar, 1993). Also, the anticipated leaf flushing might be associated with water stress, and an increase in rainfall or rather a reduction in days with no rain might stimulate the production of leaves in the subsequent month (Borchert, 1992). However, this cannot explain the peak of leaf flushing in October that was a dry month.

Chapman et al. (1999) reported the highest density of flowering and fruiting trees when the first rainy season was ending and dry season was beginning, while my data shows an opposite pattern, with the peak of flowering and fruiting coincident with the beginning of the rainy season. Also, it has been hypothesised that abnormally high rainfall might bring to fruit abortion in the subsequent month (Bollen & Donati, 2005). One possible explanation for the pattern found at Ampasy is that fleshy-fruited species should have their peak fruiting period during the rainy season due to an increased moisture level necessary for fruit production (Rathke & Lacey, 1985). In fact, flowering and fruiting at Ampasy were influenced by rainfall in the same month and the preceding month. My data support the hypothesis that a high water availability is necessary at the time of fruiting to enhance fruit maturation

(Lieberman, 1982; Rathcke & Lacey, 1985) and germination success (van Schaik et al., 1993; Justiniano & Fredericksen, 2000). Furthermore, rainfall is a proxy of clouds, which reduce solar irradiance and alter ambient temperature, and might influence the activity of insects (Wright & van Schaik, 1994). Thus, rainfall influences phenological phases in a complex way, by altering both abiotic and biotic factors.

Temperature had the strongest influence in shaping phenological patterns at Ampasy. I found a positive influence of the mean temperature of the same month and the preceding month on leaf flushing and flowering. This is in line with the finding that increased temperature might induce leaf flushing and flowering in some species (e.g. *Diospyros* sp.) in the Hathinala rainforest, India (Singh & Kushwaha, 2006). Temperature has been hypothesised as the main cue that induces community-wide flowering events (Ashton et al., 1988; Sakai et al., 1999). The flowering and fruiting patterns of many species, however, are triggered by low temperatures (Numata et al., 2003). Furthermore, the minimum temperature during the preceding dry season has been indicated as a possible cue for flowering in other rainforests (Tutin & Fernandez, 1993, Chapman et al., 1999; Anderson et al., 2005). Temperature is expected to have a strong effect on flowering and a secondary effect on fruiting (Anderson et al., 2005). Tropical trees are expected to respond in various ways to changes in rainfall and temperature because they show different adaptations to seasonal drought and cues for bud break of vegetative and flower buds (Singh & Kushwaha, 2006). Thus, the effect of temperature on the phenological phases of tropical trees is not clear-cut.

3.4.3. Conclusions

In conclusion, the lowland rainforest of TGK showed a seasonal phenological pattern with seven months of fruit scarcity. The low number of frugivorous lemurs in TGK when compared to other forests in Madagascar, might be explained by this prolonged period of fruit scarcity rather than low fruit productivity. Nine plant species with a total FAI > 10 has been indicated as “keystone species” since they were fruiting during the period of fruit scarcity. Contrary to my predictions, daylength was not the main abiotic factor influencing phenological phases at Ampasy, possibly to due confounding factors of rainfall and cloud density that may have limited solar irradiation. Temperature and rainfall were the main factors shaping flowering and fruiting at Ampasy. Previous studies in other tropical rainforests found that abiotic factors up to 11 months prior shape phenological phases (e.g. Chapman et al., 1999; Anderson et al., 2005; Bollen & Donati, 2005). Also, many tree species show irregular flowering and fruiting patterns (Chapman et al., 1999) and there are substantial differences between years (Bollen & Donati, 2005). Thus, multi-annual phenological data are necessary to test whether food availability is a factor that may affect lemur communities in the southernmost rainforests of Madagascar.

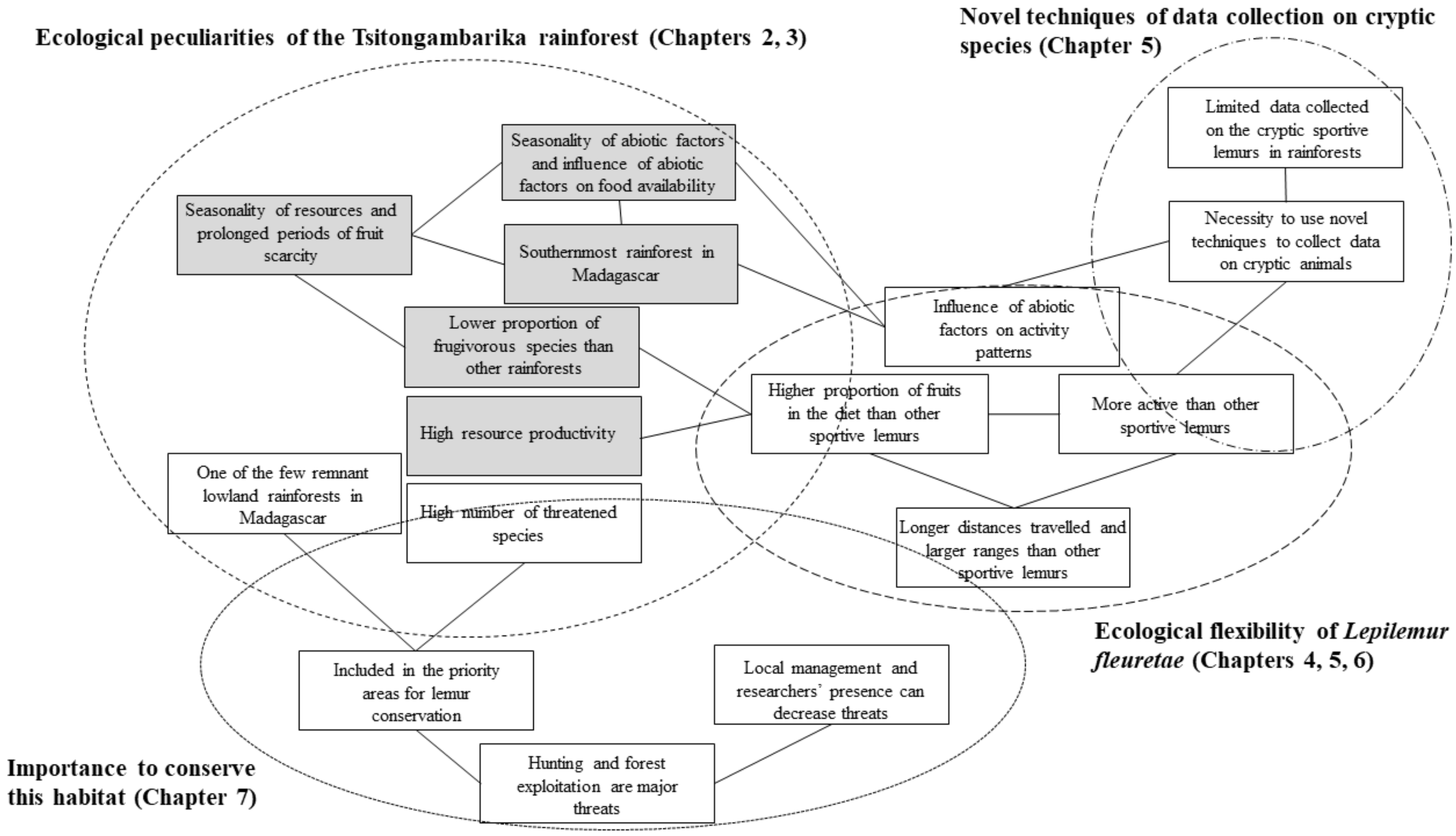

Figure 3.3: Word flowchart representing the topics of Chapter 3. Topics highlighted in grey.

Chapter 4. Why *Lepilemur fleuretae* in the Tsitongambarika lowland rainforest has large home ranges and high proportion of fruit and flowers in the diet?

In this chapter, I investigate diet and ranging patterns of Fleurette's sportive lemur at Ampasy, which differ from other species of sportive lemurs that inhabit spiny and deciduous forests. I argue that the low diversity of frugivorous lemurs (that I investigated in the previous chapter) and the presence of ecologically similar species led Fleurette's sportive lemur to include a higher proportion of fruits and flowers in its diet than the other sportive lemurs. As a consequence, Fleurette's sportive lemur exhibits larger home ranges and travels longer daily distances than the other sportive lemurs.

4.1. Introduction

Ranging patterns and feeding strategies are both influenced by resource availability and distribution (Chapman, 1988; Barton et al., 1992; Robbins & McNeilage, 2003; Hemingway & Bynum, 2005). Frugivorous species generally tend to have larger home ranges than those of folivorous species due to the more clumped distribution of fruits than leaves (Clutton-Brock, 1977; Clutton-Brock & Harvey, 1979; Mace & Harvey, 1983; Isbell, 2012). Habitat degradation seems to have a less severe influence on folivorous primates since secondary forests may produce leaves with higher protein and lower fibre content compared with those found in mature forests (Ganzhorn, 1995; Chapman et al., 2002). By contrast, frugivorous primates tend to be more sensitive to spatial and temporal fluctuations of fruiting trees and require strategies to face lean seasons (Estrada & Coates-Estrada, 1996; Rode et al., 2006).

The assumptions that folivores are less constrained by food availability than frugivores, however, have been lately questioned (Steenbeek & van Schaik, 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 (Koenig et al., 1998; Chapman & Chapman, 2002). Folivores may also select mature leaves that are highly variable in nutritional quality since they accumulate higher levels of secondary compounds, especially in rainforests when compared to deciduous forests (Hemingway, 1998). This entails that folivores may be affected by scramble competition and may be subjected to similar competitive regimes than frugivores (Snaith & Chapman, 2007).

Animals are known to adopt different strategies to face fluctuations of resource availability. In terms of feeding strategies, time-minimisers have a threshold of energy intake and, when reached, they spend their time on non-foraging activities; while resource-maximisers tend to maximise their energy intake spending more time feeding (Schoener, 1971; Hixon, 1982). In terms of ranging patterns, animals may either adopt an area-minimiser strategy by increasing their home ranges during lean periods to satisfy a minimum-resource threshold, or a resource-maximiser strategy by shifting from a random to a more selective use of the forest when resource availability decreases (Mitchell & Powell, 2004). These strategies are flexible, and animals may adopt different solutions in different periods (Hixon, 1982; Hixon & Carpenter, 1988, Mitchell & Powell, 2004).

Malagasy environments are characterised by a pronounced seasonality, climatic unpredictability, and natural fluctuations of food availability that represent a serious challenge to lemurs (Wright, 1999; Dewar & Richard, 2007). *Lepilemur* spp. have been shown to be mainly folivorous, but they can also rely on fruits and flowers in periods of food abundance (Thalmann, 2001). The biology of this genus in the rainforest is almost unknown, with no information on their diet and very limited information on their ranging patterns (Wilmet et al., 2015). Most of the information on sportive lemurs derives from dry/deciduous forests with a majority of studies investigating ranging patterns related to social structure or energetics (see Chapter 1.3).

In this chapter, I investigate the diet and ranging patterns of Fleurette's sportive lemur *Lepilemur fleuretae* in the southernmost rainforest of Madagascar: the lowland rainforest of Tsitongambarika (TGK). This rainforest is characterised by a strong resource seasonality, with a prolonged period of fruit scarcity, and by a high productivity in the months of fruit abundance (see Chapter 3). This rainforest is also characterised by the presence of only two frugivorous species, representing the rainforest area with less frugivorous lemur species in eastern Madagascar (see Chapter 3). In addition, *L. fleuretae* is in competition with another folivorous, nocturnal primate, *Avahi meridionalis*, occurring at 0.32 ind/ha, that shows similar ecological adaptations to sportive lemurs (M. Balestri, unpub. data). It has been shown that *Lepilemur* sp. has a lower quality diet when in competition with *Avahi* sp., and this has been hypothesised to lead to competitive exclusion in some cases (Ganzhorn, 1993). The presence of *Avahi meridionalis* is expected to lead *Lepilemur fleuretae* to a lower energy diet, or alternatively to rely on flowers and fruits in the season of food abundance as woolly lemurs remain folivorous year-round (Thalmann, 2001). Thus, TGK represents an ideal model to test the hypothesis that sportive lemurs may shift to a more frugivorous and energetic diet in conditions of competition with folivorous primates and low competition with other frugivores. I predict that *Lepilemur fleuretae* in TGK:

1) has a diet richer in fruits and flowers than other species of the same genus inhabiting other rainforests of Madagascar due to the lower competition with frugivores, high competition with the ecologically equivalent *Avahi*, and the high productivity of the forest in the period of food abundance.
2) has larger home ranges than other species of the same genus since fruits and flowers are more patchily distributed than leaves.
3) has smaller home ranges and longer daily distance travelled in the season of flower/fruit scarcity than in the season of flower/fruit abundance as a time-minimiser/area-minimiser strategy due to the strong resource seasonality and the prolonged season with flower/fruit scarcity.

4.2. Methods

4.2.1. Data collection

I collected data on five individuals (two adult males and three adult females) of Fleurette's sportive lemurs via continuous sampling (Altmann, 1974) for a total of 140.4 observation hours. In the season of scarcity of young leaves (March-August; see Figure 3.2), I collected 72.3 h, while in the season of abundance of young leaves (September-February) I collected 68.1 h. The total amount of hours of direct contact was 22.1 h on F-1, 5.5 h on F-2, 48.4 h on F-3, 49.5 h on M-1, and 14.9 on M-2. The data collection at the study site was particularly challenging and some areas were inaccessible during periods of heavy rain (September and October 2015 were the only months in which rainfall was below 100 mm; see Figure 2.4). To ensure systematic observations, I equipped the individuals with radio-collars (RI-2D, Holohil System Ltd, 11g; see Chapter 2.4) at the beginning of July 2015 and followed each individual from August 2015 to July 2016. An individual (LEPI-2) was killed by a fossa *Cryptoprocta ferox* at the beginning of September 2015. During behavioural observations, I collected data on activity (feeding, resting, moving) and food categories consumed (Mature Leaves, ML; Young Leaves, YL; Ripe Fruits, RP; Flowers: FL; Insects: I) (see Appendix IV). I collected lemur locations every hour via a handheld GPS (Garmin 60CSx).

Since observations were challenging in the study area, lemur locations were mainly collected via the triangulation method from July 2015 to June 2016. Firstly, I tagged the forest transects every 25 m and mapped each flag. To have a more accurate location and to reduce the error in collecting lemur locations via triangulation, I took ten GPS points with an error < 6 m for each flag and averaged them. I maintained triangulation angles between 30° and 150° (Gese, 2001) and I collected them every hour from dusk to dawn to gather independent data. I plotted bearings 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 in ArcMap.

4.2.2. Data analysis

To determine the diet of Fleurette's sportive lemur, I calculated the proportion of time spent feeding (in seconds) each food item over the total amount of time spent feeding and over the amount of time spent feeding in the two seasons. I calculated the total proportion of each food category in the diet during the entire year as well as during each season. I show the overall diet as the sum of data collected from all the individuals to overcome the different amount of time spent on each individual and the limited amount of behavioural observations. I consider preferred food items as the ones eaten more than 1% of the total feeding time (Donati et al., 2011a).

I calculated home ranges and daily travel distances (from dusk to dawn considering the locations obtained via triangulation) with the Home-Range Tools [HRT 2.0 (Rodgers & Kie, 2011)] for ArcMap 10.2.2 (ESRI, Redlands, CA). I used the 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. I employed the 100% MCP to show annual ranges because it is the most commonly reported method in the literature (Harris et al., 1990), although it is not effective in detecting differences for small-scale, within species, comparisons (Nilsen et al., 2008). Also, the MCP underestimates home ranges at small sample sizes (Downs & Horner, 2008) and overestimate home ranges at large sample sizes because of the inclusion of 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 via FK method is 30 and possibly 50 locations depending on the study species (Seaman et al., 1999). The FK analyses were performed with a bandwidth calculated using least-squares cross-validation that usually performs better than other methods (Seaman et al., 1999; Powell, 2000; Downs & Horner, 2008). Since I had small sample sizes, I performed an incremental area analysis (IAA) to determine whether annual ranges estimated via 100% MCP and 95% FK provided evidence of stability.

I ran a Repeated Measures (RM) ANOVA to evaluate differences in daily distance travelled with seasons (abundance/lean) as intra-subject factor and sex as between-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. I performed the test via SPSS v23 and considered $P < 0.05$ as significant level.

4.3. Results

4.3.1. Diet

The overall diet of *Lepilemur fleuretae* over one year included 26.3 % young leaves, 38.2 % mature leaves, 24.9 % flowers, 10.5 % ripe fruits, and 0.1 % insects. *Lepilemur fleuretae* during the lean season spent 21.0 % of time feeding on young leaves, 73.3 % of time feeding on adult leaves, and 5.7 % of time feeding on ripe fruits. Conversely, in the season of food abundance *L. fleuretae* spent 30.4 % of time feeding on young leaves, 13.5 % of time feeding on adult leaves, 42.3 % of time feeding on flowers, 13.6 % of time feeding on ripe fruits, and 0.2 % of time feeding insects (Table 4.1).

Table 4.1: Preferred food items of *Lepilemur fleuretae* at Ampasy. Plant species (vernacular and scientific names), food items, and proportion of time spent feeding by *L. fleuretae* at Ampasy in the lean season and in the period of food abundance. Only preferred food items (eaten >1 % of feeding time) are shown.

Vernacular name	**Scientific name**	**Food item^a**	**% of feeding time**	**Total feeding time (s)**
Lean season (March-August)				
Mendoravy	*Albizia* sp.	ML	27.4	17769
Mafotra	*Brochoneura acuminata*	ML	9.0	5842
Mendoravy	*Albizia* sp.	YL	8.1	5277
Mampay	*Cynometra* sp.	ML	7.0	4561
Taranta	*Micronychia bemangidiensis*	ML	6.9	4494
Voapaky	*Uapaca thouarsii*	YL	6.4	4152
Taolanambariky	*Rothmannia* sp.	RF	5.7	3697

Vernacular name	Scientific name	Food item[a]	% of feeding time	Total feeding time (s)
Lean season (March-August)				
Nanto	*Capurodendron* sp.	ML	5.6	3636
Bemavao	*Sarcostemma viminale*	YL	4.4	2852
Fanstykaitry	*Canthium medium*	ML	4.2	2721
Randrombitro	*Buddleja indica*	ML	3.5	2288
Voapaky	*Uapaca thouarsii*	ML	2.1	1369
Zora	*Scolopia erythrocarpa*	YL	2.1	1356
Taolanambariky	*Rothmannia* sp.	ML	2.0	1321
Valimafy	*Dombeya* sp.	ML	1.9	1236
Hafomena	*Dombeya oblongifolia*	ML	1.3	845
Taolana	*Hyperacanthus* sp.	ML	1.2	776
Vahimety	*Agelaea pentagyna*	ML	1.0	657
Abundance season (September-February)				
Mendoravy	*Albizia* sp.	FL	22.2	16423
Hendranendra	*Humbertia madagascariensis*	FL	20.2	15072
Voapaly	*Uapaca thouarsii*	YL	14.5	10809
Rotry	*Syzigium* sp.	RF	13.1	9765
Mampay	*Cynometra* sp.	ML	8.8	6572
Beranoampo	*Terminalia* sp.	YL	6.4	4773
Mafotra	*Brochoneura acuminata*	ML	4.5	3265
Mendoravy	*Albizia* sp.	YL	4.1	3059
Zora	*Scolopia erythrocarpa*	YL	2.9	2173
Hendranendra	*Humbertia madagascariensis*	YL	1.3	977

[a] YL=young leaves, ML=mature leaves, FL=flowers, RF=ripe fruits

4.3.2. Ranging patterns

The annual home ranges of Fleurette's sportive lemurs in Ampasy were 2.59-5.28 ha for females and 7.85-7.89 ha for males via MCP and 3.04-4.16 ha for females and 7.03-7.28 ha for males via FK (Table 4.2; Figure 4.1). The sample size for F-2 was too small to assess the annual home ranges via MCP and did not reach the asymptote via the incremental area analysis for the FK. The seasonal home ranges of Fleurette's sportive lemurs showed an opposite trend between sexes. On one hand, F-1 and F-3 showed a larger range via FK in the lean season (F-1: 4.45 ha, N = 54; F-3: 3.06 ha, N = 88) than in the season of food abundance (F-1: 2.93 ha, N = 54; F-3: 2.67 ha, N = 90). On the other hand, M-1 and M-2 showed a larger range via FK in the season of food abundance (M-1: 6.32 ha, N = 102; M-2: 7.15 ha, N = 66) than in the lean season (M-1: 6.07 ha, N = 140; M-2: 5.51 ha, N = 92).

The daily distance travelled by Fleurette's sportive lemurs were not different between the season of food abundance (758.4 ± SE 61.8 m) and the lean season (637.2 ± SE 35.9 m) (RM ANOVA, season: $F_{1,16} = 2.87$, $P = 0.112$). Males (863.6 ± SE 47.0 m, N = 20) had longer daily distance travelled than females (532.1 ± SE 53.3 m, N = 16) (RM ANOVA, sex: $F_{1,16} = 21.79$, $P < 0.001$). Males and females showed different responses between seasons (RM ANOVA, season*sex: $F_{1,16} = 5.68$, $P = 0.032$), with longer daily distance travelled in the season of abundance (1009.7 ± SE 81.8 m, N = 10) than in the lean season (717.6 ± SE 47.0 m, N = 10) for males (LSD post-hoc: $P = 0.006$) and no differences between seasons for females (abundance: 507.5 ± SE 92.8 m, N = 8, lean: 556.8 ± SE 53.4 m, N = 8, LSD post-hoc: $P = 0.341$).

Table 4.2: Home ranges of *Lepilemur fleuretae* at Ampasy. Home range comparison between the five individuals of Fleurette's sportive lemur at Ampasy. Data were collected from July 2015 to July 2016. GPS points were collected every hour.

		Annual home range size (ha)		
Individual[a]	**GPS points**	**MCP**	**95%FK**	**50%FK**
F-1	108	5.28 (60)	4.16 (68)	0.69
F-2	48	NA	2.77 (>)	0.68
F-3	178	2.59 (78)	3.04 (72)	0.76
M-1	242	7.89 (154)	7.03 (147)	1.55
M-2	158	7.85 (142)	7.28 (135)	1.72

[a] F=female; M=male

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.

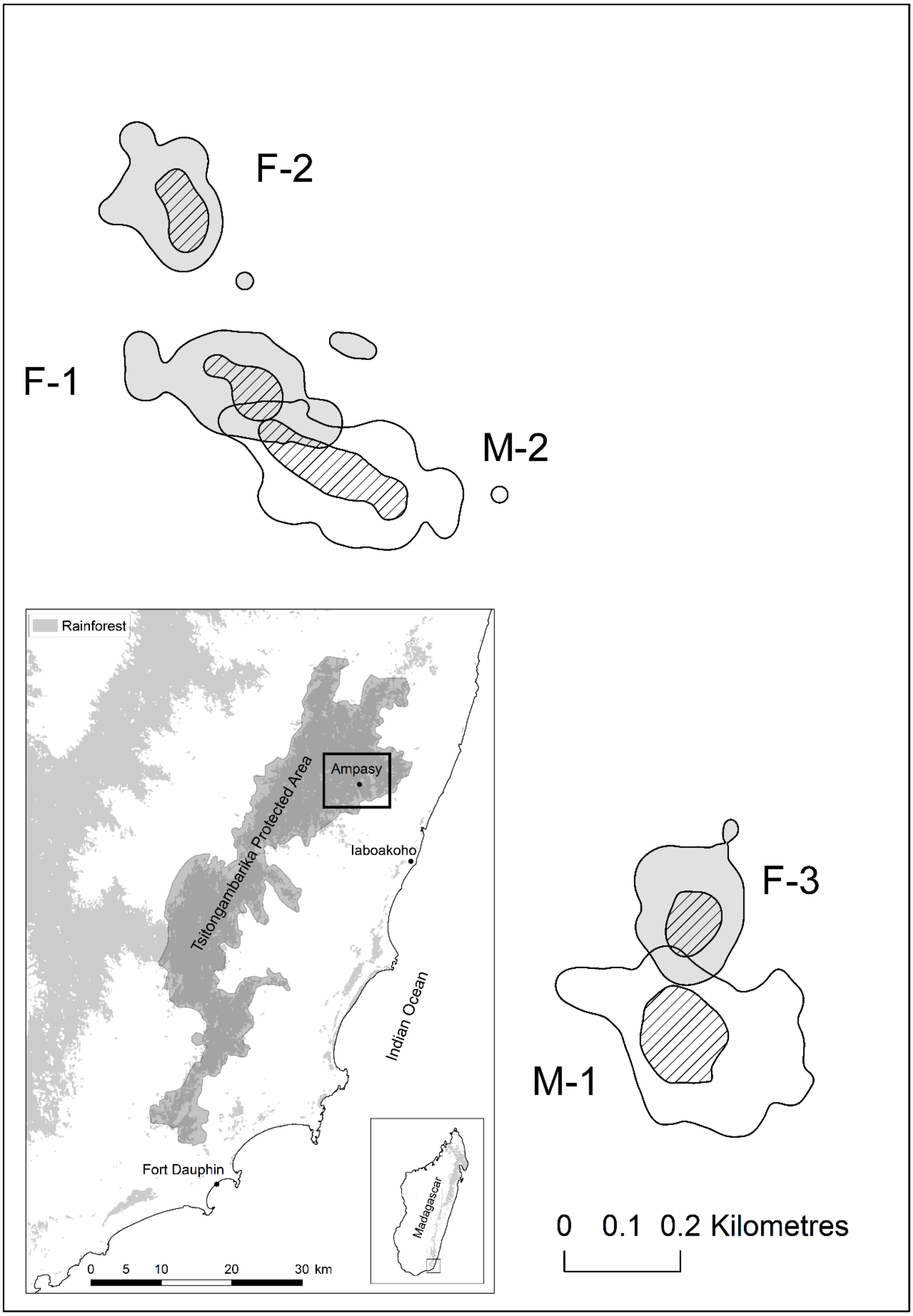

Figure 4.1: Home ranges of *Lepilemur fleuretae* at Ampasy. Home ranges and core areas are calculated via 95% and 50% FK respectively. Females are in grey background and males are in transparent background.

