Lemurs as protectors of the forest:

Red-collared brown lemur seed dispersal, forest regeneration, and local livelihoods in the littoral forest fragments of southeastern Madagascar

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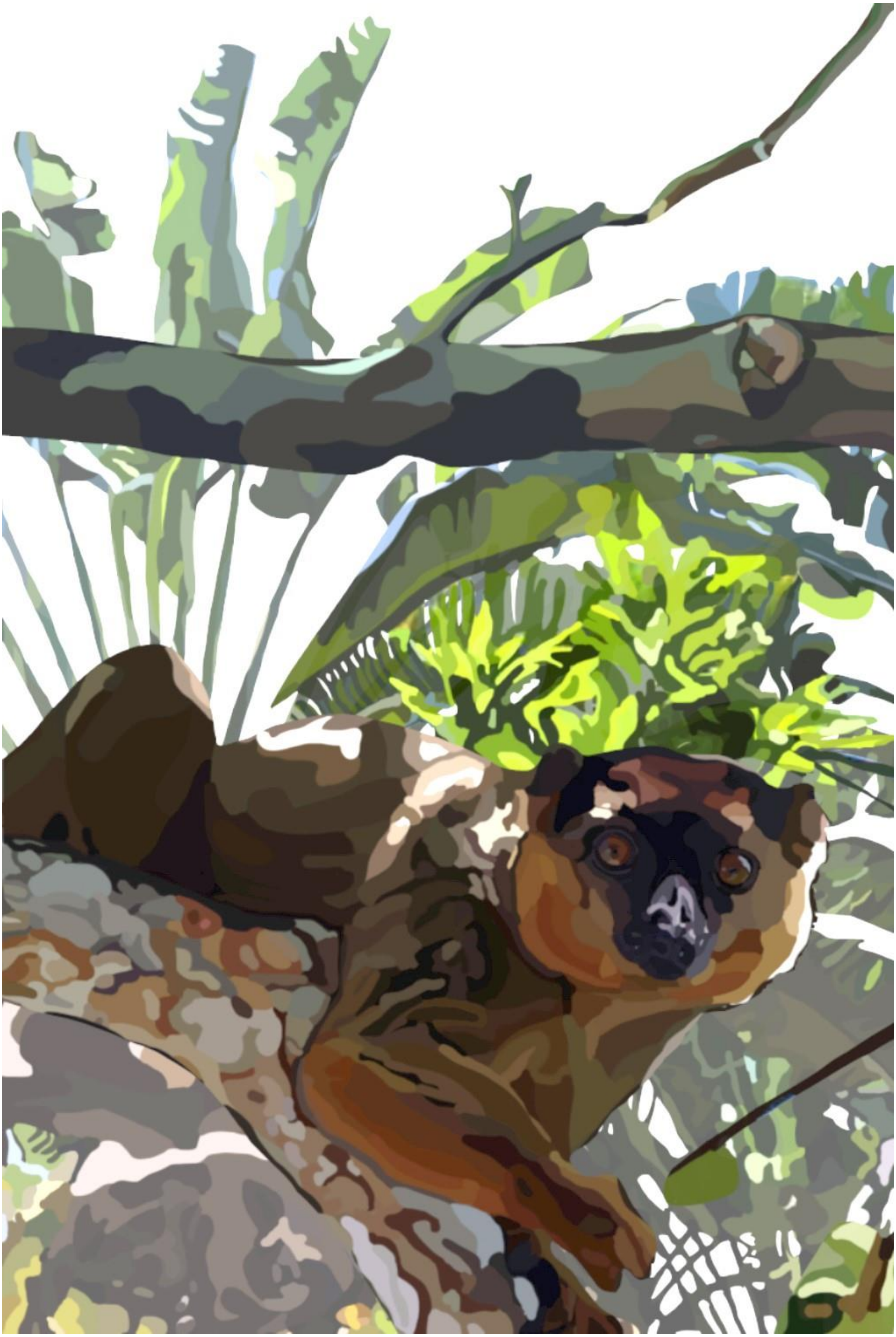

Varika. Commissioned from Annette Gunn.