4.4. Discussion

4.4.1. Large home ranges and high amount of fruits and flowers in the diet

Fleurette's sportive lemur at Ampasy had larger home ranges than other sportive lemurs studied so far in Madagascar (Table 4.3). This may be due to the habitat type, since also in a mosaic of humid and deciduous forest *L. mittermeieri* had slightly larger home ranges than other sportive lemurs in deciduous or spiny forests (Wilmet et al., 2015). In fact, the home range of *L. fleuretae* at Ampasy is significantly higher than the mean value of the home ranges for all the other species of sportive lemurs, apart from *L. mittermeieri*, using a Z test for comparison. Also, fragmentation can be a concurring effect since sportive lemurs were mainly studied in small fragments [e.g. Berenty (Nash, 1999; Dröscher & Kappeler, 2013) and Kirindy (Hilgartner et al., 2012)], while the Ampasy area is part of an almost pristine area in the continuous rainforest of the TGK Protected Area. In fact, primates that include moderate to high amount of leaves in their diet tend to have smaller home ranges when living in small forest patches than in continuous forests [e.g. *Colobus vellerosus* (Wong & Sicotte, 2007); *Alouatta palliata* (Cristóbal-Azkarate & Arroyo-Rodríguez, 2007); *Propithecus diadema* (Irwin, 2008b)].

A possible factor in determining the large home range size in *L. fleuretae* is the high proportion of flowers and fruits in the diet when compared to other sportive lemurs (see Table 4.3). As predicted due to the low diversity of frugivorous lemur species in Tsitongambarika and the possible competition with *Avahi meridionalis*, *L. fleuretae* at Ampasy had a diet rich in flowers and fruits, especially in the season of food abundance. Flowers and fruits have a clumped distribution (Isbell, 2012), and this might have contributed to the large home ranges and long distances travelled per night, especially considering that *L. fleuretae* at Ampasy was highly selective on flowers and ripe fruits (i.e. *Syzigium* sp. and *Rothmannia* sp. were the preferred trees for ripe fruits, and *Albizia* sp. and *Humbertia madagascariensis* were the preferred trees for flowers). *Syzigium* sp. trees had a high food availability index at Ampasy, *Albizia* sp. and *Humbertia madagascariensis* trees had a medium availability, while *Rothmannia* sp. trees had a relatively low availability (see Appendix III). Most of the tree species selected by *L. fleuretae* for flowers and fruits were thus abundant, so the more clumped distribution of flowers and fruits than leaves might not explain entirely the large home ranges. Also, leaves change in their nutritional content and high-quality leaves are also patchily distributed and temporally variable (Snaith & Chapman, 2007). Thus, the competition for high-quality leaves with other folivores such as *Avahi meridionalis* may have further contributed to the large home ranges of *L. fleuretae* at Ampasy. An analysis of the distribution of the plant species is required to further investigate the level of clumpiness of preferred resources.

The diet of *L. fleuretae* was rich in flowers and fruits and was probably of a higher quality when compared to the diet of other more folivorous *Lepilemur* spp. (Clutton-Brock & Harvey, 1977; Mace & Harvey, 1983; Nash, 1998; Thalmann, 2001; Dröscher & Kappeler, 2014; Seiler et al., 2014; Dinsmore et al., 2016), and this might indicate that *L. fleuretae* at Ampasy had higher energy expenditure. This was indirectly confirmed by the distance travelled at night, that were longer in *L. fleuretae* at Ampasy (~700 m) than in the other species of the same genus for which this data is available: *L. edwardsi* at Ampijoroa [~350 m (Warren & Crompton, 1997a)], *L. ruficaudatus* at Morondava [~400 m (Ganzhorn et al., 2004)], and *L. ruficaudatus* at Kirindy [~600 m (Drack et al., 1999)]. Unfortunately, there are only a few studies that investigated the diet of sportive lemurs, while there is more information on ranging patterns, although mainly related to the investigation of the social structure in this genus. This is particularly true for sportive lemurs in rainforests where the feeding ecology of this genus is almost unknown. The dietary data presented in this study were also limited by the challenges of working in this habitat at night, and can only be considered as preliminary data although collected year-round. In fact, the sampling effort in terms of hour of direct contact with the animals in this study is lower than most of the other studies on sportive lemurs (Table 4.3). The sampling effort increases when considering the ranging patterns, with accurate data also highlighted by the Incremental Area Analysis. Also, the sample size in terms of number of individuals studied is low. For these reasons, the comparison of dietary patterns, and of ranging patterns to a minor extent, may be biased by the small sample size. More information is necessary to provide further insights on the relationship between the content of flowers and fruits and the home range sizes of sportive lemurs.

Table 4.3: Previous studies on diet and/or ranging patterns of sportive lemurs.

Species	Habitat	Home range (ha) Mean (Range)	Fruits + flowers (%)	Time span (mo)	N	Sample size (h)	Source
L. septentrionalis	Dry/deciduous	1.91 (1.32-2.90) [a]	14.5	2	4	60	Dinsmore et al., 2016
L. mittermeieri	Semi-humid	3.60 (0.40-5.68) [a]	NA	4	4	NA	Wilmet et al., 2015
L. sahamalazensis	Dry/deciduous	0.38 (0.18-4.04) [b]	0.4	9	8	321	Seiler et al., 2014, 2015
L. edwardsi	Dry/Deciduous	1.09 (0.67-1.70) [b]	NA	18	4	~280	Warren & Crompton, 1997a
L. edwardsi	Dry/Deciduous	~1.00 (0.57-1.10) [b]	5.5	35	7	254	Thalmann, 2001, 2006
L. edwardsi	Dry/Deciduous	2.10 (1.49-4.10) [b]	NA	12	12	1080	Méndez-Cárdenas & Zimmermann, 2009
L. ruficaudatus	Dry/Deciduous	~0.80 [a]	NA	24	16	~2000	Hilgartner et al., 2012
L. ruficaudatus	Dry/Deciduous	0.25 (0.10-0.48) [b]	NA	2	11	NA	Drack et al., 1999
L. leucopus	Spiny	~0.25 [a]	5.0	12	14	1530	Dröscher & Kappeler, 2013, 2014
L. petteri	Spiny	NA	~11.0	7	5	NA	Nash, 1998
L. fleuretae	Rainforest	5.38 (3.04-7.28) [a]	35.4	12	5	140.4 (diet), 734 (ranges)	This study

[a] home range calculated via 95% FK, [b] home range calculated via 100% MCP. N: number of individuals

4.4.2. Seasonal variations in ranging patterns

Males and females *L. fleuretae* showed a different seasonal ranging pattern, with males that expanded their range and had longer daily distances travelled during the season of food abundance and females showing the opposite pattern. This suggests that males minimised their daily expenditure when food is scarce, as previously found in other lemur species [*Lemur catta* (Kelley, 2013); *Eulemur collaris* (Campera et al., 2014)]. An energy conservation strategy may be important for this lemur species due to its low metabolism and to the strong seasonal variations in Madagascar (Wright, 1999). A time minimiser strategy for males *L. fleuretae* was also indicated by them travelling shorter distances during the lean season (Schoener, 1971; Hixon et al., 1982). In terms of ranging patterns, however, males *L. fleuretae* did not act exactly as area-minimisers because the overall area is larger in the season of abundance (Mitchell & Powell, 2004). This may be a strategy to store energy during the season of food abundance while saving energy during the lean season, as previously found in *L. ruficaudatus* (Ganzhorn, 2002). Conversely, females *L. fleuretae* did not have different daily distance travelled between lean and abundance periods, while they had larger home ranges in the lean period, acting as area-minimisers but not as time-minimisers. This might be related to the high expenses faced during lactation, particularly challenging in this species since there is no male parental care as in other sportive lemurs (Kappeler, 2014). Females during the lactation (September-November) usually parked their infants and foraged in proximity to the infant, hence not travelling long distances.

4.4.3. Social structure

Although I do not have specific information to understand the social structure of *L. fleuretae*, my data suggest that this species has a dispersed one-male multi-female social system at Ampasy. In fact, the home ranges of males were around twice the size of the home ranges of females. Sportive lemurs with the least cohesive dispersed-pair social system had a difference in home range size between males and females [0.18 ha for female and 0.33 ha for male *L. leucopus* (Dröscher & Kappeler, 2013)]. Conversely, dispersed-pair sportive lemurs with higher cohesiveness usually show overlapping home ranges with a similar size between males and females and a considerable amount of time spent in pairs, including sleeping in pairs (Zinner et al., 2003; Méndez-Cárdenas & Zimmermann, 2009; Hilgartner et al., 2012). During behavioural observations, I rarely reported animals in proximity and they never shared sleeping sites; I thus expect *L. fleuretae* to be solitary foragers and to sleep alone contrary to other *Lepilemur* spp. that live in pairs [e.g. *L. edwardsi* (Thalmann, 2006; Méndez-Cárdenas & Zimmermann, 2009); *L. ruficaudatus* (Hilgartner et al., 2012)]. The social structure of sportive lemurs, however, can vary even among the same species in the same area from dispersed-pair to dispersed one-male multi-female (Warren & Crompton, 1997a; Thalmann, 2001) or from pair-living to dispersed-pair (Zinner et al., 2003; Hilgartner et al., 2012). To provide more insight on the social organisation of *L. fleuretae* in Tsitongambarika it may be necessary to develop a study on ranging patterns and vocalisations of more individuals (Seiler et al., 2013b). It seems, however, from the information available, that *L. fleuretae* has a dispersed harem social structure, with solitary foraging and almost no interaction between sexes. The most similar species of sportive lemur to *L. fleuretae* is the *L. leucopus* in which males have larger home ranges than females, possibly to maintain a pair bond while seeking for extra copulations (Dröscher & Kappeler, 2013). This species, however, exhibits some social interaction with the other sex and can be defined as dispersed pairs (Dröscher & Kappeler, 2013), while I rarely encountered *L. fleuretae* at Ampasy interacting with the other sex during behavioural observation or other activities in the forest. The only report of an interaction between more individuals was feeding on flowers on the same tree of *Humbertia madagascariensis.* Also, two females, both with infants (around 2-weeks old), rested in the same tree for around 1h and groomed each other. Rarely, individuals of *L. fleuretae* were encountered in pairs during transects for density estimates (M. Balestri, unpub. data). However, due to the limited amount of hours of behavioural observations, I might have missed important social interactions between individuals, and I did not manage to collect data on mating behaviours that may have given more information on the social structure of the species.

4.4.4. Conclusions

The feeding behaviour and the ranging patterns of Fleurette's sportive lemurs at Ampasy provided interesting insights since it appears that sportive lemurs in rainforests may have a different behavioural ecology than the sportive lemurs in dry and deciduous forests. Fleurette's sportive lemur at Ampasy, in fact, had a considerably higher amount of fruits and flowers in their diet than the counterparts in other habitats. Also, the ranging patterns differed from other sportive lemurs, with larger home ranges and longer daily distances travelled. Although my data are not adequate to explore this aspect, the social structure of sportive lemurs at Ampasy may be different from the one of most other sportive lemurs and the species appears to live in a dispersed one-male multi-female social system. Further studies are required to clarify the social structure and the behavioural ecology of this genus in rainforests, and the extent of its behavioural flexibility.

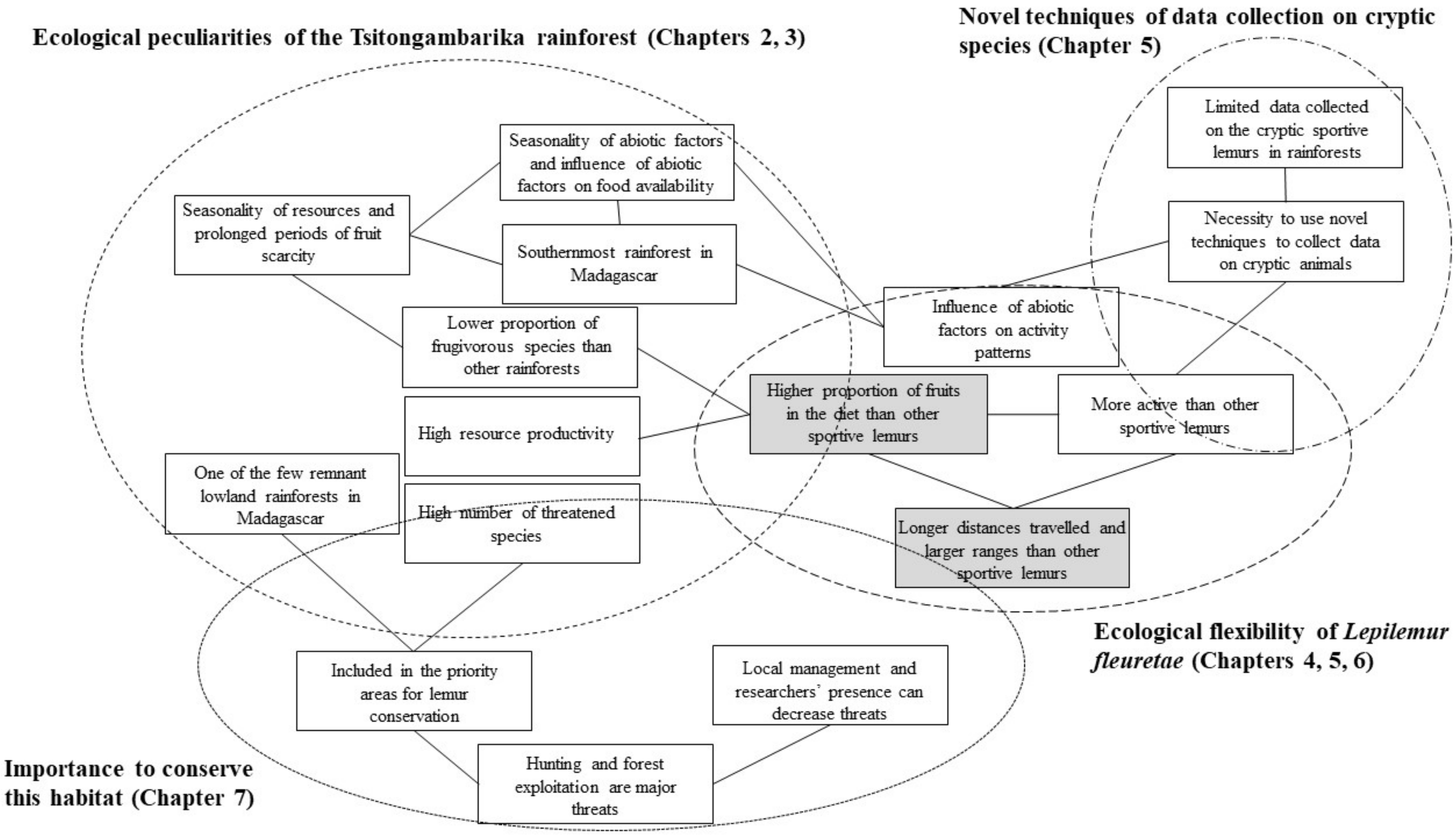

Figure 4.2: Word flowchart representing the topics of Chapter 4. Topics highlighted in grey.

Chapter 5. A novel approach to study activity patterns of cryptic primates: unsupervised learning algorithm for data from three-axis accelerometer tags.

In this chapter, I explore the potential of a novel method, the unsupervised learning algorithm on accelerometer data, to extrapolate activity patterns in cryptic animals. I discuss the advantages of this method when a low amount of behavioural observations is available. I then compare the activity patterns of Fleurette's sportive lemur at Ampasy with the activity patterns of other sportive lemurs and discuss the hyperactivity of Fleurette's sportive lemur. The hyperactivity is in line with what found on dietary and ranging patterns in the previous chapter.

5.1. Introduction

Direct observations are the main method employed to collect animal behaviours, although providing reliable data in wild animals is frequently challenging (Brown et al., 2013). In fact, direct observations require a habituation period that varies depending on the species and may last for years (Jack et al., 2008, Crofoot et al., 2010). The observer is rarely undetectable and even habituated animals may still change their behaviour in latent ways (Caine, 1990). Direct observations are also biased by intra-subject methodological differences (Altman, 1974). Furthermore, many animal species are cryptic and the amount of data collectable via behavioural observations may be very limited (Chimienti et al., 2016).

To face the difficulties of direct observations, automatic loggers have been widely used recently for several applications: ranging patterns (Lucas & Baras, 2000; Gibbons & Andrews, 2004), energy expenditure (Cooke et al., 2004), activity (van Oort, 2004), body temperature (Dausmann, 2005), and other body parameters (Cooke et al., 2013a). Also, automatic loggers are often employed to collect environmental data (Cooke et al., 2013b). As for automatic loggers to record activity, the use of three-axis accelerometers has been recently recognised as a powerful tool to register animal behaviours (Shepard et al., 2008; Brown et al., 2013), to describe activity patterns (Sakamoto et al., 2009), and to investigate energy expenditures (Halsey et al., 2009, 2011).

Despite the efficiency of this method to gather fine-grained data, the analysis of accelerometer data is not always simple and different methods have been employed, broadly classified in supervised and unsupervised learning algorithms (Sakamoto et al., 2009; Brown et al., 2013; Gris et al., 2017). Most of the studies used supervised learning algorithms to extrapolate behaviours from accelerometer data (Brown et al., 2013). In the supervised learning algorithm, it is required to manually associate part of the accelerometer data with the corresponding behaviour to create the training data necessary for the algorithm to operate. After this first stage, the algorithm [e.g. K-Nearest Neighbour algorithm (Bidder et al., 2014)] is ran to match the training data with the rest of the dataset. In spite of the relatively simple use of this method, also due to the availability of a new user-friendly software (Brown et al., 2013), the use of this approach is somehow limited by several issues. The first issue is that this approach requires extended *a priori* knowledge on the behaviours of the species, or large dataset to match behavioural data with accelerometer data. These conditions make this approach not suitable for cryptic species for which behavioural observations are challenging (Chimienti et al., 2016). The second issue is that the identification of behaviours depends on thresholds that are species-specific (Gómez Laich et al., 2008). The training data and the algorithms used on a related species may thus not be applied to obtain reliable activity estimations on a different study species. Thus, a validation of the algorithm using behavioural data on the study species is necessary. The third issue is that more advanced accelerometers allow collection of data at high rates [up to 300 Hz (Bidder et al., 2014)] and for a prolonged amount of time (up to one year if the data collection is at a frequency of 1 Hz). This produces a massive amount of data, making the manual identification of behavioural patterns difficult (Resheff et al., 2014). Finally, the same behaviour might be associated with different combinations of accelerometer data, thus each behaviour should be linked to all the possible accelerometer data to avoid misleading interpretations of the results (Gris et al., 2017).

Due to the limited applications of the supervised learning algorithms, especially in cryptic animals, the use of unsupervised learning algorithms has been recently suggested as a method to classify accelerometer data (Sakamoto et al., 2009; Brown et al., 2013; Chimienti et al., 2016; Gris et al., 2017). These algorithms automatically group the accelerometer data into different clusters based on statistical functions. The first approach used the unsupervised algorithm k-means to identify general behaviours in the European shag *Phalacrocorax aristotelis* (Sakamoto et al., 2009). This approach, however, is limited in terms of number of behaviours recognised and amount of data that this algorithm can handle (Chimienti et al., 2016). Also, the k-means clustering always gives different outputs with the same dataset since it does not estimate the optimized solution [i.e. the best results based on statistical model criteria (Sakamoto et al., 2009)]. Recently, the unsupervised learning algorithm Expectation Maximisation (EM) had been successfully used to identify latent behaviours in two seabirds: the common guillemot *Uria aalge* and the razorbill *Alca torda* (Chimienti et al., 2016). This algorithm overcomes the problems related to the k-means clustering since it allows the analysis of a large dataset and estimates an optimised solution based on the Bayesian Information Criterion (BIC) and the Akaike Information Criterion (AIC).

The use of accelerometers in primates is limited to a few studies that used accelerometers as activity sensors to estimate the percentage of activity based on cumulative locomotor counts over a period (called “epoch”) of usually 5 minutes (Erkert & Kappeler, 2004; Fernandez-Duque & Erkert, 2006). Using these devices (Actiwatch is the most popular), it is only possible to obtain a proportion of activity, while it is not possible to obtain the raw data over the three axes. For this reason, it is not possible to run supervised or unsupervised learning algorithms, and it is only possible to obtain activity/inactivity profiles. Recent studies that used Actiwatch, however, started developing algorithms to extrapolate more behaviours from the raw data collected by these accelerometers. Another issue related to Actiwatch is that it has been mainly validated in humans for different purposes (Morgan et al., 2012; Landry et al., 2015), and the parameters used to obtain activity/inactivity profiles may not be reliable for some animal species, validation is thus necessary.

The aim of this study is to test the efficiency of the unsupervised learning algorithm EM to extrapolate basic behaviours of cryptic primates. For this purpose, I used three-axis accelerometers to gather data every second over a period between two and three months on three individuals of *Lepilemur fleuretae* in the lowland rainforest of Ampasy, in the Tsitongambarika Protected Area (TGK). I validated the efficiency of the EM algorithm by comparing the profiles obtained via this analysis and the data collected via continuous behavioural observations.

5.2. Methods

5.2.1. Data collection

Details on accelerometer data collection, animal captures, and ethics statement are in Chapter 2.

5.2.2. Data preparation

I calculated variables derived from the raw accelerometer data since it has been suggested that the inclusion of integrated variables in the EM algorithm allows a more reliable calculation than the inclusion of raw data (Wang et al., 2015; Chimienti et al., 2016). The integrated variables calculated were: static acceleration over the three axes, dynamic acceleration over the three axes, amplitude (i.e. standard error) of the dynamic acceleration over the three axes, pitch (i.e. vertical orientation of the body angle), amplitude of the pitch, and Overall Dynamic Body Acceleration (ODBA; i.e. sum of the dynamic acceleration over the three axes). The integrated variables were calculated with a smoothing factor of 10 s as suggested in the previous study that employed the EM algorithm with accelerometer data (Chimienti et al., 2016). I tested the EM with different combinations of variables and parameters to empirically verify which combinations were more suitable to extrapolate the behaviours. To do this, I selected a small portion of the dataset (6 h) where I had direct observations to compare and ran different algorithms to see which one better suited the data. The variables dynamic acceleration over the three axes, amplitude of the dynamic acceleration over the three axes, and amplitude of the pitch resulted the ones more suitable to obtain the behaviours of *L. fleuretae* in this study. The integrated variables were calculated via the package “plotrix” for R software (see Appendix V).

5.2.3. Data analysis and validation

The EM algorithm is based on Gaussian Mixture Models and the package "Rmixmod" for R software was necessary for the analysis (Biernacki et al., 2006). The EM algorithm alternates between two steps called E step, in which the algorithm calculates posterior probability distributions based on input variables, and M step, in which the algorithm re-estimate input variables and associate them in clusters (Biernacki et al., 2003; Chimienti et al., 2016). The algorithm alternates these two steps to increase the log-likelihood until convergence based on BIC and AIC criteria (see Appendix VI).

For each dataset, I ran three different EM algorithms with the following variables and clustering: 1) dynamic acceleration over the three axes and amplitude of the dynamic acceleration over the three axes with two clusters (active/inactive); 2) in the active cluster, dynamic acceleration over the three axes and amplitude of the dynamic acceleration over the three axes with three clusters (inactive/low-intensity activity/high-intensity activity); 3) in the low- and high-intensity activity clusters, amplitude of the pitch with four clusters (to discern grooming from other active behaviours). The third algorithm was added after the validation with behavioural data. I selected the amplitude of the pitch as variable in the EM algorithm since the body orientation is expected to have a very small variation in the pitch compared to the other active behaviours.

To validate behavioural data, I compared the data obtained via the EM algorithm after the first two steps with the behavioural data obtained simultaneously via 23.2 h of continuous sampling (excluding out of sights) on the three animals. I calculated the percentage of correspondence with the main behaviours (resting, grooming, feeding, and moving) for each cluster. Values of correspondence shown in the results are minimum and maximum values for the three individuals.