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LIST OF ABBREVIATIONS

DBH	Diameter at breast height
e.g.,	*Exempli gratia* (for the sake of example)
etc.	*Et cetera* (and so forth)
i.e.,	*Id est* (it is)
IUCN	International Union for Conservation of Nature
LEK	Local ecological knowledge
MCZ	Mandena Conservation Zone
MND	Mandena
NA	Not available
PCQ	Point-centre quartile method
QMM	QIT Madagascar Minerals
SL	Sainte Luce
SPSS	Statistical Package for the Social Sciences

LIST OF STATISTICAL ABBREVIATIONS

B	Parameter estimate
df	Degrees of freedom
IQR	Interquartile range
H	Shannon-Wiener Index
M	Mean
N	Sample size
p	p - value, level of significance
r	Spearman rank correlation coefficient/ Pearson's correlation coefficient
Q1	The first quartile
Q3	The third quartile
SD	Standard deviation
SE	Standard error
U	Mann-Whitney U test
χ^2	Chi-square test

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ABSTRACT

Protected areas are essential to conservation. They are expected to safeguard the wildlife and their habitat, so it is important to investigate their effects on species' population and ecology. Creating a protected area can also affect local people. Positive effects can include the preservation of ecosystem services and eco-tourism, with job opportunities and increased infrastructure stemming from such socio-economic development. On the other hand, forest protection often restricts the use of natural resources, thus interfering with traditional livelihoods and local economics. These negative effects can lead to antagonistic attitudes towards the protected area, which can undermine conservation efforts. Understanding the implications of forest protection for the livelihoods local people, along with their attitudes towards, and acceptance or opposition of forest protection can help mitigate the risks of social conflict and support conservation success. In this study, I investigated how forest protection affected the ecology of red-collared brown lemurs (*Eulemur collaris*) in two littoral forests in southeastern Madagascar (Sainte Luce, Mandena). Since 1999, 14 behavioural studies have been conducted on this lemur species in these littoral forests, focusing on their diet, behaviour, activity pattern, and ranging. As protected areas were established in both Sainte Luce (in 2005) and Mandena (in 2002), I examined whether the previously observed differences have persisted. I also explored local ecological knowledge about this lemur, the impacts of forest protection on local livelihoods, and perceptions of forest protection and several stakeholders. I collected data between August 2017 and October 2018. To assess lemur diet and ranging, I collected data from three groups via focal animal instantaneous sampling (diurnally), and auditory group sampling (nocturnally). To examine the relationship between lemur presence and forest regeneration, I compared the numbers of seedlings and saplings in fragments in which this lemur was present and absent. To understand how forest protection affected local people, I surveyed 60 adults using a semi-structured interview. Similar to the results of previous studies, this study confirms that *Eulemur collaris* is frugivorous year-round. While Mandena lemurs were previously reported to have larger and more fragmented home ranges than the lemurs in Sainte Luce, in this study, Mandena lemurs' home range was smaller and less fragmented. Lemurs consumed more fruit and showed higher dietary diversity in the wet season. Their defecation was related to their resting patterns. Fragments with *Eulemur collaris* regenerated more. Most participants had a positive attitude towards *Eulemur collaris* and did not hunt it. Plant species were used locally as timber, medicine and fuelwood. *Eulemur collaris* consumed 52 utilitarian species. Perceptions of tourism and the NGO were largely positive, while perceptions of mining and forest protection were mixed due to their negative impacts on traditional livelihoods. This study shows forest protection has impacted both lemurs and people. Emphasising their interdependence might benefit both, and help preserve traditional livelihoods. As 98 % of lemurs and 70 % of primates are threatened, monitoring how conservation measures affect them is important. The urgency to conserve biodiversity should be matched with the urgency to document and conserve the cultural heritage associated with it.

CHAPTER 1: General introduction

Seed dispersal is one of the most crucial ecological processes. In the tropics, more than 75 % of all plant species are adapted to vertebrate dispersal (McKey, 1975; Howe & Smallwood, 1982; Janson, 1983; Jordano, 1992; 2000). This led to several hypotheses about possible co-evolution of fruiting plants and frugivores. These typically do not account for the animal species that might have once inhabited the same ecosystem, but were extirpated. Non-human primates (hereafter "primates") are among the most important dispersers (Chapman, 1995; Wallace & Painter, 2002; Valenta et al., 2018). As dispersal success depends on the presence of dispersers, their extirpation can lead to diminished forest regeneration (Forget & Jansen, 2007; Muller-Landau, 2007; Brodie et al., 2009). In this Introduction, I cover the topics of seed dispersal and fruit-frugivore co-evolution.

Lemurs (lat. *lemures* – ghosts, spirits) are strepsirrhine primates belonging to lemuriform infraorder (Gray, 1821), endemic to Madagascar. Like other primates of the suborder Strepsirrhini, which in addition to lemurs includes galagos, pottos and lorises, they are characterised by a wet rhinarium, and several plesiomorphic traits of early primates, such as divergent digits on hands and feet, and in most species, nails instead of claws (Gebo, 2014). The most likely hypothesis about lemurs' arrival in Madagascar states they arrived on rafts of vegetation over a period of time (Kappeler, 2000) between 40 and 60 million years ago, and adapted to fill diverse ecological niches. There are currently five lemur families comprising 15 genera and 107 species. While all are mostly arboreal, their morphology and physiology, diet, social organisation, and activity pattern vary between species. Until several hundred years ago, Madagascar was also inhabited by giant lemurs, whose subfossil remains date to as recent as about 500 years ago (Godfrey, 2016). Nearly all extant lemur species (i.e., 98 %) are threatened. The biggest threats to lemurs' survival are habitat loss, slash and burn agriculture, illegal logging, and mining. In this Introduction, I focus on the red-collared brown lemur, providing more detail on its ecology and habitat use in the littoral forests of Sainte Luce and Mandena.

It is widely regarded that the success of wildlife conservation efforts is closely tied to the species' significance to the local human population (Fiallo & Jacobson, 1995; Fulton et al., 1996; Decker et al., 2001; Mir et al., 2015). The studies of people and people-wildlife interactions, however, are still outnumbered by those focusing solely on wildlife species' ecology and behaviour. A scientific discipline focused on the investigation of human-animal interactions, both present and past, is called ethnozoology (Alves, 2012). Local ecological knowledge (LEK) of indigenous communities holds the information of wildlife perception, and is therefore valuable to these species' conservation (Charnley et al., 2007; Junqueira et al., 2011; Nash et al., 2016). Similarly, local knowledge of plants and their use is often the central focus of ethnobotanical studies (Martin, 2010). As many tropical ecosystems are facing habitat fragmentation and degradation (Ritters et al., 2000, Behin, 2000; Harper et al., 2007), protected areas have become an important component of biodiversity conservation (Brechin et al., 2002; Lele et al., 2010; Ervin, 2013; Singh et al., 2013). They can, however, have both positive and negative impacts on the local people. Understanding local perceptions of forest protection and the associate socio-economic development may benefit protected area management. In the Introduction, I cover the topics of people-wildlife interactions, local knowledge of wildlife and plants, and the impacts of forest protection on the lives and livelihoods of local people.

Littoral forests of southeastern Madagascar are inhabited by numerous species of fauna and flora, many of which are endemic to this ecosystem (Goodman & Benstead, 2005). As some of the littoral forest fragments became protected in recent decades, this change created gaps in knowledge of how these conservation policies have affected the wildlife. One of the species inhabiting these forests is the endangered red-collared brown lemur. Due to its unique ecological importance as a seed disperser (Bollen et al., 2004), it is essential to understand whether this change has affected this species' ecology, and how it may subsequently reflect in the ecological services it provides. In this study, I therefore focused on the red-collared brown lemur's seed dispersal ecology, and the regeneration of forests in which the species is present, comparing it to the regeneration of forests which this lemur no longer inhabits. As few efforts have been made to document the lives and livelihoods of the local human communities living in proximity to the littoral forests in the southeast of Madagascar, in this study I investigate their knowledge of and practices surrounding the red-collared brown lemur, as well as their reliance on the plant species growing in the littoral forest. Since local people are heavily reliant on forest resources, they have likely been affected by the forest protection measures. I therefore also explore how these changes have affected the local people's lives and livelihoods.

1. Seed dispersal

The importance of seed dispersal has been recognised since the 19th century (Darwin, 1859; Wallace, 1879; Ridley, 1930). Plant communities are both numerous and diverse, and so are their seed dispersal types. Autochory entails seed dispersal carried out by the plant itself, with no help from external vectors (Vittoz et al., 2007). Anemochorous plants disperse their seeds by wind, often with the help of specific plant organs, and the seeds of hydrochorus plants are dispersed by water. Finally, zoochory is a seed dispersal type in which the plants rely on animals for their seed dispersal. Particular species' seed dispersal type can be predicted from their growth form, height, fruit type and seed mass (Hughes et al., 1994; Guo & Zheng, 2017). A considerable number of plant species use multiple dispersal vector types (Mułler-Schneider, 1986), either alternatively or successively. While each of the main dispersal types has multiple sub-types (Van der Pijl, 1969; Vittoz et al., 2007), due to the focus of my thesis, I will direct my attention on zoochory, of which there are three subtypes: endozoochory (diaspores intentionally or accidentally transported within the animal), synzoochory (diaspores intentionally transported in animal's mouth), and epizoochory (diaspores accidentally carried on the outside of the animal). In tropical forests, endo- and synzoochory are the most common types of seed dispersal (Charles-Dominique, 2001).