5.3. Results

5.3.1. Inactivity, low-intensity activity, and high-intensity activity

The results of the first two EM algorithms indicated a clear division into three main clusters: inactivity, low-intensity activity, and high-intensity activity. The clusters were based mainly on the variance of the dynamic acceleration over the three axes and the mean amplitude over the three axes. From the first EM algorithm, I obtained the “Inactivity” that has a variance of the dynamic acceleration over the three axes of 0.0 cm/s^2 for the three individuals, a mean amplitude of 0.1 cm/s^2 over the X and Y axes, and a mean amplitude of 0.2 cm/s^2 over the Z axis (Table 5.1). In the “Activity” cluster of the first algorithm, the second algorithm highlighted another cluster with “Inactivity, with the variance of the dynamic acceleration over the three axes of 0.1 cm/s^2 for the three individuals, and the mean amplitude of 0.8-0.9 cm/s^2 over the X axis, 0.8-1.0 cm/s^2 over the Y axis, and 1.1-1.3 cm/s^2 over the Z axis. The activity clusters were divided in “Low-intensity activity” and “High-intensity activity”. The first cluster had the variance of the dynamic acceleration of 0.7-0.9 cm/s^2 over the X axis, 1.1-1.3 cm/s^2 over the Y axis, and 1.1-1.5 cm/s^2 over the Z axis. The mean amplitude of the cluster “Low-intensity activity” was 2.4-2.8 cm/s^2 over the X axis, 2.9-3.2 cm/s^2 over the Y axis, and 2.9-3.4 cm/s^2 over the Z axis. The variance of the dynamic acceleration of the cluster “High-intensity activity” was 4.7-6.6 cm/s^2 over the X axis, 6.0-6.4 cm/s^2 over the Y axis, and 8.0-9.8 cm/s^2 over the Z axis. The mean amplitude of the cluster “High-intensity activity” was 4.9-5.9 cm/s^2 over the X axis, 5.4-5.6 cm/s^2 over the Y axis, and 5.8-6.4 cm/s^2 over the Z axis.

Table 5.1: Results of the Expectation Maximisation (EM) algorithm. Parameters obtained via the EM algorithms to obtain clusters for the behaviours of *Lepilemur fleuretae*. Inactivity (1) indicates that the values are retrieved from the first algorithm, while Inactivity (2) is retrieved from the second algorithm. Values are means and variances (in brackets) and unit is cm/s^2.

	Female 1	**Female 2**	**Male**
Inactivity (1)			
Dynamic X	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Dynamic Y	0.0 (0.0)	-0.0 (0.0)	-0.0 (0.0)
Dynamic Z	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Amplitude X	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)
Amplitude Y	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)
Amplitude Z	0.2 (0.0)	0.2 (0.0)	0.2 (0.0)
Inactivity (2)			
Dynamic X	0.1 (0.1)	0.1 (0.1)	-0.0 (0.1)
Dynamic Y	0.4 (0.1)	-0.3 (0.1)	-0.2 (0.1)
Dynamic Z	0.2 (0.1)	0.1 (0.1)	0.3 (0.1)
Amplitude X	0.8 (0.0)	0.9 (0.0)	0.8 (0.0)
Amplitude Y	1.0 (0.0)	0.8 (0.0)	0.9 (0.0)
Amplitude Z	1.1 (0.0)	1.3 (0.0)	1.2 (0.0)
Low-intensity activity			
Dynamic X	0.1 (0.7)	0.1 (0.8)	-0.2 (0.9)
Dynamic Y	-0.3 (1.2)	0.3 (1.3)	0.6 (1.1)
Dynamic Z	0.9 (1.1)	0.6 (1.4)	0.9 (1.5)
Amplitude X	2.4 (0.0)	2.4 (0.0)	2.8 (0.0)
Amplitude Y	3.0 (0.0)	3.2 (0.0)	2.9 (0.0)
Amplitude Z	2.9 (0.0)	3.2 (0.0)	3.4 (0.0)
High-intensity activity			
Dynamic X	-0.2 (5.0)	-0.3 (4.7)	0.2 (6.6)
Dynamic Y	0.1 (6.2)	-0.2 (6.4)	-0.6 (6.0)

	Female 1	**Female 2**	**Male**
High-intensity activity			
Dynamic Z	-1.3 (8.0)	-0.9 (9.3)	-1.2 (9.8)
Amplitude X	5.2 (0.1)	4.9 (0.1)	5.9 (0.1)
Amplitude Y	5.6 (0.1)	5.6 (0.1)	5.4 (0.1)
Amplitude Z	5.8 (0.1)	6.3 (0.1)	6.4 (0.1)

5.3.2. Validation with behavioural data

The EM algorithm was efficient in determining the "Inactivity" cluster, that had a correspondence of 98.2-99.3 % (N = 3 animals) with resting obtained via behavioural observations. The other behaviours in the "Inactivity" clusters were feeding (0.4-1.0 %, N = 3 animals) and grooming (0.3-0.8 %, N = 3 animals). The "Low-intensity activity" cluster corresponded mainly with feeding behaviour (47.6-56.8 %, N = 3 animals), although moving (29.3-32.5 %, N = 3 animals) and grooming (14.9-19.9 %, N = 3 animals) were included in this cluster. The "High-intensity activity" cluster corresponded mainly with moving behaviour (88.2-93.6 %, N = 3 animals) with partial correspondence with feeding (3.2-5.2 %, N = 3 animals) and grooming (3.2-6.6 %, N = 3 animals) behaviours.

5.3.3. Grooming cluster and activity profiles

In the EM algorithm meant to isolate grooming from the activity cluster, the mean amplitude of the pitch for the grooming behaviour was 0.345 (variance: 0.020) degrees for female 1, 0.348 (variance: 0.021) degrees for female 2, and 0.358 (variance: 0.024) degrees for the male. The activity profiles of the three animals are shown in Figure 5.1.

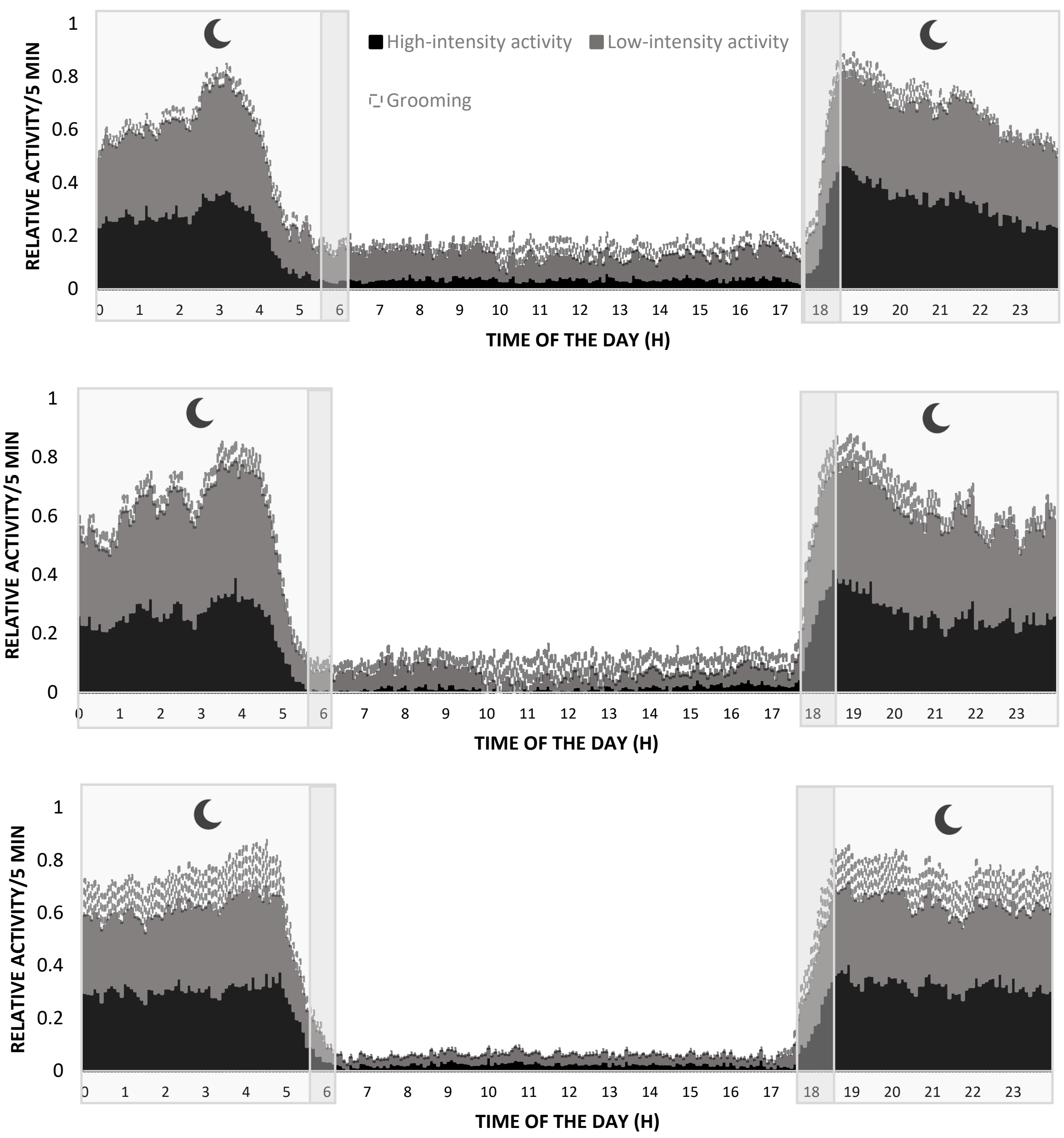

Figure 5.1. Activity profiles obtained via the Expectation Maximisation (EM) algorithm. Activity profiles of female 1 (above), female 2 (middle), and male (below) *Lepilemur fleuretae*. Night time (with sunrise/sunset variation) is in grey background. Data are average values at 5-min intervals for the period in which accelerometer data were collected: 07/07/2015 to 13/09/2015 (69 days) for female 1, from 07/07/2015 to 02/10/2015 (89 days) for female 2, and from 09/07/2015 to 29/09/2015 (83 days) for the male. See Table 5.1 for the categories obtained via the EM algorithm.

5.4. Discussion

5.4.1. Efficiency of the EM algorithm

From the results of this study, it is evident that the EM algorithm is efficient in differentiating between activity and inactivity, although more efforts should be made to extrapolate further behaviours. I found two different "inactivity" clusters that may represent the sleeping and the resting sessions respectively. The sleeping patterns of primates have been investigated with the Actiwatch before (e.g. Berro et al., 2016). The method presented in this study may represent an alternative to study sleeping patterns after a validation. Types of locomotion should be feasible to extrapolate since they are expected to have different amplitudes over the three axes based on the available information from behavioural observation on sportive lemurs. For example, leaping is expected to have a large variation over the X axis while almost no variation over the Y and Z axis; climbing is expected to have a moderate variation over the Y axis and almost no variation over the X and Z axis; jumping is expected to have a moderate variation over the three axes. Overall, leaping is expected to be at high intensity and with a higher energy expenditure than the other locomotion types (Warren & Crompton, 1998), thus I expect leaping to represent the main type of locomotion in the "High-intensity activity" cluster. It is necessary to implement the algorithm to extrapolate different locomotion types within the activity clusters. I plan to collaborate with specialists who developed the unsupervised learning algorithm on different species of birds to extrapolate more information from the data collected. Conversely, feeding behaviour is not easy to detect since it largely varies depending on the food item and on the substrate. Supervised learning algorithms, coupled with detailed behavioural information, might provide more insights than unsupervised learning algorithms to extrapolate different feeding behaviours. In fact, feeding behaviour can be associated with different combinations of accelerometer data, and detailed behavioural observations are required to match accelerometer data (Gris et al., 2017). The unsupervised learning algorithm, based on statistical differences between curves, may thus not provide the mean to discern feeding behaviour. I did not pursue further the extrapolation of behaviours since it would have required additional time (I expect I will need another 6 months at least based on previous works on other animals), and this was not the main topic of my dissertation.

I suggest that the algorithm used in this study is possibly more efficient in detecting activity profiles than the software that has been used in previous studies to extrapolate data from Actiwatch loggers in primates (e.g. Erkert & Kappeler, 2004; Fernandez-Duque & Erkert, 2006). With around 99% of correspondence between inactivity detected in this study via the algorithm and the inactivity detected via behavioural observations, the EM algorithm represents a fine-grained solution to study activity patterns in primates. The validation of Actiwatch with direct observations on other animals gave different values [~97% accuracy to detect inactive behaviour in the reindeer *Rangifer tarandus* (Van Oort et al., 2004); ~98% accuracy to detect resting behaviour in the rocky mountain elk *Cervus elaphus nelsonii* (Naylor & Kie, 2004); ~75% accuracy to detect inactivity behaviour in the sheep *Ovis aries* (McLennan et al., 2015)]. Other studies found a strong correlation between activity data from Actiwatch and behavioural observations (e.g. Muller & Schrader). Unfortunately, there is no validation of Actiwatch on primate species, while it would be appropriate to validate with direct observations the activity patterns obtained via this software. Actiwatch has been extensively validated in humans for different purposes (e.g. Morgan et al., 2012; Landry et al., 2015). It is necessary, however, to validate also the method presented in this study in several primate species to confirm the efficiency of the EM algorithm in detecting primate behaviours. For this purpose, species with different locomotion types should be compared, and diurnal species should be initially preferred for this comparison since collecting detailed behavioural data is usually more feasible than in nocturnal species. Also, it would be interesting to investigate the efficiency of accelerometers to extrapolate social behaviours (e.g. aggressive interactions, play, mating) since very limited literature is present on the application of accelerometers to studies on social behaviour (Brown et al., 2013). The same methodology used for *L. fleuretae* has been validated on four individuals of southern woolly lemur *Avahi meridionalis* with similar results (M. Balestri, unpub. data). However, since woolly lemurs are not the scope of this dissertation, the data have not been reported in this chapter.

5.4.2. Comparison of activity profiles

A comparison of activity profiles suggests that *L. fleuretae* at Ampasy was particularly active, spending less time resting at night (around 30%; see Figure 5.1) than other sportive lemurs [around 40% for *L. edwardsi* at Ampijoroa (Warren & Crompton, 1997a); around 50% for *L. petteri* at Beza Mahafaly (Nash, 1998); around 45% for *L. sahamalazensis* at Sahamalaza (Ruperti, 2007); around 65% for *L. septentrionalis* at the Montagne des Français (Dinsmore et al., 2016)].

Time spent moving at night by *L. fleuretae* at Ampasy (around 30% considering both "low-intensity activity" and "high-intensity activity" clusters and the validation with behavioural data; see Figure 5.1 and Chapter 5.3.2) was also higher than the other sportive lemurs [around 25% for *L. edwardsi* at Ampijoroa (Warren & Crompton, 1997a); around 13% for *L. petteri* at Beza Mahafaly (Nash, 1998); around 15% for *L. sahamalazensis* at Sahamalaza (Ruperti, 2007); around 12% for *L. septentrionalis* at the Montagne des Français (Dinsmore et al., 2016)].

The "high-intensity activity" and "low-intensity activity" clusters represented around 2% and 5% of activity during the day respectively, suggesting occasional leaping and possible feeding during the day. Self-grooming was also present during the day, suggesting vigilance during the day as previously reported on other species (Charles-Dominique & Hladik, 1971; Ruperti, 2007; Seiler et al., 2013b). Interestingly, the two females of *L. fleuretae* spent more time grooming and "low-intensity activity" than the male during the day (see Figure 5.1). This is probably the consequence of the data collection period, which included the gestation period for females. The movements reported for females during the day may thus include lactating and allogrooming the infant. It is interesting to report the fine-grained details possible to get via the EM algorithm on accelerometer data, even though the algorithm can still be implemented.

5.4.3. Future applications

Possible future applications may involve estimations of energy expenditure via ODBA as previously reported in many studies [see Brown et al. (2013) for a review]. In fact, it has been shown that the ODBA is correlated to the oxygen consumed across a wide range of animal species, becoming a common proxy of energy expenditure (Halsey et al., 2009, 2011). Another possible application of the accelerometers is to derive fine-grained animal's position via dead-reckoning which uses speed and change in height or depth coupled with a known start position (e.g. release point) to derive new positions (Wilson et al., 2008). However, factors such as terrain inclination can affect the calculation and lead to accumulated errors; thus, the application of accelerometers to estimate animal's position has several limitations and the use of GPS loggers to calibrate multiple times the position derived via dead-reckoning is advisable (Brown et al., 2013).

5.5.4. Conclusions

The use of three-axis accelerometers in primatology can provide detailed information and it is particularly useful for cryptic species, for which behavioural observations are challenging. The potential analyses with accelerometer data are significant, and it is recommended to apply the techniques already employed in other animal species to primates. The EM algorithm resulted a fine-grained technique to analyse a massive dataset and obtain reliable behavioural categories. The main achievement gained so far is the possibility to obtain very accurate activity profiles, and there is high potential to obtain more information, especially on the different types of locomotion. From the activity profiles, it is evident that *L. fleuretae* at Ampasy is more active than the other species of sportive lemurs studied so far. It is necessary to validate this method on several primate species, and diurnal species can potentially provide enough data for a very detailed validation since it is more feasible to collect a large amount of data via behavioural observations on them.

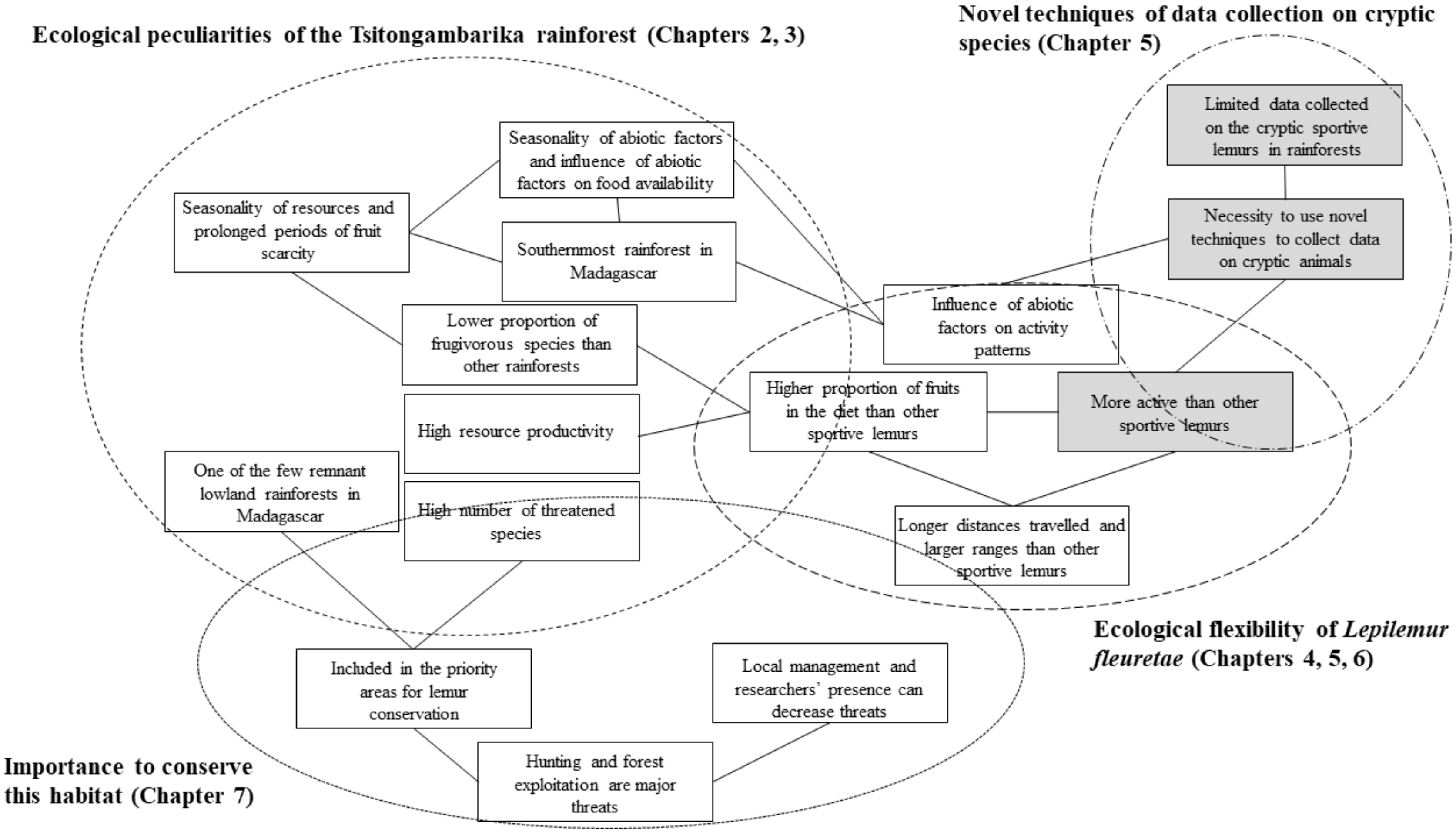

Figure 5.2: Word flowchart representing the topics of Chapter 5. Topics highlighted in grey.

Chapter 6. Influence of the proximate factors nocturnal luminosity and photoperiodic changes on the activity of the nocturnal *Lepilemur fleuretae*.

In this chapter, I am going to explore whether the activity of Fleurette's sportive lemur at Ampasy is influenced by nocturnal luminosity and photoperiodic changes. I use data collected via accelerometers and analysed with the unsupervised learning algorithm, a novel method I validated in the previous chapter. By looking at the strong seasonal patterns at Ampasy, highlighted in chapter 3, I now want to explore whether photoperiodic variations influence the activity of the species. Photoperiodic variations are, in fact, the main Zeitgeber influencing activity in habitats with seasonal and predictable food availability. Fleurette's sportive lemurs are also expected to show lunarphobia as an anti-predatory strategy due to the presence of a full set of predators at Ampasy.

6.1. Introduction

Activity patterns of animals are endogenously generated by biological clocks and empowered with mechanisms that allow adaptation to environmental challenges (Refinetti, 2016). Activity patterns rely on endogenously fixed rhythms that can be circadian (i.e. over the 24-h) and circannual (i.e. over the calendar year) (Aschoff, 1979). Circadian and circannual rhythms are shaped by predictable environmental factors, called Zeitgebers, such as photoperiodic variations, or by less predictable factors that may override the main rhythm, called masking factors, such as food quality and availability, weather conditions, nocturnal luminosity, predation, and anthropogenic disturbance (Daan & Aschoff, 1982; Halle & Stensteth, 2000; Donati et al., 2009, 2016; Brivio et al., 2017).

Photoperiodic variation is an important Zeitgeber, especially for animals living far from the equator and that experience seasonal variations in daylength and climate (Brockman & van Schaik, 2004). The endogenous clock is influenced by light that synchronises activity to the photoperiod; thus, activity is usually strongly affected by variations in sunrise and sunset (Aschoff, 1966; Aschoff et al., 1982; Erkert, 1989; Reppert & Weaver, 2002). Photoperiodic variations are important in Malagasy lemurs due to the strong seasonality in the island (Wright, 1999; Ganzhorn et al., 2003; Federman et al., 2017). In fact, photoperiodic variation has been demonstrated to function as main Zeitgeber for a variety of cathemeral lemur species (Kappeler & Erkert, 2003; Donati & Borgognini-Tarli, 2006; Donati et al., 2009), as well as an important factor in determining activity in diurnal and nocturnal lemurs (Petter-Rousseaux, 1980; Erkert & Kappeler, 2004). This is in contrast with the hypothesis that Madagascar has unpredictable environments and fruiting patterns are unreliable (Dewar & Richard, 2007). There is probably a difference between sites in terms of predictability of resource availability, and photoperiod may be the main Zeitgeber in seasonal/predictable environments, while it may have a limited influence on the activity of animals in aseasonal/unpredictable environments (Curtis & Donati, 2013).

The activity of nocturnal prey species is usually affected by the intensity of nocturnal illumination due to its correlation with predation risk (Beier, 2006; Prugh & Golden, 2014). At high luminosity conditions, nocturnal prey species can decrease activity to reduce predation risk [lunarphobia (Nash, 2007; Saldaña-Vásquez & Munguía-Rosas, 2013; Upham & Haffner, 2013)] or increase activity to increase foraging efficiency and have a better visual detection of predators [lunarphilia (Gursky, 2003; Donati et al., 2009; Brivio et al., 2017)]. The choice of one of these two strategies is thus determined by the balance between costs (increased vulnerability to predation) and benefits (improved detection of food and predators) (Prugh & Golden, 2014).

The sportive lemur *Lepilemur* sp. is considered strictly nocturnal (Dollar et al., 2007; Nash, 2007), although some species may show a high level of vigilance during daytime [e.g. *L. sahamalazensis* (Seiler et al., 2013b)]. Ruperti (2007) reported the diurnal behaviour of *L. sahamalazensis*, highlighting that the species spends around 35 % of its resting time vigilant during the day, and it can show some activity like grooming or small movements. Also, *L. sahamalazensis* always remains in the same sleeping spot during the day, thus excluding the presence of true cathemeral activity [characterized by the use of the main behaviours during the day and at night (Tattersall 1987)]. Charles-Dominique & Hladik (1971) also reported that *L. leucopus* can show hyperactive grooming behaviour in the early afternoon and it may stay vigilant to avoid predators during the entire day. Zinner et al. (2003) reported seeing four instances of *L. ruficaudatus* feeding leaves or fruit in proximity to their tree holes during the day. Other sportive lemurs were reported to rest in sunny spots near the sleeping site [*L. edwardsi* (Warren & Crompton, 1997a); *L. petteri* (Nash, 1998)]. Considering all these reports the question arises on whether a more continuous data collection on sportive lemur activity may reveal a flexible activity of this genus.