As seed dispersal away from the parent tree is essential for the successful establishment of seedlings (Janzen, 1970; Connell, 1971; Howe & Smallwood, 1982), and the majority of tropical plants are dispersed by frugivores, attracting them is of immense importance. The factors important in attracting dispersers are most often related to fruit characteristics such as fruit size and husk hardness (Janson, 1983), seed size (Zanne et al., 2005), fruit quantity (Curran & Leighton, 2000), colour (Steves et al., 2009; Valenta et al., 2013; Melin et al., 2013), odour (Valenta et al., 2013; Nevo et al., 2015; 2016), crop size (Korine et al., 2000; Bollen et al., 2004), nutritional content (Bollen et al., 2004), secondary metabolite content (Cipollini & Levey, 1997), the number of feeding sites on the tree, the presence of competitors, and the availability of alternative food sources (McKey, 1975). However, while some studies have revealed differences between taxa in their preferences for particular fruit characteristics (Gautier-Hion et al., 1985; Fleming et al., 1987; Debussche & Isenmann 1989; Galetti et al., 2000; Bollen et al., 2004; Bollen, 2003), others have argued that findings will differ depending on the chosen sampling unit (Fischer & Chapman, 1993) - comparisons at the species level will overestimate dispersal syndromes (i.e., seeds' morphological characteristics correlated to particular seed dispersal agents (Clobert et al., 2009).

Primates are among the most important seed dispersers in the tropics. This is not surprising because the primate order accounts for a significant percentage (between 25 % and 40 %) of tropical forests' biomass (Eisenberg & Thorington, 1973; Terborgh, 1983; Lambert & Garber, 1998). Moreover, a large number of primate species exhibit high rates of frugivory, from the New World primates (Hawes & Peres, 2013) to chimpanzees (Goodall, 1986) or large-bodied lemurs (Wright et al., 2005; Donati et al., 2007; Sato et al., 2014). Some of the primate species whose seed dispersal has been well studied include capuchins (*Cebus* spp.) (Wehncke & Domínguez, 2007; Valenta & Fedigan, 2010), spider monkeys (*Ateles* spp.) (Link & Di Fiore, 2006), woolly monkeys (*Lagothrix lagotricha*) (Stevenson, 2000), chimpanzees (*Pan troglodytes*) (Wrangham et al., 1994), and several lemur species (Razafindratsima et al., 2014). Apart from their role as seed dispersers, some species of primates are considered seed predators, due to them destroying the seeds or feeding on the unripe fruit (McKey, 1978; Kinzey, 1992; Kaplin et al., 1998; Stevenson, 2000). In the majority of cases, however, primates act as both dispersers and predators of seeds (Gautier-Hion et al., 1993; Norconk et al., 1998).

Seed dispersal type affects dispersal distances. Autochory enables for the shortest dispersal distance, and hydrochory has the potential for carrying the seeds furthest, but this seed dispersal type is highly unpredictable and typically not documented (Vittoz et al., 2007). During the zoochorous dispersal process, seeds can be destroyed, dropped under the parent tree, spat out nearby or transported far away from the parent tree. The distance of transport will depend on the behaviour and the anatomy of the animal by which the seeds are consumed, with larger animals often comprising more efficient dispersers (Vittoz et al., 2007). Interestingly, seed dispersal distances tend to be the largest in the tropics, likely due to tropical plants' life history traits, such as dispersal mode and plant height (Chen et al., 2019). According to the Janzen-Connell hypothesis (Janzen, 1970; Connell, 1971), the main benefit of seed dispersal is that it enables seeds and seedlings to escape the high density-dependent mortality, caused by pathogens, seed predators and herbivory directly under the parent plant. With an increased research interest in the link between animal-mediated seed dispersal and the establishment and the distribution of seedlings, it has become increasingly clear that where the seeds are initially dropped is often not where they stay (Wang & Smith, 2002). Studying seeds' post-dispersal fate is necessary, as it has important implications for vegetation structure (Forget, 1996; Vander Wall & Joyner, 1998; Forget et al., 1999; Forget & Vander Wall, 2001).