The aim of this study was to test whether nocturnal luminosity and photoperiodic variations are significant factors in determining activity patterns of the Fleurette's sportive lemur *L. fleuretae* in the lowland rainforest of Ampasy, Tsitongambarika Protected Area (TGK). This study area represents a good model to test the influence of these Zeitgebers and masking factors on nocturnal primates since this area represents the southernmost rainforest in Madagascar, thus one of the habitats with the largest photoperiodic variation for primates. Also, this area is one of the last remnant continuous lowland rainforest in Madagascar, representing a site with no or minimal anthropogenic disturbance to the natural biorhythm of this species (Donati et al., 2016). In addition, the site still hosts the main predator of this species (the cathemeral fossa *Cryptoprocta ferox*) as well as other possible predators (the diurnal harrier hawk *Polyboroides radiatus* and Henst's goshawk *Accipiter henstii*, and the cathemeral Dumeril's boa *Acrantophis dumerili*) (Colquhoun, 2006). I predicted:

1) Photoperiodic variations to be highly influential on the activity patterns of *L. fleuretae* in TGK that is a habitat with strong seasonal luminosity variations (see Chapter 3);
2) *L. fleuretae* to be lunarphobic to reduce the risk of being detected by predators at night;
3) *L. fleuretae* to be strictly nocturnal but to show, as shown in previous studies, some diurnal activity such as vigilance from predators that are mainly diurnal and cathemeral, and extensions of feeding activity into the day during short nights due to the seasonal photoperiodic variation at TGK (see Chapter 3).

6.2. Methods

6.2.1. Data collection.

See Chapter 2.1 for details on the study area, Chapter 2.4 for details on study animals, animal captures, and accelerometer data collection, and Chapter 2.5 for the ethics statement. Refer to Chapter 5 for detailed information on the use of accelerometers, data analysis, and validation in three individuals of *Lepilemur fleuretae*.

6.2.2. Data analysis

I calculated the daily proportion of activity during the day, at twilight, and at night. As twilight, I measured 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 after sunset). 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 2.3). Using moon phase as a proxy of luminosity may affect the interpretation of the results since luminosity is also affected by other factors such as cloud density and rainfall. Nevertheless, using moon phase as a proxy of moon luminosity is a common procedure while investigating the effects of moon luminosity of activity patterns [e.g. Kappeler & Erkert (2003); Donati et al. (2009); Rode-Margono & Nekaris (2014)].

To evaluate the influence of night-length and moon phase on the activity of *Lepilemur fleuretae*, I used a General Linear Model (normal distribution and identity link function) with activity (during the day, at twilight, and at night) or the Nocturnal vs Diurnal (ND) ratio [with twilights included in the nocturnal activity to compare with previous studies (e.g. Fernandez-Duque & Erkert, 2006; Donati et al., 2013; Eppley et al., 2015b)] as dependent variables, night-length and moon phase as covariates, and individual as subject and random factor. I considered the twilight in the nocturnal activity, comparably to other studies on diurnal animals that included twilight in the daily activity, since both diurnal and nocturnal animals have been shown to be active at this low luminosity condition (Donati & Borgognini-Tarli 2006; Fernandez-Duque & Erkert, 2006).

To represent the activity profiles over the 24 h, I divided the daily activity into 2-h intervals. I considered two moon light 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, day and individuals as subjects, and individuals as random factors. I included the interaction effect between time-block and moon luminosity to test whether *Lepilemur fleuretae* 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. I performed the tests via SPSS v23 considering $P < 0.05$ as level of significance.

6.3. Results

6.3.1. Influence of night-length and moon phase

The three individuals of *Lepilemur fleuretae* were at their peaks of activity at night (70.65 ± SE 0.62 %, N = 218 days), although with medium proportion of activity at twilight (40.49 ± SE 0.65 %, N = 217 days), and a low proportion of activity during the day (12.41 ± SE 0.41 %, N = 218 days) (Figure 6.1). Photoperiodic variations negatively influenced activity of *L. fleuretae*: at night (night-length effect: $F_{1,216} = 141.21$, $\beta = -15.99$, $P < 0.001$), at twilight (night-length effect: $F_{1,215} = 177.38$, $\beta = -$

18.79, $P < 0.001$), during the day (night-length effect: $F_{1,216} = 18.43$, $\beta = -3.83$, $P < 0.001$). Moon phase negatively influenced the activity of *L. fleuretae* at night (moon phase effect: $F_{1,216} = 10.44$, $\beta = -5.73$, $P = 0.001$) and positively influenced the activity at twilight (moon phase effect: $F_{1,215} = 6.18$, $\beta = 4.60$, $P = 0.014$), while it did not influence activity during the day (moon phase effect: $F_{1,216} = 2.59$, $\beta = 1.90$, $P = 0.109$). The ND ratio was 11.47 ± SE 2.77 (95% CI: 6.02-16.92, N = 217 days), and it was not influenced by night-length (night-length effect: $F_{1,215} = 0.27$, $\beta = 3.15$, $P = 0.604$) nor by moon phase (moon phase effect: $F_{1,215} = 0.27$, $\beta = -4.15$, $P = 0.601$).

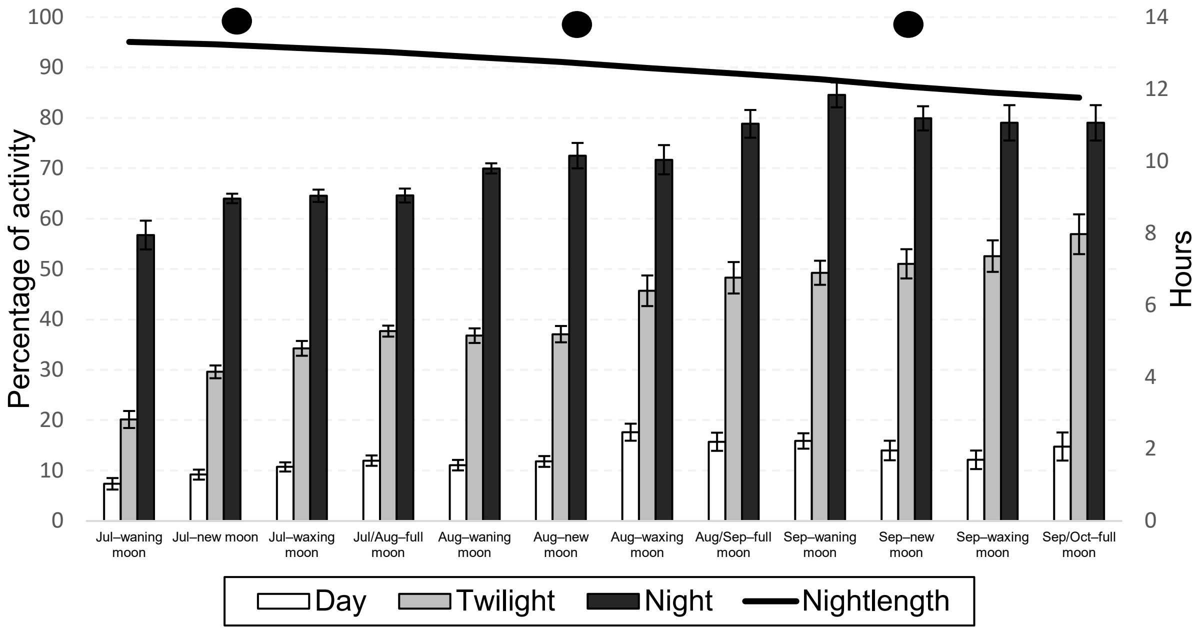

Figure 6.1: Variation of activity of *Lepilemur fleuretae* at Ampasy during the day, at twilight, and at night. Means and standard errors for successive moon phases from 07/07/2015 to 02/10/2015 are shown. Black circles indicate new moon phases.

6.3.2. Daily activity pattern

The 24-h activity pattern of *Lepilemur fleuretae* showed two main peaks between 2 am and 4 am and between 6 pm and 10 pm. There was a significant variation of the activity in the 24-h (Time-block effect: $F_{11,354.14} = 1394.02$, $P < 0.001$) (Figure 6.2).

A Sidak post-hoc test revealed a significant difference between all the time-blocks except between 22-24 and 0-2, between 20-22 and 2-4, and between 6-8, 8-10, 10-12, 12-14 and 14-16. *Lepilemur fleuretae* can have a maximum activity of around 35% during the day (Figure 6.2).

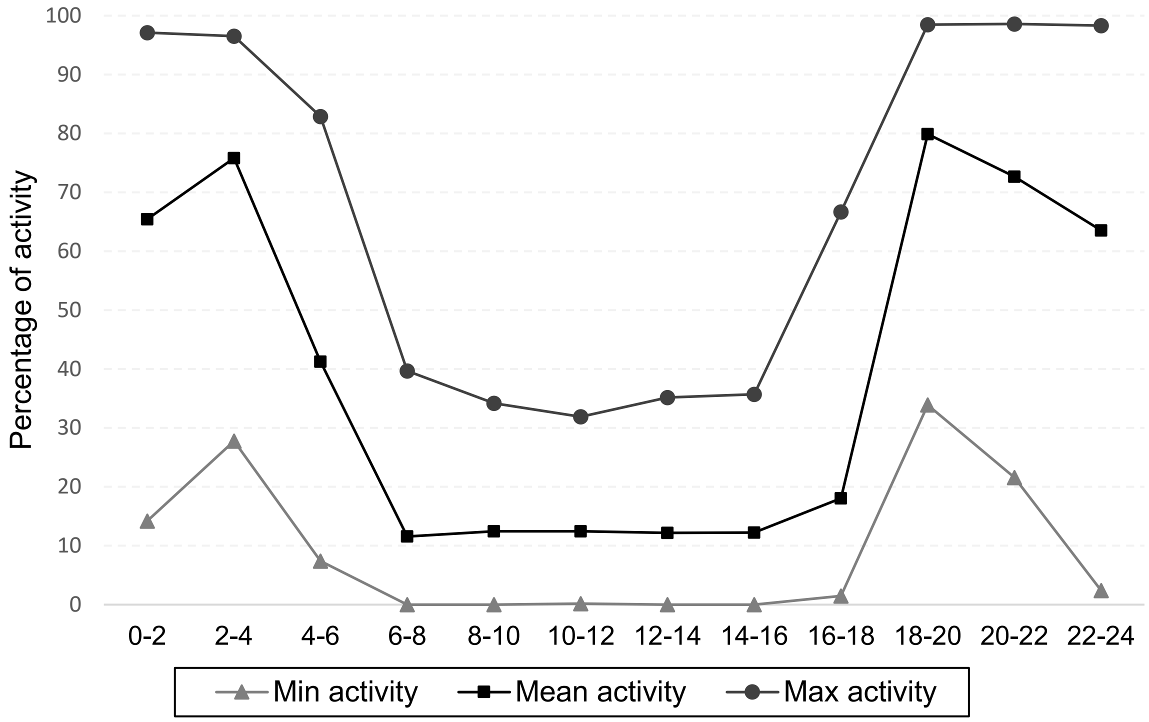

Figure 6.2: Daily activity of *Lepilemur fleuretae* at Ampasy. Hourly distribution of activity (mean, minimum, and maximum) of three individuals of *L. fleuretae* over the 24-h from 07/07/2015 to 02/10/2015. Sunset: 17:17-17:51; evening astronomical twilight: 18:37-19:08; morning astronomical twilight: 4:14-5:16; sunrise: 5:31-6:36.

The 24-h activity pattern of *L. fleuretae* was significantly different between low and high luminosity conditions (Time-block*moon luminosity effect: $F_{11,354.15} = 1.85$, P = 0.044) (Figure 6.3). The overall activity was different between high and low luminosity conditions (moon luminosity effect: $F_{1,1533.88} = 8.16$, P = 0.004), with more activity at high luminosity (40.52 ± SE 0.38 %) than at low luminosity (39.07 ± SE 0.34 %).

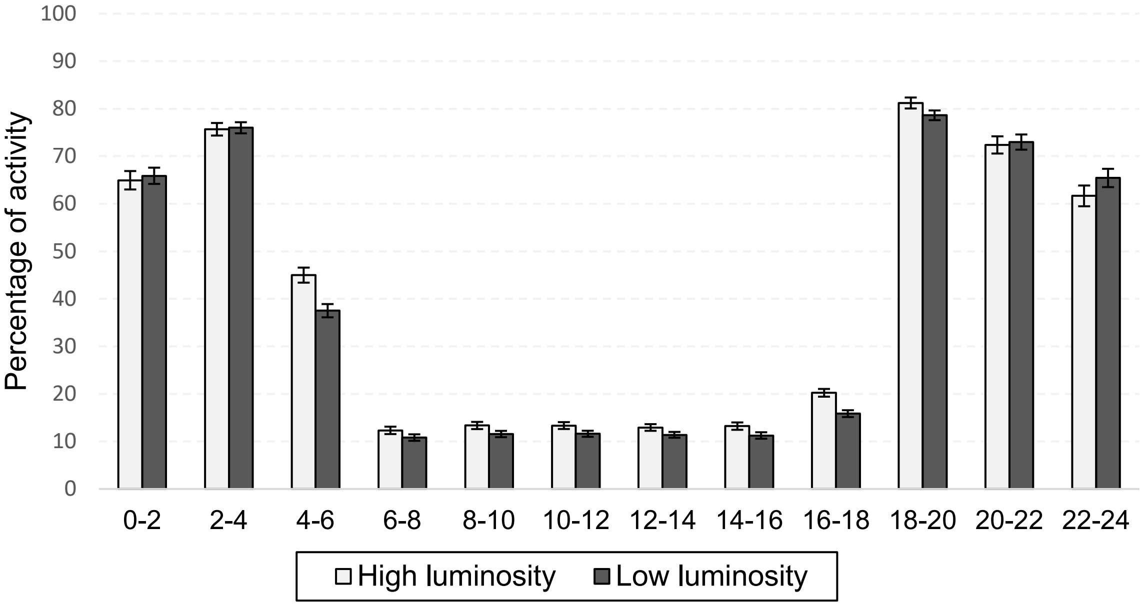

Figure 6.3: Daily activity at high and low moon luminosity conditions. Hourly distribution of activity (mean and standard error) of three individuals of *Lepilemur fleuretae* over the 24-h at low and high luminosity conditions from 07/07/2015 to 02/10/2015. Sunset: 17:17-17:51; evening astronomical twilight: 18:37-19:08; morning astronomical twilight: 4:14-5:16; sunrise: 5:31-6:36.

6.4. Discussion

6.4.1. Influence of photoperiodic variations

As predicted, photoperiodic variation was the main Zeitgeber influencing activity patterns of *Lepilemur fleuretae* at Ampasy. This confirms that the activity pattern of these nocturnal lemurs is strongly synchronised with variations of sunset and sunrise (Brockman & Van Schaik, 2004). Malagasy environments are highly seasonal and the influence of photoperiodic variation on activity patterns of lemurs was reported on a variety of species [*Eulemur collaris* (Donati & Borgognini-Tarli, 2006); *E. collaris X E. fulvus rufus* (Donati et al., 2009); *E. fulvus rufus* (Kappeler & Erkert, 2003); *E. mongoz* (Curtis et al., 1999)]. On the contrary, other studies found no correlation between activity profiles in cathemeral lemur species and photoperiodic variation [*E. macaco* (Colquhoun, 1998); *Lemur catta* (Donati et al., 2013); *Hapalemur meridionalis* (Eppley et al., 2015b)]. Beyond lemurs, seasonal changes in ambient temperature, precipitation, and food abundance had a stronger effect than photoperiodic variations for owl monkeys in the Argentinean Chaco [*Aotus azarai azarai* (Erkert et al., 2012)]. The different influence of photoperiodic variation in the activity of primates may be the consequence of the different predictability of resources at different sites (Curtis & Donati, 2013). In fact, the Ampasy forest had a seasonal peak of resources influenced by photoperiodic variations (see Chapter 3), while the sites where the activity is not influenced by daylength tend to show unpredictable phenological patterns between years (Halle & Stensteth, 2000).

The more likely explanation for the increase in activity with the decrease of night-lengths is that they had a shorter time to meet their energetic requirements. The increase of activity in *L. fleuretae* at Ampasy with the decrease of night-length may also be the consequence of the diet change during periods of food abundance. In particular, *L. fleuretae* was found to feed on flowers of *Albizia* sp. (see Table 4.1) that are mainly available in September (see Appendix III). Feeding on flowers requires longer distances travelled and higher activity levels than feeding on leaves, and this might partially explain the strong effect of photoperiodic variation on the activity patterns of this species.

Temperature may also play a role in shaping the activity profiles of *L. fleuretae* with lower activity during colder months as an energy-saving strategy as previously found in other lemur species (Kappeler & Erkert, 2003; Donati & Borgognini-Tarli, 2006; Donati et al., 2009). Temperature may also explain why *L.*

fleuretae increases the diurnal activity with the decrease of night-length and animals may have needed to thermoregulate more by sunbathing as previously reported in other sportive lemurs (Warren & Crompton, 1997a; Nash, 1998). However, phenological patterns, as well as other environmental variables, are dependent on photoperiodic variations (van Schaik et al., 1993) and it is difficult to isolate single factors (see Chapter 3.4.2). Also, the reproductive state may have played an important role in shaping activity patterns since two out of three animals were females and gave birth around the end of August. This can be another explanation why I found an increase in mean activity starting at the end of August since mothers might have spent more time allogrooming and lactating their infants, with a consequent increase in activity while resting, especially during the day. This is also evident from the activity profiles (with grooming behaviour highlighted) where the two females showed higher activity during the day than the male (see Figure 5.1).

The activity of *L. fleuretae* at Ampasy showed a bimodal pattern, with one peak of activity starting at the end of the evening astronomical twilight and one peak before the beginning of the morning astronomical twilight. The fact that the timing of the circadian activity rhythm of *L. fleuretae* varies depending on sunset and sunrise variations corresponds to the predictions of the two-oscillator model of circadian rhythmicity (Pittendrigh & Daan, 1976). This model hypothesises that circadian rhythms are regulated by an evening oscillator entrained to dusk and a morning oscillator entrained to dawn. Peaks at dawn and dusk have been found in other primates (Aschoff et al., 1982; Curtis et al., 1999; Kappeler & Erkert, 2003; Fernández-Duque, 2003; Donati & Borgognini-Tarli, 2006; Schwitzer et al., 2007; Donati et al., 2009; Fernández-Duque et al., 2010; Donati et al., 2013; Eppley et al., 2015b) and mammals (Aschoff, 1966; Ryan et al., 1993; Pagon al., 2013; Brivio et al., 2016). Bimodality may be an adaptation to reduce daily energy expenditure (Baldellou & Adam, 1998) and to avoid overheating (Erkert, 2000). The bimodal pattern in *L. fleuretae* at Ampasy, however, is not as evident as in other species since activity is high even in the central hours of the night. This indicates that *L. fleuretae* at Ampasy might shift from a bimodal to a unimodal activity profile depending on environmental conditions. In fact, *L. fleuretae* showed a unimodal activity profile in 22 days out of 217. Other mammal species were reported to shift from bimodal to unimodal circadian activity due to changes in weather conditions or predator risk [agouti *Dasyprocta azarae* (Cid et al., 2015); big cypress fox squirrel *Sciurus niger avicennia* (Ditgen et al., 2007); Mexican fox squirrel *Sciurus nayaritensis chiricahuae* (Koprowski & Corse, 2005); Eurasian red squirrel *Sciurus vulgaris* (Wauters et al., 1992)].

A female and a male *L. fleuretae*, however, showed a unimodal and a bimodal activity pattern respectively during the same day (Figure 6.4). Since the environmental conditions were the same, in this case the unimodal pattern showed by the female might be the consequence of the fact that the female had an infant (around 1-2 weeks old from my estimates) that required a constant parental care. The male *L. fleuretae* also showed a unimodal pattern in other days, so environmental conditions should have played an important role in shaping this response, although other factors might concur.

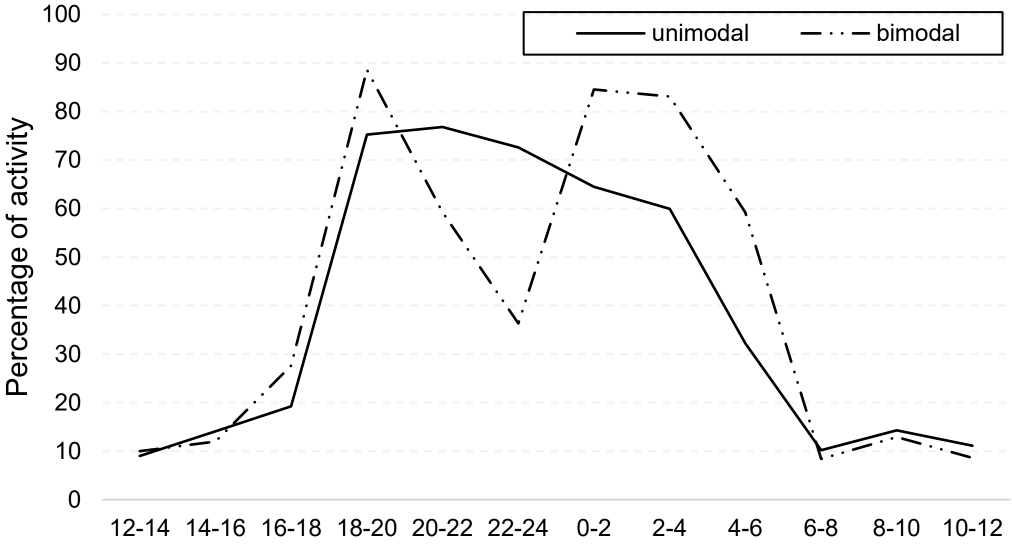

Figure 6.4: Unimodal and bimodal activity of *Lepilemur fleuretae* at Ampasy. Examples of a unimodal and a bimodal activity pattern shown by two different individuals of *L. fleuretae* on the same day (14/08/2015) at Ampasy.

6.4.2. Influence of moon luminosity

As predicted, Fleurette's sportive lemurs at Ampasy showed lunarphobia at night, with lower activity at high luminosity conditions. This might be the consequence of the presence at TGK of a full set of predators, including the main predator of this lemur species, the cathemeral fossa. The fossa, in fact, is expected to be lunarphilic as other large predators since they increase prey detection at high luminosity conditions (Prugh & Golden, 2014). Lunarphobia is a common strategy to reduce predatory risk in many mammalian species [e.g. bare-tailed woolly opossum *Caluromys philander* (Julien-Laferriere, 1997); beach mouse *Peromyscas polionotus* (Wolfe & Summerlin, 1989); European badger *Meles meles* (Cresswell & Harris, 1988); Kangaroo rats *Dipodomys* sp. (Upham & Hafner, 2013); Mexican fruit bat *Artibeus jamaicensis* (Morrison, 1978); Javan slow loris *Nycticebus javanicus* (Rode-Margono & Nekaris, 2014)]. Despite this antipredatory behaviour, two animals were killed by the fossa. I did not notice any other antipredatory behaviour in this lemur apart from freezing to reduce the likelihood of detection. Contrary to my expectations, *L. fleuretae* showed higher levels of activity at twilight in high luminosity conditions, thus behaving in a more lunarphilic way at twilights. As a possible explanation, *L. fleuretae* at Ampasy may be more vigilant when starting its activity and scan in search for predators as a consequence of the increased predation risk. The species might also take advantages in being more active at twilight in high luminosity conditions to find more food resources and compensate for the relative inactivity during the rest of the night. By looking at behavioural observations, it seems that *L. fleuretae* at twilight spent more time scanning, grooming, and moving in proximity to the sleeping sites rather than feeding. Thus, the first hypothesis might be the one that better explains lunarphilia at twilight. Further data, however, are required to reach a clear conclusion.

6.4.3. Disturbed resting during the day

As expected from previous studies, *L. fleuretae* showed some opportunistic diurnal activity, around 10%. Since the mean ratio between nocturnal and diurnal activity was 11.47:1, the species cannot be considered cathemeral. It fact, previous species reported to be occasionally cathemeral had a nocturnal vs diurnal ration lower than 5:1 [3.98:1 for *Hapalemur meridionalis* (Eppley et al., 2015b); 4.8:1 for *Lemur catta* (Donati et al., 2013)]. The species is probably vigilant during the day, as previously reported (Charles-Dominique & Hladik, 1971; Ruperti, 2007; Seiler et al., 2013b) and may show some activity to thermoregulate (Warren & Crompton, 1997a; Nash, 1998). I cannot exclude that *L. fleuretae* may feed during daytime as previously reported in *L. ruficaudatus* (Zinner et al., 2003). The activity profile showing the low and high peaks of activity suggests that there can be some occasional feeding in proximity to the sleeping site during the day (see Figure 5.1). In fact, *L. fleuretae* had an average high-intensity activity of around 2% during the day that very likely corresponds to movements such as leaping (see Chapter 5.4.1). Behavioural observations, however, are necessary to confirm this hypothesis.

6.4.4. Conclusions

Photoperiod was the main Zeitgeber influencing the activity of *L. fleuretae* at Ampasy, probably due to the seasonal pattern of the Ampasy forest in terms of food availability and temperature. The species is lunarphobic and reduces the activity at high luminosity conditions, although it increases the activity at twilight when at high luminosity, maybe to increase vigilance towards predators. The activity profile of *L. fleuretae* is bimodal, although with a high mean proportion of activity during the night, suggesting that the species may shift to a unimodal activity profile depending on environmental conditions. Reproductive state and ambient temperature might also play a role in shaping activity patterns of this species. Further studies should be performed to explore more in-depth the proximate and ultimate determinants of activity patterns of this species.

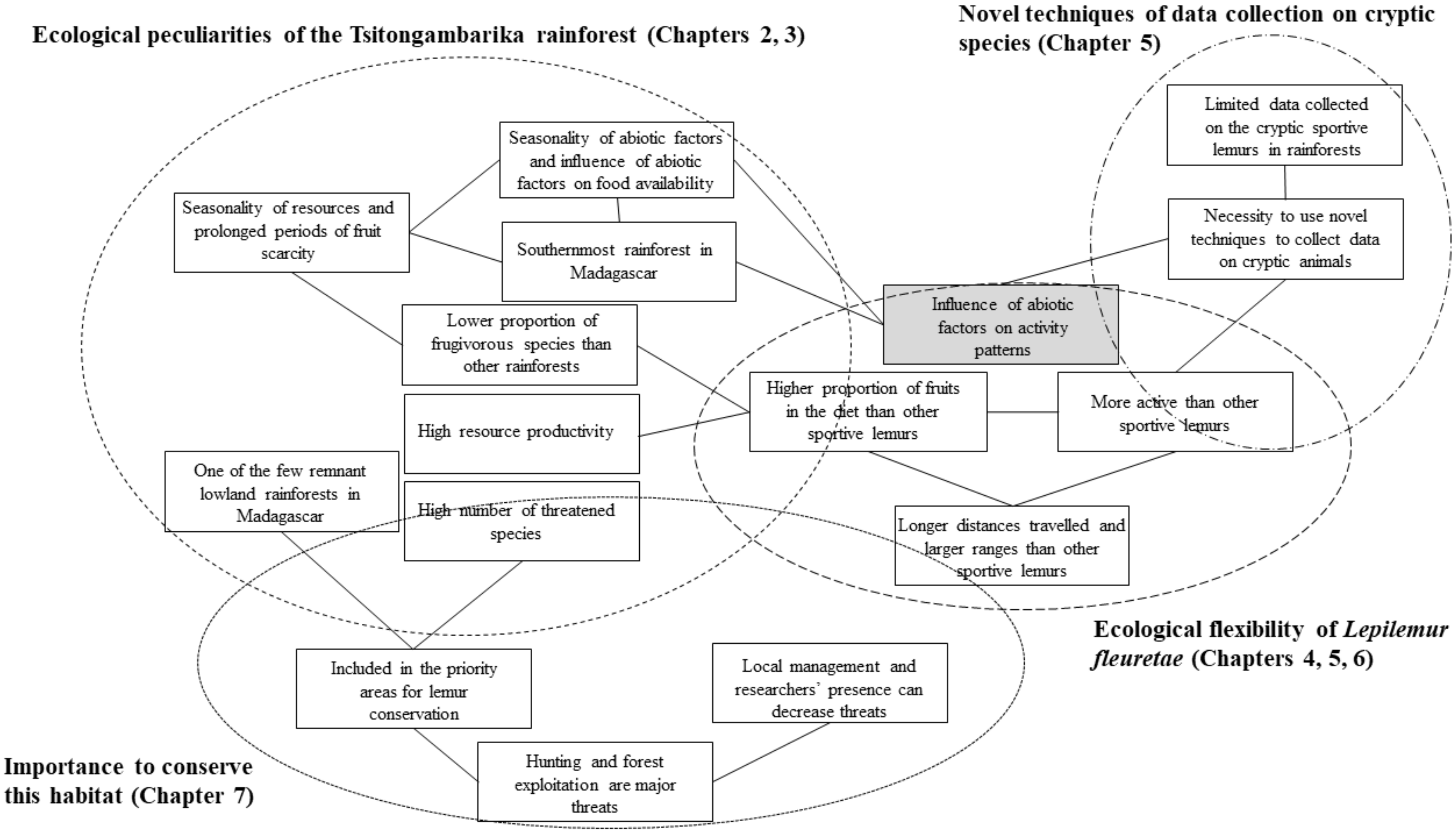

Figure 6.5: Word flowchart representing the topics of Chapter 6. Topics highlighted in grey.

Chapter 7. Does forest management and researchers' presence reduce hunting and forest exploitation by local communities in Tsitongambarika?

Chapter published in *Oryx* journal

In this chapter, I explore whether specific conservation strategies may help to increase the protection of Fleurette's sportive lemur in Tsitongambarika. Despite the ecological flexibility showed by this sportive lemur in the previous chapters, this species is classified as Critically Endangered and implementing conservation strategies is essential for the survival of this species. Sportive lemurs are, in fact, subjected to hunting pressure since they do not show a flight response towards humans even in areas where hunting occur. In addition, sportive lemurs are subjected to habitat degradation, logging, and fragmentation since they have the tendency to stay in the interior part of the forest and they require large trees as sleeping sites.

7.1. Introduction

Hunting of wildlife, mainly for commercial purposes, is one of the major threats to biodiversity (Nijman, 2010; Jenkins et al., 2011) and has significantly reduced wildlife populations (Rao et al., 2011; Melo et al., 2015). Long-lived species with slow reproductive rates are particularly affected (Rao et al., 2011). Various methods have been used to estimate hunting pressure, each with strengths and weaknesses. Market surveys are a common way to estimate the level of hunting (Allebone-Webb et al., 2011), although this method does not account for subsistence hunting (Golden et al., 2013). An alternative method is to estimate the density of snares (Barelli et al., 2015) but this does not consider opportunistic hunting. Interviews are frequently used to estimate hunting pressure or bushmeat consumption (Rao et al., 2011; Golden et al., 2013), but obtaining reliable responses is a challenge, as participants may be reluctant to declare illegal activities (Knapp et al., 2010; Nuno & St John, 2015). Another approach involves estimating population fluctuations by monitoring the density of animals over time, although in this case it is difficult to separate the effects of hunting from those of other ecological factors (Barelli et al., 2015; Melo et al., 2015).

For effective conservation programmes in countries where hunting and shifting agriculture are the main sources of subsistence, forest management and the creation of alternative sources of income should bring about a reduction in hunting pressure and forest exploitation, but local stakeholder and community perceptions should be taken into account (Hill, 1997). Previous studies (e.g. Newmark et al., 1993; Little, 1994) have suggested that even a minor interaction between NGOs, research organizations and local communities can have a positive impact on attitudes towards wildlife. However, several studies have reported failure of forest management programmes, mainly as a result of a lack of long-term funding (e.g. Little, 1994; Webber et al., 2007).

In addition to forest management, the presence of researchers has been recognised as a factor in reducing anthropogenic pressures on threatened species (Marsh et al., 1999; Wrangham & Ross, 2008; Schwitzer et al., 2014). This is based on the rationale that local communities may decrease their hunting activity and exploit the forest less, as a consequence of receiving direct benefits from researchers' presence, such as new job opportunities (Wrangham & Ross, 2008; Schwitzer et al., 2014). Researchers can also provide training to local assistants, as well as increase awareness of the importance of the forest, and this is likely to facilitate future research and ecotourism (Schwitzer et al., 2014). Evidence to support the hypothesis that researcher presence decreases hunting pressure comes from two studies that investigated the abundance of primates in Tai National Park, Ivory Coast (Campbell et al., 2011; N'Goran et al., 2012); these studies found a positive association between species densities and distance to the research station, as a result of lower hunting pressure close to the research station. Furthermore, long-term research in an area has been linked to an increase in wildlife population size (Fedigan & Jack, 2012; Nakamura, 2012), although this has not been linked directly to the presence of a research station. However, the opposite has also been reported, with a population of primates having been hunted to near-extirpation despite the presence of a large, fully operational field station (Nijman, 2005). Similarly, but without presenting data to support their claims, Bezanson et al. (2013) argued that the presence of researchers, and especially the establishment of extensive trail systems, facilitates greater access and increased opportunities for poaching.

Madagascar is a biodiversity hotspot in which many endemic species are threatened (Myers et al., 2000). Ninety-four percent of lemurs, one of the island's flagship taxonomic groups, are threatened with extinction (Schwitzer et al., 2014). Hunting of wildlife is mostly for subsistence (Razafimanahaka et al., 2012; Golden et al., 2014), as bushmeat is a cheap alternative to domesticated meat (Golden et al., 2014; Borgerson et al., 2016), and poverty, poor health and child malnutrition are strong predictors of illegal hunting (Borgerson et al., 2016). It has been suggested that bushmeat consumption is more widespread than previously thought (Golden, 2009), based on recent studies (e.g. Razafimanahaka et al., 2012; Golden et al., 2014; Borgerson et al., 2016).

The Tsitongambarika (TGK) Protected Area, in south-eastern Madagascar, was established in 2008 (BirdLife International, 2011) and has been co-managed by the NGO Asity Madagascar (BirdLife Madagascar) and KOMFITA (Community Forest Management) since 2013. A research station was established in 2015 at Ampasy, in the northernmost portion of the protected area. The TGK forest is a good model with which to test the influence of a research station on a forest area, as no long-term research had been conducted in the area prior to the establishment of the research station, thus local communities had not had prolonged exposure to researchers. Furthermore, this area has no exposure to tourism, which can be a potentially confounding factor (Krüger, 2005; Wright et al., 2014).

My aim was to evaluate the determinants reducing pressure on lemur populations in the northernmost portion of TGK. I hypothesised that the presence of researchers and local forest management significantly benefit lemur communities and the forest. In particular, I predicted that:

1) anthropogenic pressure on the forest was reduced after local management commenced;
2) people from villages close to the research station and involved in the local management of the forest decreased their forest use following the establishment of the research station more than people from villages further away, and villages not involved in the local management did not decrease their impact on the forest;
3) the occurrence of active snares was greater prior to the start of local management, and decreased substantially after the research station was established;

4) rates of encounter with cathemeral [i.e. active at any time of night or day (Donati et al., 2016)] lemurs increased after the research station was established, as they are expected to be the main targets of hunting, given their comparatively large body size.

7.2. Methods

7.2.1. Study area

The study was conducted at the Ampasy research station, in the northernmost portion of Tsitongambarika (see Chapter 2.1). The research station is located at the forest edge in the Ampasy Valley, c. 7.6 km from Iaboakoho (c. 60 km north of Fort Dauphin). Local people depend mainly on fishing and traditional practices, including shifting agriculture (BirdLife International, 2011). They also depend on the forest for timber, firewood, medicinal plants, and lianas to make lobster traps, although the importance of hunting in the area is not well-known and has potentially been underestimated in previous reports (BirdLife International, 2011). Hunting in Tsitongambarika has been reported to be a major threat to the collared brown lemur *Eulemur collaris*, and other endemic species are also targeted, including the southern bamboo lemur *Hapalemur meridionalis*, the Malagasy flying fox *Pteropus rufus*, the fossa *Cryptoprocta ferox* and the blue coua *Coua caerulea* (BirdLife International, 2011).

7.2.2. Interviews

I collected data via semi-structured household interviews (Golden, 2009) from nine villages in the municipality of Iaboakoho, selecting a maximum of 10 people from each village. In total, 72 people were interviewed in June 2016 (Table 7.1). I included all villages within two hours' walk of the research station.

Table 7.1: **Estimated and censused number of households in the study area.** Number and percentage of households censused during semi-structured interviews in villages in the municipality of Iaboakoho, in south-east Madagascar (Figure 1). The villages are categorized based on distance from the research station of Ampasy and continuous forest, and whether or not they are involved in local forest management.

Village category	No. of households censused (%)	Estimated no. of households in village*
Close-involved	22 (40)	55
Close-not involved	20 (36)	55
Far-involved	30 (14)	210
Total	72 (23)	320

*Based on observations by the researchers and published data from BirdLife International (2011).

A translator with previous experience and who speaks the local dialect was hired to assist with the interviews. Additionally, a local guide helped in recruiting male heads of households, asking for their participation in interviews. Convenience sampling was used to select interview participants, selecting those available in the village at a given time (Henn et al., 2009). The interview included eight questions (Table 7.2), starting with general questions on forest use, followed by more specific questions about hunting. Indirect questioning techniques (Nuno & St John, 2015) were employed to minimise dishonest answers, although I cannot exclude the presence of false negatives.

Table 7.2: Questionnaire design. Questionnaire used to estimate the level of forest exploitation by inhabitants of villages at various distances from the Ampasy research station (Figure 2.1), in the northernmost part of the Tsitongambarika Protected Area.

Question	**Potential answers**
1. How often do you go into the forest now?	Daily, weekly, monthly, rarely, never
2. Did you visit the forest more often before local management by Asity began?	Yes, no
3. Why do you use the forest? (Tick all that apply)	Firewood, timber, pirogues, hunting, other
4. Which animals did you hunt?	Open question
5. What did you do the last time you went into the forest?	Open question
6. When was the last time you ate a lemur[1], and how did you get it?	Before 2013, after 2013[2]; second part was open question
7. Do you think people from your village hunt now?	They hunt, they do not hunt, do not know
8. Do you think people from the neighbouring villages hunt now?	They hunt, they do not hunt, do not know

[1] *Gidro* in the local dialect. [2] The translator asked if the last time they ate a lemur was before or after local management began in 2013.

Following the questions, a series of 16 photographs were presented (Table 7.3), each of a different endemic animal species I had observed in Tsitongambarika since research began at Ampasy. I asked if the respondent had seen each animal, and whether or not they had eaten it. Pictures were tested with four local guides to ensure easy recognition. I asked interviewees to independently (i.e. one-by-one) provide the vernacular names of the species shown, assuring the overall consensus for each picture. To maximise the reliability of data, images were not limited to lemur species, as I did not want to reveal my main research focus [participants may have avoided answering honestly if they knew the focal species (Nuno & St John, 2015)].

7.2.3. Snare and lemur counts

I established 11 transects of 1 km length using pre-existing trails (See Chapter 2.2). I evaluated the number of snares by walking all transects after the research station was established (May 2015) and at the end of the study (July 2016). I counted all traps visible up to 20 m from the transect. Local people cut down an area of forest and put a series of snares along wood pieces that animals are required to cross if they want to pass the open area. Snares are thus easy to spot, and, when spotted, we informed the local authorities who destroyed them. I also considered data collected in July 2012, before local management began in the Ampasy Valley (Nguyen et al., 2013). The same transects were walked in 2012 and 2015, although more areas were surveyed in 2012. I plotted the global positioning system coordinates of the snares found, to compare the data collected in 2012 with my data, considering only traps along the established transects. Eleven of the 16 traps found in 2012 (Nguyen et al., 2013) were located within the area monitored in 2015. Nine of the 11 transects occurred in the forest, and I walked each transect once per month during May–July 2015 and May–July 2016 to estimate encounter rates of collared brown lemurs and southern bamboo lemurs. Transects were walked at a mean speed of c. 1.0–1.5 km per hour, starting in the early morning (06.30–07.30) or late afternoon (15.00–16.00).

Table 7.3. List of species shown during the interviews. Vernacular, common and scientific names, order and IUCN status, and percentages of interview participants who reported having eaten and seen the species shown in photographs during interviews in villages in the municipality of Iaboakoho.

Species	**Vernacular name**	**Order**	**IUCN status***	**Ate the species (%)**	**Saw the species (%)**
Striped civet *Fossa fossana*	Aparo	Carnivora	VU	63.8	87.0
Fossa *Cryptoprocta ferox*	Fossa	Carnivora	VU	26.1	56.5
Broad-striped mongoose *Galidictis fasciata*	Voatsira fotsy	Carnivora	VU	18.8	66.7
Ring-tailed mongoose *Galidia elegans*	Voatsira mena	Carnivora	VU	49.3	98.6
Malagasy flying fox *Pteropus rufus*	Fanihy	Chiroptera	VU	68.1	100.0
Peters's sheath-tailed bat *Paremballonura atrata*	Kananavy	Chiroptera	LC	72.5	100.0
Aye-aye *Daubentonia madagascariensis*	Aye-aye	Primates	EN	0.0	29.1
Southern woolly lemur *Avahi meridionalis*	Fotsy fe	Primates	EN	43.5	89.9
Southern bamboo lemur *Hapalemur meridionalis*	Halo	Primates	VU	75.4	98.6
Greater dwarf lemur *Cheirogaleus major*	Matavirambo	Primates	DD	31.9	84.1
Fleurette's Sportive lemur *Lepilemur fleuretae*	Pondiky	Primates	CR	32.9	80.0
Anosy mouse lemur *Microcebus tanosi*	Tsitsidy	Primates	NA	39.1	95.7
Collared brown lemur *Eulemur collaris*	Varika	Primates	EN	79.7	95.7
Blue coua *Coua caerulea*	Tesso	Cuculiformes	LC	55.1	100.0

Species	**Vernacular name**	**Order**	**IUCN status***	**Ate the species (%)**	**Saw the species (%)**
Brown mesite *Mesitornis unicolor*	Deho	Mesitornithiformes	VU	92.8	100.0
Madagascar red owl *Tyto soumagnei*	Vorondolo	Strigiformes	VU	1.4	97.1

*DD, Data Deficient; LC, Least Concern; VU, Vulnerable; EN, Endangered; CR, Critically Endangered; NA, Not Assessed

7.2.4. Data analysis

For interviews, I grouped villages into three categories depending on the distance from the research station/continuous forest and the potential influence of local management: close-involved, close-not involved, far-involved. Villages in the close-involved category were those closest to the research station (4.3–5.0 km) and continuous forest (2.1–3.3 km) that were involved in the local management of the forest, especially after the research station was established, and for which the Ampasy Valley was the preferred point of access to the forest. Villages categorized as close-not involved were those close to the research station (4.3–5.0 km) and continuous forest (2.1–3.3 km) that were not involved, or were only marginally involved, in the local management and for which another valley was the preferred point of access to the forest. Villages categorized as far-involved were those furthest from the research station (6.2–7.6 km) and continuous forest (4.2–4.7 km) that were involved in the local management from the beginning, and for which the Ampasy Valley was the preferred point of access to the forest. To calculate the distance from the research station/continuous forest, I plotted global positioning system coordinates for each village in ArcGIS v. 10.4 (ESRI, Redlands, USA) and calculated the straight-line distance to the research station/continuous forest. I considered a village to be involved in the local management of the forest when more than half of the inhabitants were employed by Asity-KOMFITA, received funding from Asity-KOMFITA to support sustainable agriculture, and/or participated in conservation education programmes promoted by Asity-KOMFITA (Razafitsalama & Ravoahangy, 2010). I considered the household a statistical unit, and I ran multiple generalized linear models to test the influence of distance/management on the variables derived from the interviews. Villages were considered as subjects, as people within each village may show similar habits more often than people from different villages in the same distance-management category. Variables were linked to logistic/probit (in the case of binary and ordinal variables) or log-linear Poisson/log-negative binomial (in the case of counts) distributions. The lower value of the Quasi-likelihood under Independence Model Criterion was used to select the link function. In the case of open questions, I categorised answers (see Results) to facilitate statistical comparison. Fisher's least significant difference post-hoc tests were performed for pairwise comparisons in the case of significant effects. I reported only significant results for post-hoc tests.

For snares, I performed Wilcoxon tests between trap counts per transect in 2012 and 2015 to test whether there was a reduction as a result of local management, and between 2015 and 2016 to test whether there was a further reduction as a result of the presence of the research station. To test whether encounters with cathemeral lemurs increased from May–July 2015 to May–July 2016 I performed a Wilcoxon test, comparing the same transect per month between years. Statistical tests were performed in SPSS v23, using a significance level of $P < 0.05$.

7.3. Results

7.3.1. Interviews

Overall, 20.8% of participants entered the forest daily, 38.9% weekly, 16.7% monthly, 18.1% rarely, and 5.6% never. No significant differences were found between villages in the number of people who used the forest at least once per week (Figure 7.1; distance-management effect: Wald $\chi^2 = 1.861$, $P = 0.394$).

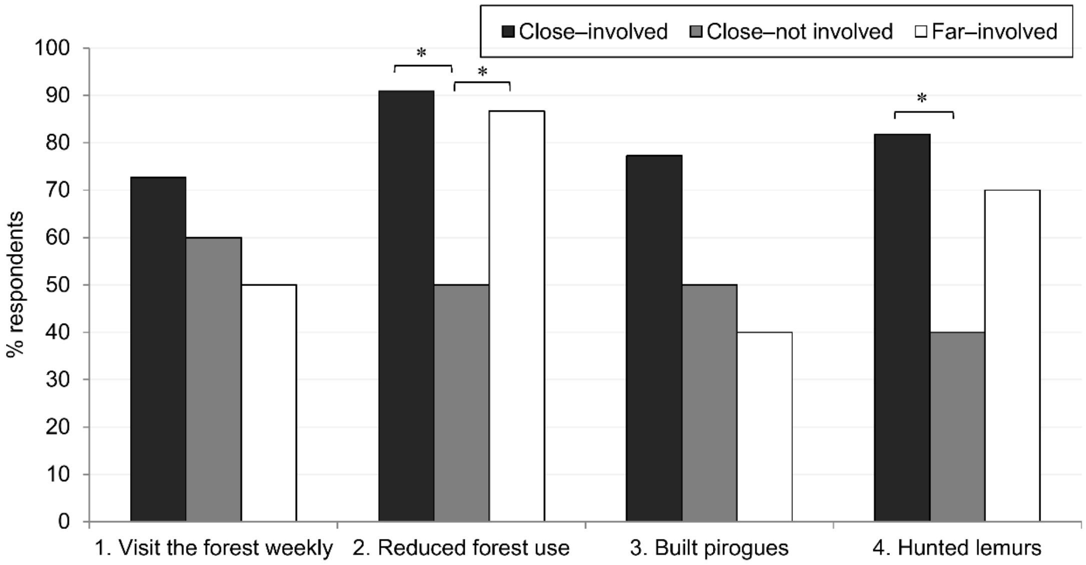

Figure 7.1: **Forest use in the municipality of Iaboakoho.** The percentage of interview participants who reported visiting the forest weekly, having reduced their forest use since local management by Asity began, building pirogues in the forest, and hunting lemurs, in response to questions 1–4 (Table 7.2), categorized according to distance from the research station at Ampasy and continuous forest, and involvement in local forest management. $^*P < 0.05$.

Before local management began, 77.8% of participants used the forest more frequently than they do now, with significant differences between villages (Figure 7.1; distance-management effect: Wald $\chi^2 = 13.536$, $P = 0.001$). Fewer people from villages in the close-not involved category acknowledged they had reduced their forest use after the introduction of local management compared to villages in the close-involved ($P = 0.001$) and far-involved ($P = 0.001$) categories.

All participants used the forest for timber and firewood. Many participants (54.2%) used the forest to build pirogues (dug-out canoes made mainly from the tree *Calophyllum inophyllum*). The percentage of people who built pirogues (Figure 7.1) did not vary between villages (distance-management effect: Wald $\chi^2 = 2.022$, $P = 0.364$). For hunting, I considered only participants who said they hunted lemurs.

Overall, 65.3% of participants used the forest to hunt lemurs. This percentage varied between villages (distance-management effect: Wald $\chi^2 = 7.289$, $P = 0.026$; Figure 7.1). People in villages categorized as close-not involved reported hunting lemurs less frequently than people living in villages categorized as close-involved ($P = 0.003$).

The answers to question 5 (What did you do the last time you went into the forest?) were 'collected timber or firewood' (57.8%), 'collected fruits, lianas or crops' (26.6%), 'built pirogues' (14.1%), and 'fished' (1.6%) (Figure 7.2). Distance-management was a significant factor determining the answer 'collected timber or firewood' (Wald $\chi^2 = 14.016$, $P = 0.001$). In particular, people from villages categorized as far-involved gave this answer more than those in close-involved ($P = 0.046$) and close-not involved ($P < 0.001$) villages.