To enable better understanding of seeds' post- (primary) dispersal seed fate, it would be necessary to observe or otherwise document their encounters with seed predators, as well as these potential predators' interest in, or efficiency in, processing seeds that arrive by different dispersal vectors. The latter could be used to reach conclusions regarding whether or not particular dispersers may be beneficial to the seed, increasing its chances to escape predation simply by digesting it. If so, this could have implications for the regeneration of plant species in the dispersers' diet. As forests are used not only by wildlife, but very often also by people, information pertaining to forest regeneration (and therefore resource availability and longevity) is important. Finally, a clearly beneficial seed-seed disperser connection could provide important evidence for the debate on the fruit-frugivore co-evolution.

2. Fruit-frugivore co-evolution

The large percentages of zoochorous plants in the tropics and a high variation in their seed dispersers have led many authors to hypothesise a co-evolution between the fruiting plants and frugivorous animal species (van der Pijl, 1969). The most limiting hypothesis, stemming from the assumed mutual dependency of plants, their diaspores and their consumers, proposes a tight co-evolutionary relationship between one single fruiting plant and a specialised disperser. This type of co-evolution would be dependent on directional selection, for which consistent and mutual ecological interaction patterns are essential (Janzen, 1980; Howe & Westley, 1988). If particular taxa preferences are reflected in an increased reproductive success of the plants the seeds of which they disperse, then their seed dispersal should also affect these plants' fruit traits (Valenta et al., 2018). This is an unlikely scenario, as plants do not possess an ability to control intentionally which frugivores will feed on them and disperse their seeds, the viability of which should be unaffected by the process (Lambert & Garber, 1998). Even when a particular plant species is reliant on multiple seed dispersers, their individual importance can differ (Schupp, 1993; Valenta et al., 2018). In these cases, the traits which are more likely to be selected are those that allow for a more successful dispersal by the most efficient frugivore (Valenta et al., 2018). So far, no evidence has been found in support of the hypothesis regarding the existence of a tight co-evolutionary relationship between single fruiting plants and highly specialised dispersers (e.g., Howe & Smallwood, 1982; Howe, 1984; Herrera, 1985; Gautier-Hion et al., 1985; Fisher & Chapman, 1993; Chapman, 1995; Erikkson & Ehrlen, 1998; Lambert & Garber, 1998; Bollen et al., 2004).

In a less exclusive model, McKey (1975) differentiates between generalist and specialist plants. The low investment plants (i.e., generalists) invest little in single fruits and more in large fruit crops displayed during a short fruiting period, in order to attract a large variety of frugivores. On the other hand, the high investment plants (i.e., specialists) produce fruits with higher nutrient content, but in more limited quantities and during an extended fruiting season, thus attracting specialist frugivores (Howe, 1979). The validity of this model rests on qualitative, rather than quantitative predictions, making some of its elements (for example, what exactly entails high or low investment) difficult to specify. Moreover, as it was developed with bird-dispersed trees of the Neotropics in mind, and it largely depends on the composition of the frugivore guild, it may not work as well in ecosystems of few frugivorous species. It should perhaps not come as a surprise that it has also not found a lot of empirical support (Dowsett-Lemaire, 1988; Wenny, 2000; Wütterlich et al., 2001).

The third model focuses on dispersal syndromes – the sets of fruit traits hypothesised to have evolved under the selective pressures of specific seed dispersers. Plants benefit more from visits of mutualists that do not specialise in particular plant types (Herrera, 1985; Johnson & Steiner, 2000), which is also evident from a lower degree of specialisation towards dispersers than pollinators (Blüthgen et al., 2007). Unrelated plants that share the same dispersers will show convergent fruit traits. This is known as the signal convergence hypothesis, which emphasises the broad morphological adaptations of fruit traits that frugivores use as reliable signals. These traits tend to be associated with different frugivore taxa, mostly enabling a distinction between bird- and mammal-dispersed fruits, or those dispersed by both, and are typically related to fruit size, husk hardness, and colour (Van der Pijl, 1969; Janson, 1983; Knight & Siegfried, 1983; GautierHion et al., 1985; Martinez del Rio, 1994; Corlett, 1996; Kalko et al., 1996; Korine et al., 2000; Pizo, 2002). Mammals tend to show a preference for fruits rich in sugar, while birds prefer fruits of high lipid and protein content (Fleming et al., 1987; Debussche & Isenmann, 1989; Galetti et al., 2000). Fruits of bird-dispersed plants also tend to be smaller, more colourful, and of a more elongated shape than those of plants dispersed by primates. Plants that rely on primate seed dispersal are usually consumed by more than one species of primates (Janson, 1983;