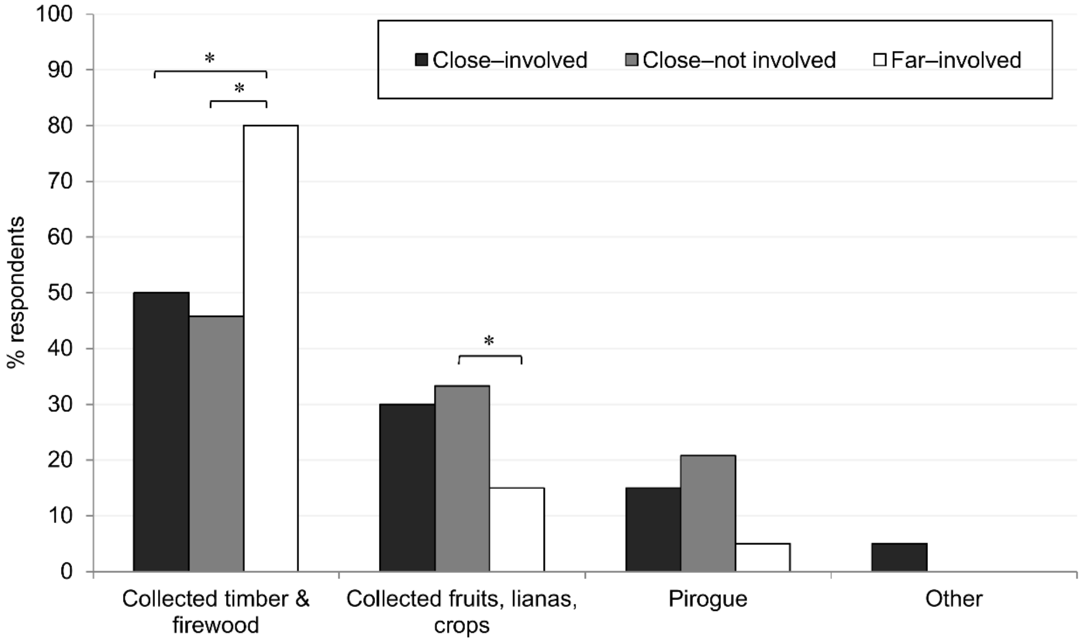

Figure 7.2: **Recent activities in the forest declared by participants.** The percentage of interview participants who chose each of the responses to question 5 (What did you do the last time you went into the forest? Table 7.2), categorized according to distance from the research station at Ampasy and continuous forest, and involvement in local forest management. $^*P < 0.05$.

Distance-management was also a significant factor determining the answer ‘built pirogues’ (Wald $\chi^2 = 8.306$, $P = 0.016$; Figure 7.2). In particular, people from villages categorized as close-not involved gave this answer more often than those in far-involved villages ($P = 0.008$). There were no differences between villages for the answer ‘collected fruits, lianas or crops’ (distance-management effect: Wald $\chi^2 = 0.594$, $P = 0.743$).

When asked about the last time they ate lemurs, 18.6% of participants said it was after local management had begun, and 8.6% stated they never ate lemurs. In response to a follow-up question (How did you procure it?), 63.0% answered ‘opportunistic hunting’ (mainly via slingshot), 20.4% answered ‘snares’, and 16.7% answered it was a ‘gift’ from relatives/friends. Opportunistic hunting was not dependent on distance-management (Wald $\chi^2 = 2.151$, $P = 0.341$) but the use of snares was (Wald $\chi^2 = 23.390$, $P < 0.001$), with more participants who reported using snares in close-involved than in far-involved villages ($P < 0.001$; Figure 7.3).

In response to the question ‘Do you think that people from your village hunt now?’ 45.8% of participants said that people in their village still hunted, 25.0% said that people from their village hunted previously, and 29.2% did not know. The answer was different between villages (distance-management effect: Wald $\chi^2 = 8.712$, $P = 0.013$), with participants in villages categorized as close-not involved responding less frequently that people in their village still hunted than participants in far-involved ($P = 0.016$) and close-involved ($P = 0.048$) villages. Overall, 37.5% of people interviewed answered that people in neighbouring villages still hunted, 19.5% said that people from their village hunted previously, and 43.1% did not know. The answer to the question ‘Do you think that people from the neighbouring villages hunt now?’ differed significantly between villages (distance-management effect: Wald

$\chi^2 = 6.438$, $P = 0.040$). Fewer people living in close-not involved villages declared that people from neighbouring villages still hunted, compared to people living in close-involved villages ($P = 0.049$; Figure 7.3).

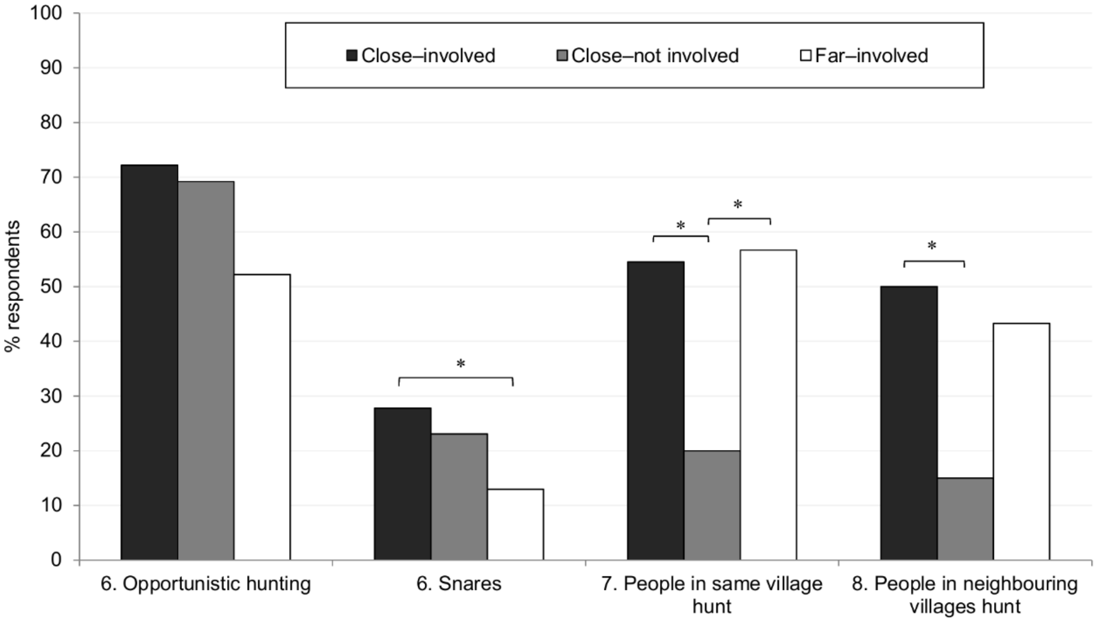

Figure 7.3: Hunting pressure in the municipality of Iaboakoho. The percentage of interview participants who reported catching lemurs by opportunistic hunting and snares, that people in their village hunted, and that people in neighbouring villages hunted, in response to questions 6-8 (Table 7.2), categorized according to distance from the research station at Ampasy and continuous forest, and involvement in local forest management. $*P < 0.05$.

The number of species eaten by participants (Figure 7.4) differed significantly between villages (distance-management effect: Wald $\chi^2 = 15.393$, $P < 0.001$). People living in villages categorized as close-not involved declared they ate fewer species than those living in villages categorized as close-involved ($P < 0.001$) or far-involved ($P = 0.006$). Also, people living in villages categorized as close-involved ate more species than those living in villages categorized as far-involved ($P = 0.049$). The number of lemur species that participants had eaten differed significantly between villages (distance-management effect: Wald $\chi^2 = 15.793$, $P < 0.001$). People living in villages categorized as close-involved declared they ate more lemur species than those living in villages categorized as close-not involved (P < 0.001) or far-involved (P = 0.001).

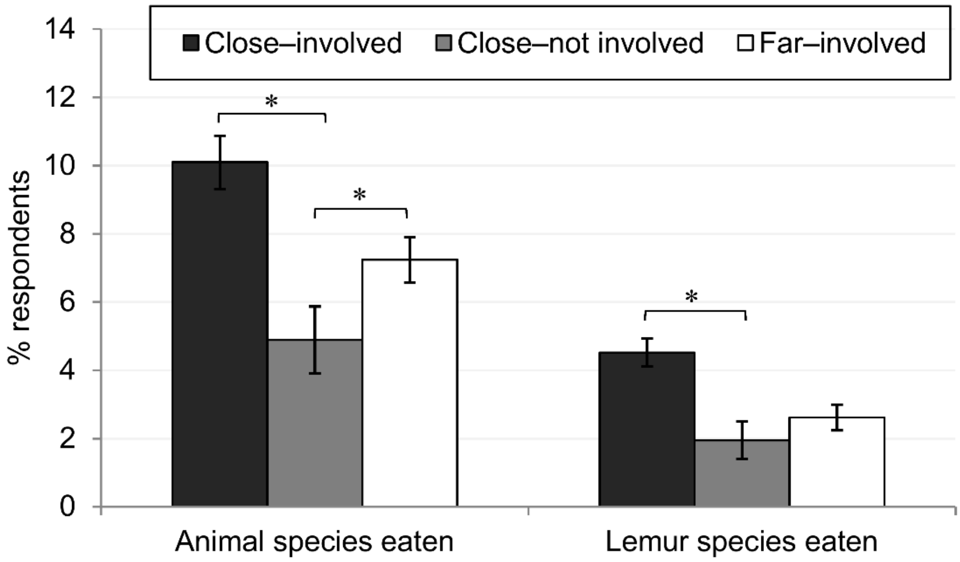

Figure 7.4: Number of species eaten. Numbers (mean ± SE) of animal and lemur species eaten by people in villages in the municipality of Iaboakoho, in south-east Madagascar, categorized according to distance from the research station at Ampasy and continuous forest, and involvement in local forest management. The taboo species aye-aye *Daubentonia madagascariensis* and Madagascar red owl *Tyto soumagnei* are not included. *P < 0.05.

The most widely consumed species in the area was the brown mesite *Mesitornis unicolor*, and the most commonly eaten lemur species was the collared brown lemur, followed by the southern bamboo lemur (Table 7.3). The aye-aye *Daubentonia madagascariensis* and Madagascar red owl *Tyto soumagnei* are taboo, although one person admitted to eating the latter. Most participants had eaten small Peters's sheath-tailed bats *Paremballonura atrata* and Anosy mouse lemurs *Microcebus tanosi* when young, or caught them for their children. Several participants sold ring-tailed mongoose *Galidia elegans* tails to Chinese people for traditional medicinal purposes.

The participants who declare to have eaten individuals of Fleurette's sportive lemur indicated that they took them from the tree hole or cut down the tree hole during the day. They also declared that, when spotted during the day, it is relatively easy to capture them.

7.3.2. Snare and lemur counts

The number of snares decreased significantly from 11 in 2012 (1.00 traps per km) to four (0.36 traps per km) in 2015 ($N = 11$, $Z = -2.121$, $P = 0.034$), and further decreased significantly from 2015 to 2016, when zero snares were found ($N = 11$, $Z = -2.000$, $P = 0.046$).

The number of observations of cathemeral lemurs increased significantly between May–July 2015 and May–July 2016 ($N = 27$, $Z = 2.575$, $P = 0.010$). During May-July 2015 I counted nine southern bamboo lemurs (0.33 individuals per km and 0.07 groups per km) and six collared brown lemurs (0.22 individuals per km and 0.04 groups per km), and during May-July 2016 I counted ten southern bamboo lemurs (0.37 individuals per km and 0.22 groups per km) and 54 collared brown lemurs (2.00 individuals per km and 0.41 groups per km).

7.4. Discussion

According to my findings the number of traps decreased after local management of the forest began, and decreased further after the installation of the research station. Furthermore, the encounter rate of cathemeral lemurs (the main targets for hunting) increased after the installation of the research station. Seventy-eight percent of participants declared they frequented the forest more often prior to local management commencing. These are indications that anthropogenic impacts on the area have been alleviated to some degree via forest management by Asity and KOMFITA. Impacts continued to decrease after the installation of the research station, mainly as a consequence of the increased involvement of villages categorized as close-involved.

7.4.1. Impact of forest management

The impact of local management is likely to be linked to the new job opportunities offered to local people and the actions to reduce impact on the forest. Approximately 20 people from villages categorized as far-involved were hired by Asity-KOMFITA to patrol the forest and reprimand those carrying out illegal activities. Other people, mainly from far-involved villages, were supported via training in sustainable agriculture. As part of the local management of the area a buffer zone was created in which local people are allowed to extract timber and firewood, and hunt exotic species [e.g. wild boar *Sus scrofa* (Razafitsalama & Ravoahangy, 2010)]. The buffer zone includes small forest patches close to far-involved villages. Conversely, the core zone, in which most of the Ampasy Valley is located, is patrolled regularly, and activities there are more strictly regulated. The effectiveness of this patrolling may be limited, however, as the agents do not have direct enforcement authority and they live in close proximity to the people they are meant to be reporting on (Reuter et al., 2017). Conflicting interests are thus likely to arise from this situation.

Some illegal activities, such as pirogue construction, appear to be still important in the area, as the municipality of Iaboakoho is the main pirogue supplier for Fort Dauphin (BirdLife International, 2011). Building a pirogue usually takes c. 1 month to complete, and pirogue builders often engage in other activities, such as opportunistic hunting (Gardner & Davies, 2014). According to Asity reports, many pirogue builders have ceased this activity and are now employed within the community (F. Rakotoarimanana, pers. comm.). The dina (i.e. local law) includes fines (c. USD 3) for people caught building pirogues without permission, and to obtain this permission (only one pirogue is allowed per person) a tax must be paid to the local community (BirdLife International, 2011). However, pirogues can command prices of MGA 400,000-1,200,000 (USD 120-360), which is well above the typical local monthly salary of c. MGA 150,000 (USD 45) (Faniry Rakotoarimanana, pers. comm.). One of the actions decided by the area local management committee is to destroy illegal pirogues found in the forest, which has effectively reduced pirogue production in recent years (Rakotoarimanana, 2016), although this previously created conflict between the NGO and local communities. The necessity to understand the needs of the community and mediate these with conservation goals is clear. It is crucial to consider the link between enforcement and incentives by implementing projects that could encourage individuals to engage less intensively in extractive activities, and ultimately modify these destructive behaviours (Reuter et al., 2017). Encouraging individuals to participate in alternative activities with similar profits, such as forest patrolling or sustainable agriculture, is an approach that needs to be strengthened, and is evident in the fact that most of the personnel hired at the research station were previously hunters and/or pirogue builders in the area.

Despite the use of indirect questioning techniques (Nuno & St John, 2015), I realise that the results obtained via interviews could be biased, as participants may have been hesitant to declare their illegal activities (Knapp et al., 2010; Jenkins et al., 2011), especially if ongoing. In particular, inhabitants of villages categorized as close-not involved may have been more reluctant to admit to hunting and eating lemurs. They may also have been reluctant to declare that people from their villages or from neighbouring villages hunted at the same level as people living in close-involved and far-involved villages. From speaking informally with my collaborators, it emerged that inhabitants of close-not involved villages have access to other areas of the forest far from the research station where opportunistic and snare hunting persists.

7.4.2. Impact of researchers' presence

The increase in encounter rates of cathemeral lemurs after the installation of the research station is probably not a result of factors such as patrolling and improved environmental conditions (e.g. habitat quality), as these factors remained stable between 2015 and 2016 (M. Balestri, unpub. data). Rather, it is likely that the presence of researchers favoured an increase in lemur encounter rates as a consequence of habituation of lemurs to human observers, and indirect deterrence of hunting. The main impact of researcher presence in terms of decreasing anthropogenic pressure is related to the creation of new job opportunities (Wrangham & Ross, 2008; Schwitzer et al., 2014). Despite the limited number of full-time employees (Table 7.4), the Ampasy research station employs several part-time workers from the local community. Employees were hired from various villages, with equal selection between sexes. Salaries are higher than the mean local salary, to favour positive community involvement, but not too high, to avoid social disequilibrium, as favouring individuals with high social standing and creating social disequilibrium has been indicated as a possible cause of failure of another forest management programme (Webber et al., 2007).

Table 7.4: **Employment at the research station.** Details of local people employed by the research station at Ampasy, with job, number of people employed, mean number of days worked per month, mean daily wage and mean monthly salary.

Job	No. employed	Mean no. of days worked per month	Mean daily wage per person (MGA)	Mean monthly salary per person (MGA)
Guide	2–4[a]	25	9,500	237,500
Cook	2	18	8,500	153,000
Guardian	2	18	8,000	144,000
Porter	8–20[a]	4	9,000	36,000
Cleaner	2	3	8,500	25,500
Total	16–30[a]	8.6–10	8,800–8,900	77,000–88,000

[a] Depending on the number of researchers at the research station (minimum: October–March; maximum: April–September).

Another important consequence of the research station was the contribution to the local economy through the purchase of food (Table 7.5). Thus, the food market for a fully operational research station near a small community such as Iaboakoho has the potential to generate new job opportunities and increase the income of local farmers. However, the management of the research station needs further improvement (e.g. constant and long-term presence of researchers) to increase the benefits across the local community. Also, a few local people associated the arrival of researchers with the almost concomitant law enforcement that prohibited them to do illegal activities in the core zone. It will be important to involve more villages in the local management and in the research station to reduce problems with the local community in the future.

Table 7.5: Consumption of local products at the research station. Estimated monthly consumption of products from the municipality of Iaboakoho by the personnel (researchers, volunteers and full-time employees) at the research station at Ampasy.

Food type	**Estimated monthly cost (MGA)[a]**
Meat	80,000–110,000
Fish	40,000–70,000
Rice & manioc	130,000–180,000
Vegetables & legumes	65,000–95,000
Other	40,000–60,000
Total	355,000–515,000

[a] Depending on the number of people at the research station (minimum: October–March; maximum: April–September).

7.4.3. Implications

Longitudinal involvement by Asity-KOMFITA and the continuation of research projects in the area are pivotal in ensuring local sustainable development. Continuous monitoring is necessary to control the impact of anthropogenic activities over time and reliably estimate wildlife populations (Fedigan & Jack, 2012; Nakamura, 2012). Promoting ecotourism may also increase community income and create alternative job opportunities for local people by conserving the forest [(Schwitzer et al., 2014); but see Krüger (2005) for the negative impacts of ecotourism on wildlife conservation]. At present, however, promoting ecotourism in the Iaboakoho community is challenging because of the lack of a paved national road from Fort Dauphin (making an already remote site further inaccessible) and inadequate infrastructure. Besides the research station, additional development strategies are implemented by Asity-KOMFITA, such as sustainable farming, a tree nursery and reforestation, effective enforcement of the dina, and environmental education

(Razafitsalama & Ravoahangy, 2010; Rakotoarimanana, 2016; Balestri et al., 2017). All these activities have been shown to create long-term benefits for both local ecosystems and communities (Manjaribe et al., 2013). However, the effectiveness of these actions in the Tsitongambarika area and the timeline for their implementation remains to be seen.

7.4.4. Conclusions

It is evident that a combination of local management and related development strategies, such as the installation of a research station, can assist in significantly reducing forest exploitation by local communities. However, a prolonged effort to maintain conservation management is necessary to avoid failure of conservation programmes (Webber et al., 2007). Furthermore, illegal activities still persist in the area, especially in villages not involved in the local management. A full integration between community needs and conservation plans needs to be in place to maintain long-term benefits. Overall, the forest near Ampasy is well preserved but there is the need to continue local management and research in the area to avoid losing this rare habitat.

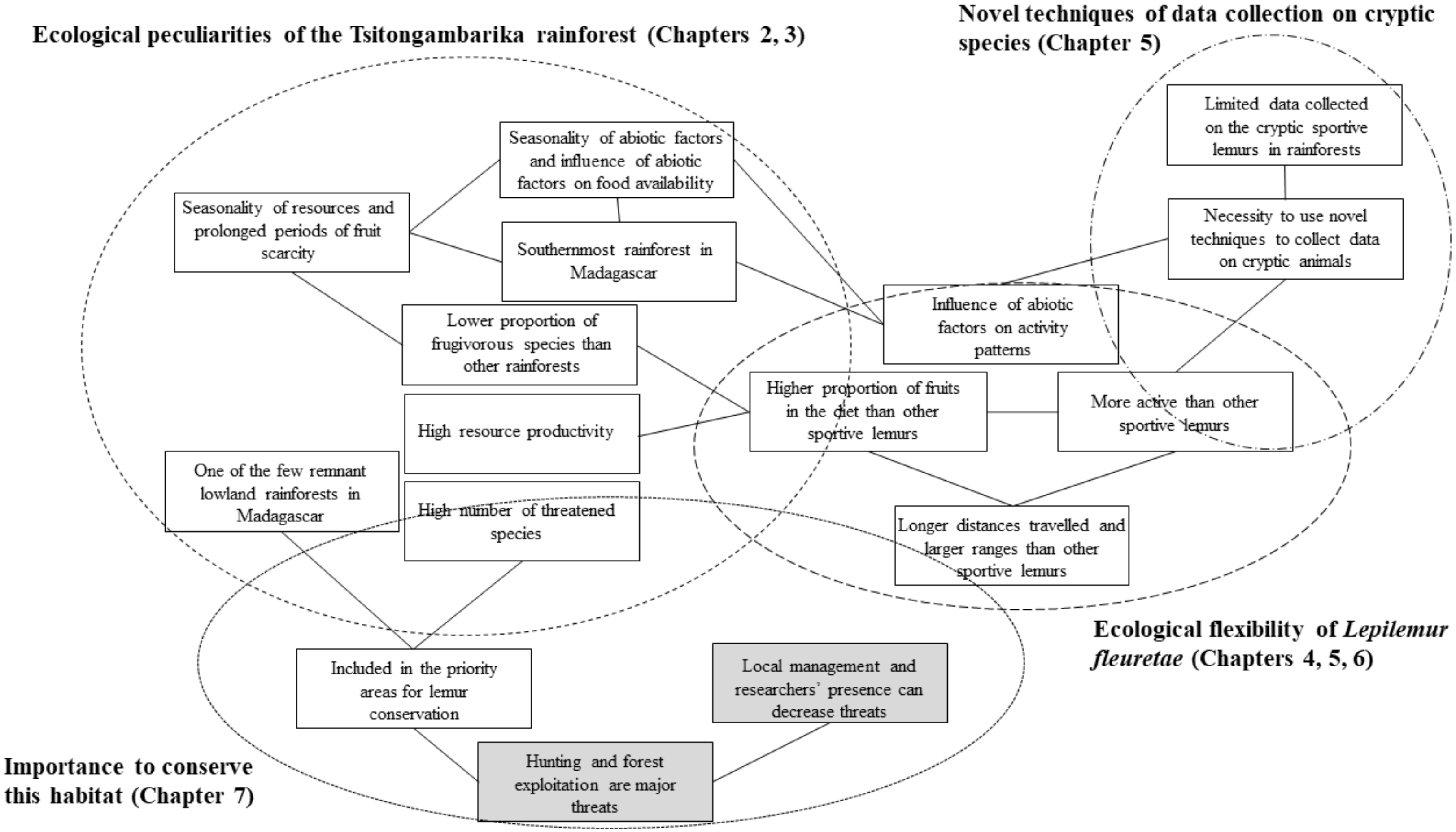

Figure 7.5: Word flowchart representing the topics of Chapter 7. Topics highlighted in grey.

Chapter 8. General discussion

The aim of this chapter is to provide a summary of the key findings of the previous chapters and to discuss them in a broader perspective. Overall, the behavioural ecology of the Critically Endangered Fleurette's sportive lemur at the Ampasy lowland rainforest in the Tsitongambarika Protected Area provided important insights into the understanding of the ecology of this genus.

8.1. Main findings

As shown in Chapter 3, the Tsitongambarika (TGK) rainforest represents a peculiar habitat since it is one of the rainforests with the lowest number of frugivorous lemur species in eastern Madagascar. One possible explanation for this pattern may be the prolonged bottle-necks of fruit scarcity since TGK seems to be the rainforest with the longest time-window of fruit scarcity in Madagascar. Conversely, the peak of fruit production is comparable to other rainforests in Madagascar and other continents (see Table 3.2). This is not supporting the hypothesis that low peaks of fruit availability may explain the paucity of frugivorous primate in Malagasy rainforests (Federman et al., 2017). The southern position of the TGK rainforest may play an important role in shaping seasonal patterns of phenological profiles, and the prolonged periods of food scarcity are suggested as possible ecological drivers for the low number of frugivorous lemurs in the area. My ecological explanation is in addition rather than mutually exclusive to the existing hypotheses explaining the patterns of species assemblages in Malagasy rainforests, including the one claiming that species distribution is constrained by the geometry of the rainforest area left on the island (Lees et al., 1999; Goodman & Ganzhorn, 2004). Daylength, however, had a lower influence than expected on phenological patterns, possibly due to rainfall and cloud density that may have limited solar irradiation (Wright & van Schaik, 1994).

Patterns of fruiting and flowering in TGK were mainly influenced by rainfall and ambient temperature that contributed to the high synchrony of phenological patterns between tree species at Ampasy. Apart from the strong seasonality, this lowland rainforest hosts the folivorous species *Avahi meridionalis* that has been shown in other habitats to limit the food intake of *Lepilemur* spp. when in sympatry (Ganzhorn, 1993). These two factors, resources availability and competition, are suggested as significant drivers of the peculiar ecological traits of *L. fleuretae* at Ampasy.

Considering the low metabolism and the previous findings on other species of this genus (see Chapter 1), I expected *L. fleuretae* to show evidence of low energy expenditure such as short distances travelled, small home ranges, and a considerable amount of time spent resting. In fact, other sportive lemurs were found to rely on behavioural and physiological adaptations to cope with a low-quality diet despite their small body size [*L. edwardsi* (Hladik & Charles-Dominique, 1974); *L. petteri* (Nash, 1998); *L. ruficaudatus* (Schmid & Ganzhorn, 1996)]. Conversely, *L. fleuretae* in TGK is particularly active when compared to other species of this genus. In fact, *L. fleuretae* travelled longer distances and had larger home ranges than any species of sportive lemurs studied so far (see Chapter 4). This is coupled with and probably a consequence of the higher proportion of fruits and flowers in the diet of this species when compared to the other sportive lemurs in Madagascar (see Table 4.3). *Lepilemur* spp. are also known to rely on abundant resources to reduce dietary overlap with the ecologically equivalent *Avahi* spp. (Thalmann, 2001), and the shift to flowers and fruits in *L. fleuretae* at Ampasy may be a consequence of this competition. Contrary to what has been hypothesized for a long time, these might be indications that in some habitats there is between-group scramble competition even between folivorous species as postulated by Snaith & Chapman (2007). The low competition with frugivorous species may have favoured the choice of this strategy. *Lepilemur fleuretae* was very selective in the plant species from where to feed fruits and flowers, suggesting that these food items were particularly high in nutritional quality, although I cannot test this hypothesis since I do not have nutritional values of random plants in the forest. By looking at the nutritional content of the priority food items of *L. fleuretae*, flowers of *Albizia* sp. (main food item during the season of food abundance, see Table 4.1) were particularly rich in nitrogen (3.09%; M. Balestri, unpub. data) and thus a high-quality resource, considering that the average content of fruit nitrogen in Madagascar is 0.98% (Donati et al., 2017). Further studies are required, however, to have detailed information on the diet of *L. fleuretae* at Ampasy due to the relatively low amount of hours of behavioural observations collected in this study. In particular, the data collection was fragmented during the season of food abundance due to heavy rains, especially from December to February when most of the trees at Ampasy had the peak of flowering and fruiting (see Appendix III). It is thus possible that the diet of *L. fleuretae* is even richer in fruits and flowers than what I reported. The social structure of this species of *Lepilemur* was not among the aims of this study, although I suggested a solitary living and polygynous dispersed social system based on the data collected. This is another aspect in which *L. fleuretae* differs from other sportive lemurs inhabiting other habitats (see Chapter 4.4.3), and further investigation is required on this species as well as on the other species inhabiting the Malagasy eastern rainforests.

In Chapter 5, I reported the validation of a new approach to describe activity pattern and time-budget in primates, the use of the unsupervised learning algorithm to extrapolate behaviours from accelerometer data. I discussed the need for a validation with direct behavioural observations when reporting activity patterns obtained from accelerometer data. I also suggested that the unsupervised learning algorithm can potentially provide fine-grained information that was previously impossible to collect, such as detailed information on locomotory behaviours. The activity profiles of *L. fleuretae* at Ampasy suggests that this species is more active than other species of sportive lemurs inhabiting other habitats (see Chapter 5.4.2). As prevously mentioned, this may be due to changes in dietary preferences, with flowers of *Albizia* sp. included in the diet. Flowers may have a more clumped distribution than leaves, and this may have required longer distances travelled and higher activity. It is important to collect activity data over a longer period to have a clearer picture of the relationship between dietary choices, spatial distribution of resources, and activity patterns. Accelerometer data can have other applications such as estimations of energy expenditure. The potential of automatic loggers in primatology, especially on cryptic species, is significant and it is important to collaborate with researchers with more experience using these technologies in this field, such as ornithologists and herpetologists. The use of automatic loggers for reconstructing activity can provide detailed information and the unsupervised learning algorithm can be particularly useful to extrapolate data collected on cryptic species, for which behavioural observations are challenging. This allowed us the collection of novel information on the activity patterns and the influence of photoperiodic variations and moon phase on them (see Chapter 6).

Photoperiodic variation strongly influenced the activity patterns of *L. fleuretae* at Ampasy, probably due to the seasonal synchrony of resources that are thus relatively predictable for the animals (Curtis & Donati, 2013). *Lepilemur fleuretae* was lunarphobic at night, possibly as an anti-predator strategy due to the presence at TGK of a full set of predators, including the main predator of this lemur species, the cathemeral fossa *Cryptoprocta ferox*. Conversely, the species was lunarphilic at twilights. The observation of the individuals very vigilant when starting their activity and scanning in search for predators suggests that predation risk may also explain this pattern. The peaks of activity of *L. fleuretae* at Ampasy were at different times than the ones of *A. meridionalis* (M. Balestri, unpub. data), suggesting an additional dimension to reduce niche overlap, i.e. a different temporal niche (Ganzhorn, 1989). In fact, *L. fleuretae* was more active during the central hours of the night, while *A. meridionalis* was more active at twilight and showed opportunistic cathemeral activity (M. Balestri, unpub. data).

Another indication that *L. fleuretae* at Ampasy avoid the between-group scramble competition with *A. meridionalis* by increasing the niche separation is the high density in the area [0.81 ind/ha (M. Balestri, unpub. data)]. The encounter rates of *L. fleuretae* at Ampasy [2.26 ind/km (M. Balestri, unpub. data)] were higher than the encounter rate of the same species at Andohahela [0.46 ind/km in the transects below 600m (Feistner & Schmid, 1999)]. During my study at Ampasy, I observed that *L. fleuretae* tend to stay more in the interior part of the forest than in the forest edge, supporting previous findings in the Vohibola rainforest (Lehman, 2007). This preference for mature, interior forest indicates that Fleurette's sportive lemurs, in fact, may be strongly threatened by habitat fragmentation, that also increases exposure to hunting pressure (Craul et al., 2009). In fact, sportive lemurs are mainly hunted when spotted in sleeping trees during the day, and they do not show a flight response towards humans (Rabesandratana & Zimmermann, 2005). From the interviews in the villages surrounding the Ampasy area (see Chapter 7), it also emerged that it is easy to capture *L. fleuretae* when found in sleeping trees during the day since the animals freeze and do not try to escape. Fleurette's sportive lemur, however, was one of the species less eaten in the area (32.9% of the participants reported to have eaten this species, see Chapter 7), probably due to the difficulty in spotting this animals in this continuous forest. Despite its low occurrence as hunted species, it is important to limit the forest exploitation in the area to avoid dramatic habitat loss that may compromise this unique habitat and the Critically Endangered Fleurette's sportive lemurs. A combination of local management and related development strategies, such as the installation of a research station, is suggested to assist in preserving this habitat; although a balance between community needs and conservation plans in necessary to maintain long-term benefits (see Chapter 7). Overall, the forest near Ampasy is well preserved, but there is the need to continue local management and research in the area to avoid losing this rare habitat.

8.2. Limitations

The main limitation of this study was the small sample size related to behavioural observations. In fact, other studies on sportive lemurs in deciduous and spiny forests collected data for more than 1000 h of direct observations [e.g. Méndez-Cárdenas & Zimmermann (2009); Hilgartner et al. (2012); Dröscher & Kappeler (2013, 2014)]. In these studies, researchers also captured all the overlapping animals in an area of the forest, thus having at least 10 animals. The capture of animals at Ampasy, however, was complicated and even a specialist team had difficulties. The team would have required at least two weeks to capture all the overlapping individuals in an area of the forest. Furthermore, two animals were killed by the fossa during the study period, and the two animals equipped with backpacks removed them after a few weeks. Nevertheless, even if all the individuals present in an area were captured, it would have been likely that other individuals would have had part of their home ranges in the area considering the relatively large home ranges of this species and the continuous habitat. It is thus very difficult to conduct a detailed study on the social structure of Fleurette's sportive at Ampasy.

To partially overcome the problem of behavioural data collection, I collected the locations of animals via triangulation, thus obtaining reliable ranging patterns of four individuals. The activity patterns were estimated via accelerometers allowing a continuous sampling over three months on three individuals. Even if I reduced the sample size by limiting the sampling period and the number of individuals, the data presented on activity patterns are much more reliable than using behavioural data. This is because of the large amount of out of sights during the behavioural observation of this cryptic species, which is particularly difficult to follow in a hilly area of rainforest such as the Ampasy valley. Activity (locomotion in particular) would have been underestimated since the animals were difficult to follow due to their rapid movements. It would be important to extend the data collection via accelerometers to different seasons to have a clearer activity pattern. The diet of Fleurette's sportive lemurs at Ampasy is one of the aspects that requires more investigation. The dietary data can be considered as preliminary, although they provided interesting insights. That is the reason why I showed dietary data with descriptive statistics, avoiding inferential statistics.

The data collected, despite the small sample size, gave statistically significant results and, overall, provided interesting insights on the ecological flexibility of the genus *Lepilemur*. Furthermore, all the data collected on the behavioural ecology of Fleurette's sportive lemur will be compared with the data collected on Southern woolly lemur in future publications. This will partially overcome the problem of a low sample size, similar to what done before at Ampijoroa (Warren & Crompton, 1997a, 1997b; Thalmann, 2001, 2006).

8.3. Future directions

Future research focusing on the behavioral ecology of *Lepilemur* spp. living in rainforests will help elucidate the full extent of the ecological flexibility and/or intra- and inter-specific variability withing this genus. In particular, it will be important to determine whether the hyperactivity, the large home range, and the large amount of fruits and flowers in the diet of *L. fleuretae* can be found in other species in rainforests or whether the Tsitongambarika forest is a peculiar habitat that determined this different behavioural ecology. Also, a detailed study on the energetics of *L. fleuretae*, as well as of other sportive lemurs in rainforests, may elucidate whether there is a physiological flexibility in the genus. Another interesting aspect to explore is the absence of *Lepilemur* from littoral forest fragments of Mandena and Sainte Luce. A possible reason is the lack of suitable trees for sleeping, and a comparative study on the presence/absence of this genus in different fragments of littoral forests related to the habitat characterisation may help explain this aspect.

A project meant to determine which native tree species have higher rates of germination and growth rate is advisable, similar to what was done at Kianjavato (Manjaribe et al., 2013). The Ampasy research station can host a plant nursery that can provide new job opportunities for local people and give important data for future habitat restoration projects. The habitat restoration project should be coordinated with Asity and should be meant to expand the buffer zone (to provide timber and firewood for local people) and restore area subjected to slash and burn agriculture in the past.

The hunting project I presented in this dissertation can also be extended to other valleys close to Ampasy to determine the anthropogenic pressure in neighbouring areas. This is necessary to determine which villages should be prioritised for future projects meant to give alternative job opportunities to local people to decrease anthropogenic pressure on the forest. A project on conservation education with the schools in the municipality of Iaboakoho is also necessary to raise awareness on lemur ecology and promote pro-environmental behaviours in future generations.

An important research project to continue is the one related to the niche separation between Fleurette's sportive lemur and Southern woolly lemur. Other aspects should be investigated such as the temporal niche separation, with accelerometer data collected for an entire year. Another aspect to explore more in depth is the role of the gut bacterial community in detoxification processes by comparing the genes associated with the two species and determine analogies and differences (Fackelmann, 2017). Also, sensory adaptations related to colour, odour, hardness and taste of food items eaten should be explored in depth to determine hidden aspects of the dietary niche separation between the two species.

The use of three-axis accelerometers is suggested to provide detailed information on the activity patterns of cryptic species, for which behavioural observations are challenging. The EM algorithm resulted a fine-grained technique to analyse a massive dataset and obtain reliable behavioural categories, and it is necessary to extend the analysis suggested in this thesis to other primates, but also to other nocturnal mammals. Accelerometers, as well as other automatic loggers (e.g. loggers for animal locations and body temperature), can provide novel information on the behavioural ecology of cryptic species and unveil new behavioural and ecological patterns.

8.4. Conclusion

In conclusion, this study highlighted the ecological flexibility of the genus *Lepilemur* that occupies all the forested habitats in Madagascar with different ecology depending on the habitat type. With the recent discovery of 26 species belonging to this genus (Hoffmann et al., 2009), and detailed information on only five of them (six including *L. fleuretae*), it is clear that the ecology of this genus is still far to be completely understood. Due to the difficulties in gathering data on this genus in rainforests, automated data loggers can assist in providing new insights on the more cryptic species of this genus. As it occurred in other lemur taxa in recent years, long-term data from habitats where species have been poorly studied reveal that many lemurs are less constrained by their specializations than previously assumed. Further studies are necessary to clarify the extent of flexibility of this genus in the rainforest. The use of automatic loggers such as accelerometers may lead to a new approach on the study of cryptic animals and provide novel information on poorly known species.

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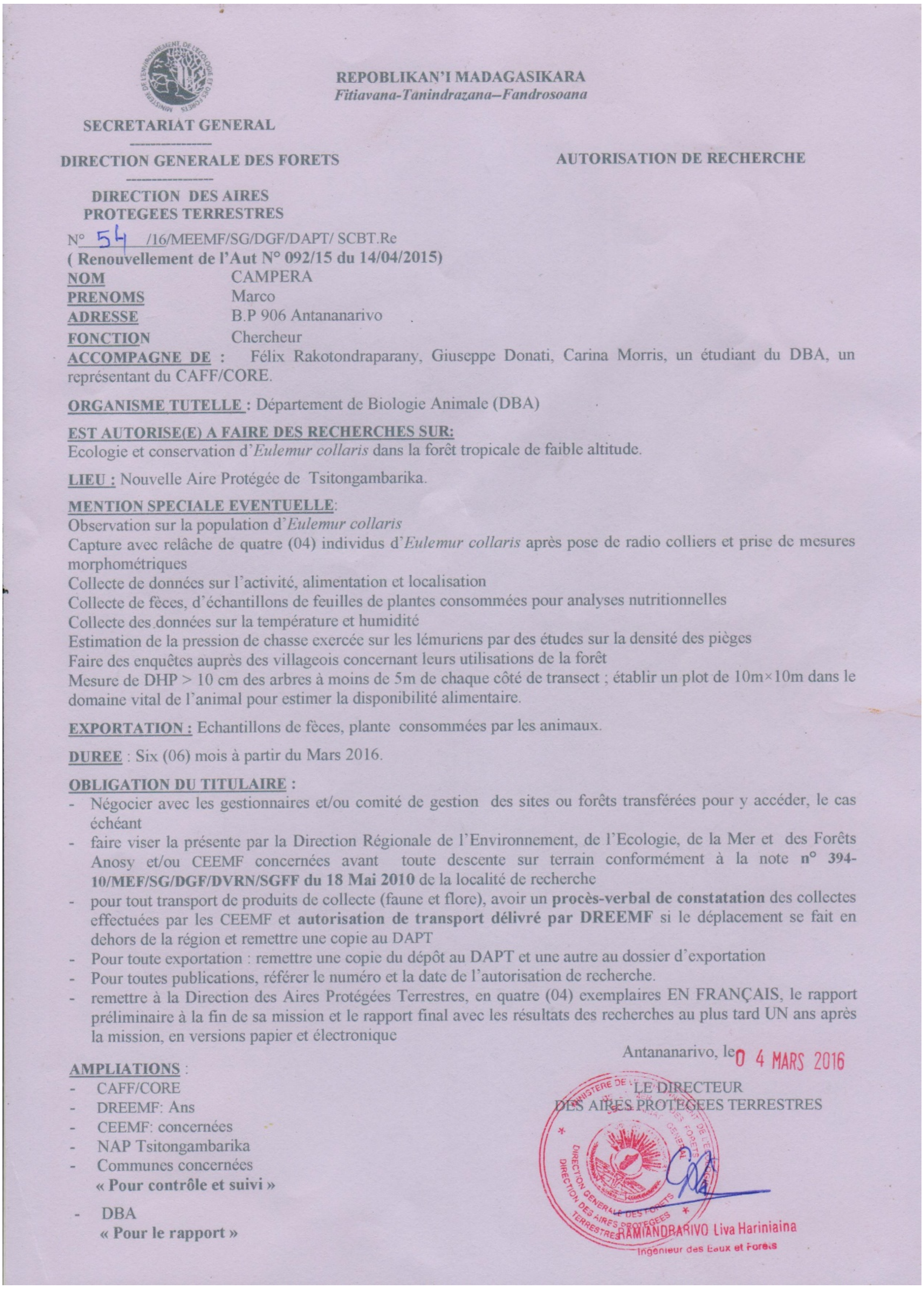
Appendix I: research permits.



SECRETARIAT GENERAL

DIRECTION GENERALE DES FORETS

DIRECTION DES AIRES PROTEGEES TERRESTRES

REPOBLIKAN'I MADAGASIKARA
Fitiavana-Tanindrazana–Fandrosoana

AUTORISATION DE RECHERCHE

N° 54 /16/MEEMF/SG/DGF/DAPT/ SCBT.Re

(Renouvellement de l'Aut N° 092/15 du 14/04/2015)

NOM	CAMPERA
PRENOMS	Marco
ADRESSE	B.P 906 Antananarivo
FONCTION	Chercheur

ACCOMPAGNE DE : Félix Rakotondraparany, Giuseppe Donati, Carina Morris, un étudiant du DBA, un représentant du CAFF/CORE.

ORGANISME TUTELLE : Département de Biologie Animale (DBA)

EST AUTORISE(E) A FAIRE DES RECHERCHES SUR:
Ecologie et conservation d'*Eulemur collaris* dans la forêt tropicale de faible altitude.

LIEU : Nouvelle Aire Protégée de Tsitongambarika.

MENTION SPECIALE EVENTUELLE:
Observation sur la population d'*Eulemur collaris*
Capture avec relâche de quatre (04) individus d'*Eulemur collaris* après pose de radio colliers et prise de mesures morphométriques
Collecte de données sur l'activité, alimentation et localisation
Collecte de fèces, d'échantillons de feuilles de plantes consommées pour analyses nutritionnelles
Collecte des données sur la température et humidité
Estimation de la pression de chasse exercée sur les lémuriens par des études sur la densité des pièges
Faire des enquêtes auprès des villageois concernant leurs utilisations de la forêt
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

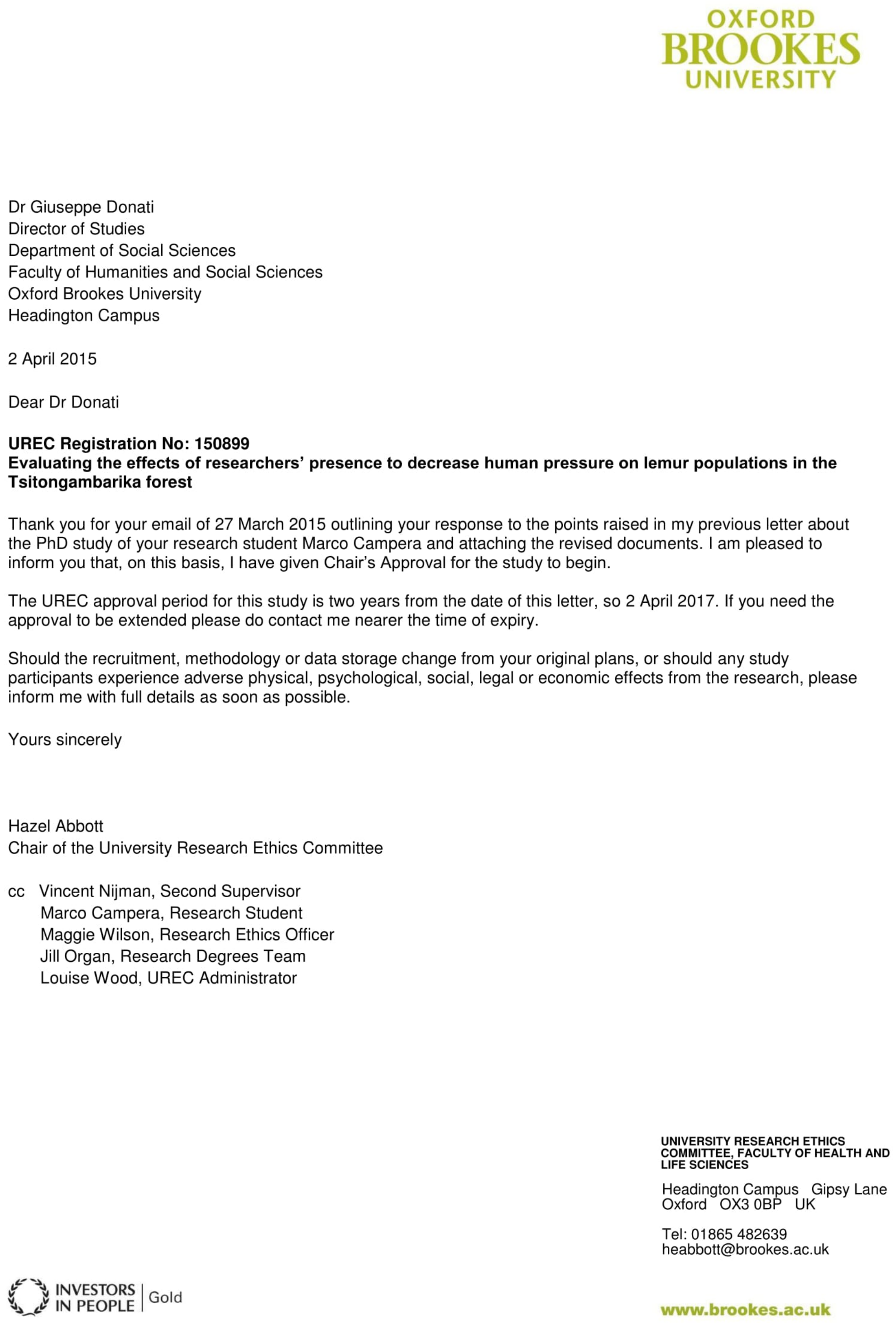
LE DIRECTEUR
DES AIRES PROTEGEES TERRESTRES

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 II: 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

2 April 2015

Dear Dr Donati

UREC Registration No: 150899
Evaluating the effects of researchers' presence to decrease human pressure on lemur populations in the Tsitongambarika forest

Thank you for your email of 27 March 2015 outlining your response to the points raised in my previous letter about the PhD study of your research student Marco Campera 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 2 April 2017. 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

Hazel Abbott
Chair of the University Research Ethics Committee

cc Vincent Nijman, Second Supervisor
Marco Campera, Research Student
Maggie Wilson, Research Ethics Officer
Jill Organ, Research Degrees Team
Louise Wood, UREC Administrator

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Appendix III: Phenology of the tree species at Ampasy. Food Availability Index (FAI) and peaks of Young Leaves (YL), Flowers (FL), and Ripe Fruits (RF) production per species at Ampasy from July 2015 to June 2016. The max FAI is stem density (trees/ha) * mean DBH (dm). Peak of production indicates that more than 1/3 of trees are in the corresponding phenological phase. YR: multiple peaks in the same year.

Order[1]	**Family**	**Species**	**Common name**	**Max FAI**	**YL**	**FL**	**RF**
	Clade: Magnoliids						
Laurales	Lauraceae	*Cryptocarya lacrimans*	Viary	10.4	Oct-Dec	Nov-Dec	Dec-Jan
		Cryptocarya sp. 1	Remilaza	0.5	Nov-Jan	Dec-Jan	Jan
		Cryptocarya sp. 2	Tavolohazo	16.5	Oct-Jan	Nov-Dec	Jan
		Ocotea racemosa	Varongy	28.9	Oct-Jan	Nov-Dec	Jan-Feb
		Ocotea sp.	Valotry	5.3	Oct-Dec	Oct-Nov	Jan
		Potameia madagascariensis	Tsalela	0.4	Oct-Jan	Oct-Nov	Dec-Jan
	Monimiaceae	*Tambourissa religiosa*	Ambora	16.2	Oct-Dec	Nov-Dec	Feb
		Tambourissa trichophylla	Bety	0.4	Oct-Jan	Nov	Dec-Jan
Magnoliales	Annonaceae	*Monanthotaxis madagascariensis*	Rangomafotry	12.5	Oct-Jan	Nov-Dec	Dec-Feb
		Polyalthia sp.	Hazaomby	0.3	Nov-Feb	Jan-Feb	Mar-Apr
		Xylopia sp.	Fotsivavy	18.6	Oct-Jan	Oct-Nov	Dec-Feb
	Myristicaceae	*Brochoneura acuminata*	Mafotra	117.3	Nov-Jan	Nov	Dec-Feb
	Clade: Monocots						
Alismatales	Araceae	*Pothos scandens*	Mandrio	1.0	Sep-Dec	Nov-Dec	Jan
Arecales	Araliaceae	*Polyscias pentamera*	Batsiala	1.4	Oct-Dec	Nov-Dec	Jan
		Schefflera voantsilana	Voantsila	13.7	Dec-Jan	Dec	Jan
		Cuphocarpus aculeatus	Tsitongampossa	4.3	YR	YR	YR
	Arecaceae	*Dypsis arenarum*	Hirihiry	3.2	Jan-Feb	Jan	Feb-Mar
		Dypsis lilacina	Telopoloambilany	6.1	Feb	Feb	Mar
		Dypsis mananjarensis	Lafa	2.8	Jan-Mar	Jan-Feb	Mar-Apr
		Dypsis pilulifera	Tavilokoko	0.5	Feb-Mar	Feb-Mar	Mar-Apr

Order[1]	**Family**	**Species**	**Common name**	**Max FAI**	**YL**	**FL**	**RF**
Clade: Monocots							
		Dypsis prestoniana	Mangidy	6.9	YR	YR	YR
		Dypsis pustulata	Vonotry	7.6	YR	YR	YR
		Orania longisquama	Tsindro	1.7	Jun-Aug	Jun-Jul	Jul-Aug
		Ravenala madagascariensis	Ravinala	1.2	Apr-May	Apr-May	May-Jul
		Ravenea lakatra	Lakatry	1.2	Dec	Dec	Jan
		Ravenea sp.	Hanivo	4.3	YR	YR	YR
Asparagales	Asparagaceae	*Dracaena reflexa*	Falinandro	2.8	YR	YR	YR
	Iridaceae	*Aristea angustifolia*	Midinigiavy	0.8	Dec-Feb	Dec-Jan	Feb-Mar
Pandanales	Pandanaceae	*Pandanus* sp.	Fandra	37.4	YR	YR	YR
Clade: Eudicots							
Asterales	Asteraceae	*Brachylaena* sp.	Hazotona	3.2	Oct-Feb	Nov-Dec	Jan
		Centauropsis antanossi	Fotsivaliky	3.1	Nov-Feb	Nov-Dec	Jan-Feb
Boraginales	Boraginaceae	*Ehretia macrocarpa*	Vatoa	5.3	Aug-Jan	Nov-Dec	Jan-Feb
Brassicales	Capparaceae	*Crateva obovata*	Faritraty	2.6	Nov-Feb	Dec-Jan	Jan-Feb
Buxales	Buxaceae	*Buxus angustifolia*	Retsiriky	0.7	YR	Nov-Dec	Jan
		Didymeles perrieri	Fanala	0.3	Sep-Dec	Nov	Dec-Jan
Caryophyllales	Asteropeiaceae	*Asteropeia micraster*	Fanolantolo	0.6	Nov-Feb	Dec-Jan	Jan-Mar
		Asteropeia multiflora	Fanolabemavao	3.1	YR	YR	YR
		Asteropeia rhopaloides	Fanola	3.7	Aug-Jan	Nov-Dec	Dec-Feb
	Physenaceae	*Physena madagascariensis*	Retsonzo	0.8	Oct-Dec	Oct	Nov-Dec
Celastrales	Celastraceae	*Brexiella* sp.	Resilaitry	2.6	Sep-Jan	Nov-Dec	Jan-Feb
		Cassine micrantha	Harambohazo	3.7	Sep-Jan	Nov-Dec	Dec-Feb
		Polycardia orientalis	Tsimahasoky	2.3	Oct-Jan	Oct-Nov	Dec-Jan
		Polycardia phyllantoides	Fandrianakanga	2.9	Oct-Jan	Nov-Dec	Dec-Jan
Crossosomatales	Aphloiaceae	*Aphloia theiformis*	Fandramana	5.8	Oct-Jan	Nov-Dec	Dec-Feb

Order[1]	Family	Species	Common name	Max FAI	YL	FL	RF
Clade: Eudicots							
Cucirbitales	Anisophylleaceae	*Anisophyllea phallax*	Hazomamy	5.3	Nov-Jan	Nov	Dec-Feb
Dilleniales	Dilleniaceae	*Dillenia triqueta*	Varikanda	16.2	Oct-Jan	Dec	Jan-Feb
Ericales	Ebenaceae	*Diospyros* sp. 1	Hazomety	22.6	Nov-Jan	Nov-Dec	Dec-Feb
		Diospyros sp. 2	Hazomasy	4.1	Oct-Jan	Oct-Nov	Dec-Jan
	Lecythidaceae	*Barringtonia* sp.	Kamboky	1.3	Oct-Feb	Nov-Dec	Dec-Feb
	Primulaceae	*Oncostemum* sp. 1	Hazotoho	3.6	Nov-Jan	Dec	Jan
		Oncostemum sp. 2	Lona	6.8	Oct-Jan	Nov-Dec	Jan
	Sapotaceae	*Capurodendron androyense*	Hazomiteraky	8.8	Oct-Feb	Nov-Dec	Jan-Mar
		Capurodendron pervillei	Beladitra	4.9	YR	YR	YR
		Capurodendron sp.	Nanto	79.5	Sep-Jan	Nov-Dec	Jan
		Chrysophyllum boivinianum	Rehiaky	13.3	Sep-Jan	Oct-Nov	Dec-Feb
		Faucherea tampoloensis	Natoroboky	1.6	Aug-Jan	Oct-Nov	Dec-Feb
		Mimusops sp.	Tendrokazo	3.7	Sep-Jan	Nov-Dec	Jan-Feb
		Sideroxylon tambolokoko	Tambolokoko	1.1	Oct-Dec	Dec	Jan
Fabales	Fabaceae	*Albizia* sp.	Mendoravy	22.2	Sep-Nov	Sep	Oct-Nov
		Calliandra thouarsiana	Menbolazo	3.3	YR	Nov-Dec	Dec-Jan
		Cynometra cloiselii	Voariotry	13.6	Oct-Jan	Oct-Nov	Nov-Dec
		Cynometra sp.	Mampay	25.8	Nov-Feb	Nov-Dec	Dec-Feb
		Dalbergia baronii	Manary	3.5	Oct-Jan	Dec	Jan
		Dalbergia maritima	Tombobisy	4.2	Oct-Dec	Nov-Dec	Jan-Mar
		Dalbergia emirnensis	Andromena	1.6	Oct-Feb	Dec	Jan-Feb
		Indigofera sp.	Hengitry	1.3	Oct-Feb	Dec-Jan	Jan-Feb
		Intsia bijuga	Harandrato	0.9	Oct-Jan	Dec	Jan-Feb
		Intsia sp.	Hintsy	4.1	Oct-Jan	Nov-Dec	Jan
		Mimosa latispinosa	Romino	2.0	Oct-Jan	Dec	Jan-Feb

Order[1]	Family	Species	Common name	Max FAI	YL	FL	RF
	Clade: Eudicots						
		Phylloxylon sp.	Mahasalama	3.2	YR	YR	YR
		Sylvichadsia grandiflora	Fanamo	9.1	Aug-Dec	Sep-Nov	Dec-Jan
		Viguieranthus alternans	Hazomallany	10.9	Sep-Jan	Nov	Dec-Jan
		Viguieranthus brevipennatus	Kingiza	1.3	Nov-Apr	Dec-Jan	Jan-Feb
Gentianales	Apocynaceae	*Cabucala madagascariensis*	Kabokala	3.8	YR	YR	YR
		Carissa madagascariensis	Hazolahy	0.5	YR	Dec-Jan	Jan-Feb
		Mascarenhasia speciosa	Hazondrano	14.1	Nov-Mar	Dec-Jan	Jan-Mar
		Plectaneia sp.	Hazomanahaky	1.5	YR	YR	YR
		Sarcostemma viminale	Bemavao	0.9	Jan-Mar	Feb-Mar	Mar
	Loganiaceae	*Anthocleista madagascariensis*	Lendemilahy	2.2	YR	YR	YR
	Rubiaceae	*Bremeria* sp. 1	Tangalavo	1.7	YR	YR	YR
		Bremeria sp. 2	Fantora	5.0	Sep-Jan	Nov	Dec-Feb
		Breonia sp.	Hafovalotry	4.0	YR	YR	YR
		Canephora madagascariensis	Hazongalala	3.5	Nov-Feb	Nov-Dec	Dec-Feb
		Canthium medium	Fantsikaitry	21.1	YR	YR	YR
		Coffea sp.	Manibary	8.1	YR	YR	YR
		Enterospermum madagascariensis	Mangavoa	1.7	YR	YR	YR
		Gaertnera macrostipula	Hazondengo	3.0	Nov-Mar	Dec-Jan	Jan-Feb
		Gaertnera raphaelii	Tanatananala	3.0	Sep-Feb	Nov-Dec	Jan-Mar
		Hyperacanthus rajeriarisonae	Taolanampossy	3.7	Oct-Feb	Dec	Jan-Feb
		Hyperacanthus sp.	Taolana	11.2	Oct-Jan	Nov-Jan	Jan
		Ixora sp.	Masosoraky	3.1	Oct-Dec	Jan	Feb
		Janotia macrostipula	Valopangady	2.5	YR	YR	YR
		Peponidium sp.	Robelo	3.1	Oct-Feb	Dec-Jan	Jan-Feb
		Psychotria sp. 1	Fotsivoho	1.0	Nov-Feb	Dec	Jan

Order[1]	**Family**	**Species**	**Common name**	**Max FAI**	**YL**	**FL**	**RF**
	Clade: Eudicots						
		Psychotria sp. 2	Hazombato	0.5	YR	YR	YR
		Rothmannia sp. 1	Taolanamainty	2.9	Nov-Feb	Jan	Jan-Feb
		Rothmannia sp. 2	Taolanambariky	5.3	YR	YR	YR
		Rothmannia thouarsii	Valopossy	0.6	Oct-Feb	Dec-Jan	Jan-Mar
		Saldinia proboscidea	Lengohazo	2.3	Oct-Jan	Oct-Nov	Dec-Jan
		Saldinia sp.	Hazondranoka	3.0	Oct-Dec	Jan	Feb
Lamiales	Acanthaceae	*Anisotes madagascariensis*	Beravy	1.2	Oct-Jan	Dec	Jan-Mar
	Bignoniaceae	*Phyllarthron ilicifolium*	Zahambe	0.3	YR	Nov-Dec	Jan-Feb
		Phyllarthron sp.	Zaha	2.0	Sep-Jan	Nov-Dec	Jan
		Rhodocolea sp.	Sikondrokondro	0.4	Aug-Jan	Oct-Nov	Nov-Jan
	Verbenaceae	*Coelocarpum humbertii*	Rombavola	0.9	Dec-Mar	Feb	Mar
	Lamiaceae	*Vitex beraviensis*	Hazomahavelo	1.8	YR	YR	YR
Malpighiales	Chrysobalanaceae	*Magnistipula tamenaka*	Tamenandrano	1.0	Aug-Jan	Nov-Dec	Jan
	Clusiaceae	*Calophyllum inophyllum*	Vitao	52.2	Oct-Feb	Nov-Jan	Jan-Feb
		Garcinia aphanophlebia	Ditsaky	15.6	Oct-Feb	Dec-Jan	Jan-Feb
		Garcinia madagascariensis	Betsivo	0.5	Oct-Dec	Nov-Dec	Jan-Feb
		Garcinia chapelieri	Akily	1.4	YR	Nov	Dec-Jan
		Garcinia verrucosa	Zambo	5.5	Oct-Feb	Dec	Jan-Feb
		Symphonia tanalensis	Haziny	59.9	YR	YR	YR
	Erythroxylaceae	*Erythroxylum* sp.	Menahihy	50.5	Oct-Jan	Nov-Dec	Jan-Feb
	Euphorbiaceae	*Acalypha* sp.	Maintsoravy	2.7	Nov-Feb	Dec	Jan-Feb
		Anthostema madagascariensis	Bamby	15.9	Sep-Dec	Sep-Nov	Nov-Dec
		Croton boiteaui	Tolaky	0.7	YR	?	?
		Croton louvelii	Singena	1.3	Oct-Jan	Dec-Jan	Jan
		Drypetes madagascariensis	Remboky	1.5	Oct-Jan	Nov	Dec-Jan

Order[1]	Family	Species	Common name	Max FAI	YL	FL	RF
Clade: Eudicots							
		Macaranga cuspidata	Talaka	0.8	YR	YR	YR
		Macaranga obovata	Mokarana	4.9	Oct-Feb	Oct-Dec	Dec-Feb
		Suregada crenulata	Kalavelo	1.9	Nov-Feb	Nov-Dec	Jan
	Hypericaceae	*Harungana madagascariensis*	Haronga	2.1	Jan-Mar	Feb-Mar	Mar-May
		Psorospermum nervosum	Harongampanihy	1.9	Oct-Jan	Nov-Dec	Jan-Feb
	Ochnaceae	*Ouratea anceps*	Hazondraotry	15.8	Nov-Jan	Dec-Jan	Jan-Feb
		Ouratea obtusifolia	Marandravy	1.3	YR	Nov-Dec	Jan
	Phyllanthaceae	*Cleistanthus* sp.	Tainbarika	13.0	Oct-Jan	Nov-Dec	Jan-Feb
		Flueggea virosa	Tsimarefy	2.2	YR	YR	YR
		Thecacoris madagascariensis	Hazondranoha	3.4	YR	YR	YR
		Uapaca ferruginea	Hazondandy	7.9	Nov-Jan	Nov-Dec	Dec-Feb
		Uapaca thouarsii	Voapaky	156.0	YR	YR	YR
		Wielandia leandriana	Votakala	4.0	Oct-Feb	Nov-Dec	Dec-Feb
		Wielandia mimosoides	Korofoky	9.9	YR	YR	YR
	Salicaceae	*Homalium axillare*	Lapivahatry	9.3	YR	Nov-Jan	Jan-Mar
		Homalium brevipedunculatum	Roandrano	3.1	YR	YR	YR
		Homalium microphyllum	Hazofotsy	52.5	YR	Nov-Jan	Jan-Mar
		Ludia sp.	Hazofotsindroka	1.3	YR	YR	YR
		Ludia spinosa	Fantsikoho	3.1	Nov-Feb	Nov-Dec	Dec-Jan
		Scolopia erythrocarpa	Zora	30.1	Sep-Nov	Nov-Dec	Dec-Jan
		Scolopia orientalis	Tsimalanilamba	2.2	Nov-Jan	Dec-Jan	Jan
	Violaceae	*Rinorea angustifolia*	Voafontsy	1.6	Oct-Feb	Nov-Dec	Dec-Feb
		Rinorea arborea	Hazondomohy	0.5	Oct-Jan	Dec-Feb	Feb-Mar
Malvales	Malvaceae	*Dombeya oblongifolia*	Hafomena	16.9	Oct-Jan	Nov-Dec	Dec-Feb
		Dombeya sp. 1	Berehoky	2.5	Sep-Dec	Oct-Nov	Dec-Feb

Order[1]	Family	Species	Common name	Max FAI	YL	FL	RF
Clade: Eudicots							
		Dombeya sp. 2	Valimafy	11.6	YR	Nov	Dec-Feb
		Grewia sp. 1	Akolahikafitra	2.0	Oct-Jan	Dec	Jan-Feb
		Grewia sp. 2	Hafopossy	2.1	Nov-Jan	Nov	Jan
		Grewia sp. 3	Vaoreoky	1.0	Oct-Feb	Nov-Jan	Jan-Feb
	Sarcolaenaceae	*Leptolaena pauciflora*	Fonto	7.2	Nov-Jan	Nov-Dec	Dec-Feb
		Schizolaena exinvolucrata	Sokazo	0.9	YR	?	?
	Sphaerosepalaceae	*Rhopalocarpus coriaceus*	Tsilavimbinato	1.2	Oct-Jan	Nov-Jan	Jan-Feb
		Rhopalocarpus sp.	Lombirinbarika	0.7	Oct-Feb	Oct-Dec	Dec-Feb
	Combretaceae	*Combretum grandidieri*	Tamenaroanga	1.0	YR	Oct-Dec	Dec-Jan
		Combretum subumbellata	Tamenakanga	4.5	Oct-Feb	Nov-Dec	Dec-Feb
		Poivrea villosa	Voatotkala	2.7	Oct-Dec	Nov-Dec	Dec-Feb
		Terminalia fatraea	Fatra	1.3	Oct-Jan	Dec	Jan
		Terminalia sp.	Beranoampo	4.8	Nov-Jan	Nov-Dec	Dec-Feb
	Melastomataceae	*Memecylon longipetalum*	Tomizo	5.6	Oct-Jan	Nov-Dec	Jan-Mar
	Myrtaceae	*Eugenia cloiselii*	Roapasy	22.7	YR	YR	YR
		Eugenia sp. 1	Mahalaza	0.4	YR	YR	YR
		Eugenia sp. 2	Robavy	12.3	YR	YR	YR
		Syzygium emirnensis	Rotry	122.5	YR	YR	YR
Oxalidales	Cunoniaceae	*Weinmannia stenostachya*	Lalo	13.4	Oct-Feb	Oct-Dec	Jan-Feb
		Weinmannia baehniana	Ringitry	3.0	Oct-Jan	Nov-Dec	Jan
	Elaeocarpaceae	*Sloanea rhodantha*	Voandoza	3.9	Oct-Dec	Nov-Dec	Dec-Feb
Proteales	Proteaceae	*Dilobeia tenuinervis*	Hivao	4.7	YR	YR	YR
		Dilobeia thouarsii	Tamenaky	69.8	Sep-Jan	Sep-Oct	Dec-Jan
		Faurea forficuliflora	Tolabao	0.3	Dec-Jan	Dec-Jan	?
Rosales	Moraceae	*Streblus dimepate*	Dipaty	7.5	Sep-Jan	Nov	Dec-Jan

Order[1]	**Family**	**Species**	**Common name**	**Max FAI**	**YL**	**FL**	**RF**
	Clade: Eudicots						
		Treculia africana	Tsarepaly	2.5	Oct-Feb	Nov-Dec	Dec-Jan
		Trilepisium madagascariensis	Vetitindaza	1.3	YR	YR	YR
Sapindales	Anacardiaceae	*Micronychia bemangidiensis*	Taranta	12.9	Oct-Feb	Oct-Dec	Dec-Jan
		Poupartia chapelieri	Sisikandrongo	2.2	Aug-Feb	Nov-Dec	Jan-Mar
		Rhus taratana	Fonofononanahary	0.4	Dec-Jan	Dec-Jan	Jan
		Soreindeia madagascariensis	Voatsiringy	0.8	Dec-Feb	Dec-Jan	Jan
	Burseraceae	*Canarium boivinii*	Haramy	9.3	Sep-Nov	Sep-Nov	Oct-Dec
	Meliaceae	*Astrotrichilia rakodomena*	Rakodimena	2.1	Oct-Feb	Nov-Dec	Jan-Feb
		Khaya madagascariennsis	Hazomena	0.5	Dec-Feb	Dec-Feb	Jan-Mar
		Malleastrum sp.	Mirangasoa	0.8	Oct-Feb	Oct-Nov	Dec-Feb
		Neobeguea leandreana	Hazolava	2.2	YR	YR	YR
		Neobeguea mahafaliensis	Bemahova	2.5	YR	Nov-Dec	Dec-Feb
		Turraea sp.	Tandria	2.4	Oct-Feb	Nov-Jan	Jan-Mar
	Rutaceae	*Vepris ampody*	Ampodinala	5.5	Oct-Dec	Dec-Jan	Jan-Mar
		Vepris elliotii	Ampoly	3.9	Nov-Jan	Nov-Jan	Dec-Feb
		Vepris fitoravina	Fitoravina	6.3	Nov-Jan	Nov-Jan	Dec-Feb
		Zanthoxylum madagascariense	Monongo	2.5	YR	YR	YR
	Sapindaceae	*Allophyllus decaryi*	Malamaravy	0.8	YR	Oct-Dec	Nov-Jan
		Plagioscyphus sp.	Takombohazo	1.4	Oct-Mar	YR	YR
		Tina fulvinervis	Vilo	5.4	Nov-Feb	Dec-Jan	Jan-Mar
		Tina striata	Hazomoro	0.8	Jan-Mar	Feb-Mar	Mar-Apr
		Tina thouarsiana	Sanirambaza	8.6	Oct-Feb	Dec-Jan	Jan-Mar
		Tinopsis conjugata	Sanira	39.2	YR	YR	YR
	Simaroubaceae	*Quassia indica*	Mangaroky	71.8	YR	Oct-Dec	Dec-Feb
Solanales	Convolvulaceae	*Humbertia madagascariensis*	Hendranendra	17.3	Sep-Dec	Sep-Nov	Nov-Dec

Order[1]	Family	Species	Common name	Max FAI	YL	FL	RF
	Other						
NA	NA	*?*	Marotana	1.3	Dec-Feb	Dec	Jan-Feb
		?	Bemisiry	0.4	Nov-Jan	Dec	Jan-Feb
		?	Homamata	0.7	YR	YR	YR
		?	Latakasosoa	0.3	Dec-Feb	Dec-Jan	Jan-Mar
		?	Marovola	1.5	Oct-Feb	YR	YR
		?	Masoranonandroa	1.5	Oct-Feb	Nov-Jan	Dec-Feb

[1] Plant classification is based on the APG IV system [Angiosperm Phylogeny Group (2016)].

Appendix IV: Ethogram used for the behavioural data collection on *Lepilemur fleuretae* 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); RF (Ripe Fruits); FL (Flowers); I (Insects)
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 V: Script for the calculation of integrated variables

```
start_msec <- 10 # decide period over which you want to run the smoothing
dorso_ventral_mean <- rep (NA, nrow (Acc_Data))
lateral_mean <- rep (NA, nrow (Acc_Data))
back_forward_mean <- rep (NA, nrow (Acc_Data))
dorso_ventral_amplitude <- rep (NA, nrow (Acc_Data))
lateral_amplitude <- rep (NA, nrow (Acc_Data))
back_forward_amplitude <- rep (NA, nrow (Acc_Data))
pitch_amplitude = rep (NA, nrow (Acc_Data))
library (plotrix)
#calculate amplitute of acceleration
dorso_ventral <- Acc_Data$Z
lateral <- Acc_Data$Y
back_forward <- Acc_Data$X
#running mean
for (i in (start_msec+1): (nrow (Acc_Data)-start_msec)) {
dorso_ventral_mean[i] <- mean (dorso_ventral [(i-start_msec): (i+start_msec)])
lateral_mean[i] <- mean (lateral [(i-start_msec): (i+start_msec)])
back_forward_mean[i] <- mean (back_forward [(i-start_msec): (i+start_msec)])
dorso_ventral_amplitude[i] <- std.error (dorso_ventral [(i-start_msec):
(i+start_msec)])
lateral_amplitude[i] <- std.error (lateral [(i-start_msec): (i+start_msec)])
back_forward_amplitude[i] <- std.error (back_forward [(i-start_msec):
(i+start_msec)])
}
```

```
Acc_Data$Static_DorsoVentral <- dorso_ventral_mean
Acc_Data$Static_Lateral <- lateral_mean
Acc_Data$Static_BackForward <- back_forward_mean
Acc_Data$Amplitude_DorsoVentral <- dorso_ventral_amplitude
Acc_Data$Amplitude_Lateral <- lateral_amplitude
Acc_Data$Amplitude_BackForward <- back_forward_amplitude
Acc_Data <- Acc_Data [-c (1: start_msec, nrow (Acc_Data): (nrow(Acc_Data)-
start_msec)),]
#acc_MRs$Roll <- atan2(acc_MRs$Static_Lateral, sqrt
(acc_MRs$Static_BackForward*acc_MRs$Static_BackForward +
acc_MRs$Static_DorsoVentral*acc_MRs$Static_DorsoVentral)) * 180/pi
Acc_Data$Pitch <- atan2(Acc_Data$Static_BackForward, sqrt
(Acc_Data$Static_Lateral*Acc_Data$Static_Lateral +
Acc_Data$Static_DorsoVentral*Acc_Data$Static_DorsoVentral)) * 180/pi
Acc_Data$Dynamic_DorsoVentral <- Acc_Data$Z-Acc_Data$Static_DorsoVentral
Acc_Data$Dynamic_Lateral <- Acc_Data$Y-Acc_Data$Static_Lateral
Acc_Data$Dynamic_BackForward <- Acc_Data$X-Acc_Data$Static_BackForward
Acc_Data$OBDA_vec<- sqrt((Acc_Data$Dynamic_DorsoVentral)^2 +
(Acc_Data$Dynamic_Lateral)^2 + (Acc_Data$Dynamic_BackForward)^2)
for (i in (start_msec+1): (nrow(Acc_Data)-start_msec)) {
  pitch_amplitude[i] <- std.error (Acc_Data$Pitch[(i-start_msec):(i+start_msec)])}
Acc_Data$Amplitude_Pitch <- pitch_amplitude
```

Appendix VI: Script for the execution of the Expectation Maximisation algorithm.

```
library (Rmixmod)
data_Prova <- Acc_Data [,c ("Dynamic_DorsoVentral", "Dynamic_Lateral",
"Dynamic_BackForward", "Amplitude_DorsoVentral", "Amplitude_Lateral",
"Amplitude_BackForward" #seleziona le variabili #can also use Amplitude_Pitch
system.time (xemOW <- mixmodCluster (data_Prova,2, models =
mixmodGaussianModel (), criterion= c("BIC","ICL"), strategy = mixmodStrategy
(algo = "EM", nbTry = 1,initMethod = "smallEM", nbTryInInit = 50,
nbIterationInInit = 5, nbIterationInAlgo = 200,epsilonInInit = 0.001, epsilonInAlgo =
0.001, seed =NULL))) # can also be data_Prova, 3
# show a summary of the best model containing the estimated parameters, the
likelihood
summary (xemOW)
#plot(xem)
Acc_Data$Partition <- (xemOW@bestResult@partition)
unique (Acc_Data$Partition)
```