Stevenson et al., 2000; Link & Stevenson, 2004; Yamagiwa & Basabose, 2009). Similarly, it appears that all frugivorous primates possess anatomical and behavioural characteristics associated with their diet, such as their dentition (Kinzey, 1992), even though they often differ in body mass, feeding behaviour, foraging group size and movement patterns (Campbell et al, 2010). When it comes to fruit-frugivorous primates, it is more likely that fruit traits are not shaped by the primate species that disperse them, at least not consistently. Instead, primates are only one of the numerous selective pressures affecting fruit traits, such as colour (Valenta et al., 2018) or odour (Nevo & Valenta, 2018). Fruit evolution may, according to some authors, be driven more by abiotic factors, such as water availability, than by frugivore pressures (Bollen et al., 2005).

A less debatable relationship, however, is the one between the sizes of fruit and their potential seed dispersers, in which fruit (and seed) sizes are limiting factors (Leighton & Leighton, 1983; Janson, 1983; Kitamura et al., 2002; Zanne et al., 2005). As a result, larger frugivores are able to disperse a wider range of seeds (Noma & Yumoto, 1997; Kitamura et al., 2002), thus preventing selection for smaller fruit size (Westcott et al., 2005). Many of the larger-body frugivore species are increasingly hunted (Terborgh & Winter, 1980; Lehman & Wright, 2000; Peres & Lake, 2003; Fa et al., 2005; Lehman et al., 2006; Corlett, 2007). Their local extirpations may also endanger the plants which they disperse. Plants that are dispersed by large-bodied frugivores typically attract them by producing large, fleshy fruit (Howe & Smallwood, 1982). Interspecific differences in the consumption of fruit of particular characteristics within the same plant could be affected by the group size differences and intragroup competition for resources arising from it (Overdorff & Strait, 1998). One of the main difficulties with studying co-evolution of plants and animals is that the former have a much slower generation time, but a much larger gene flow. This makes it extremely hard for animals to apply a consistent selective pressure (Lomáscolo et al., 2010). Cases where certain plant species seem to be exclusively reliant on a single frugivore species for their seed dispersal may offer some indication of fruit-frugivore co-evolution. Conclusions, however, should not be drawn based solely on the current species makeup, without considering their specific diet-related behaviours, as well as the (previous) existence of other frugivores of similar ecology, which are now extirpated from the area.

Madagascar's isolation from continental Africa for more than 165 million years (Rabinowitz et al., 1983) has resulted in limited colonisation of both animals and plants, as well as the possible evolutionary interactions between the two (Goodman & Ganzhorn, 1997). This isolation has, however, provided an opportunity for different evolutionary processes, which have shaped its unique frugivore community, in which many of the expected frugivores - namely, the frugivorous birds and bats - are under-represented in comparison with continental and other insular tropical areas (Hawkins & Goodman, 2003; Bollen, 2004). This is also true in the littoral forests in the southeast of Madagascar (Bollen, 2004), well-known for their plant species diversity (Ganzhorn et al., 2007) and high levels of endemism (Lowry et al., 2008). The littoral forests of Mandena, Sainte Luce and Petriky are, due to heavy fragmentation and anthropogenic use, among the most threatened ecosystems in the country (Bollen & Donati, 2006; Vincelette et al., 2007) (Figure 1). When it comes to seed dispersal, the majority of the tree species growing in these forest fragments appear to be generalists (Bollen et al., 2004). This suggests that tree species' life history traits have not been shaped under the specific-vertebrate species' constraints, and all observed specialist relationships could therefore simply be the result of frugivores' morphological and physiological heritage, and not of co-evolution. Moreover, a large number of Malagasy frugivores have gone extinct, many of which could have played a crucial role in the dispersal of large seeds (up to 30 mm in length) (Godfrey et al., 2004; Federman et al., 2016). These are now solely reliant on red-collared brown lemurs (*Eulemur collaris*) for their seed dispersal. Due to their body size, red-collared brown lemurs are likely to be the only lemur currently inhabiting the littoral forest in the southeast that can ingest large-sized seeds. For this reason, they were chosen as the focal study species for this research project.

Figure 1. Littoral forest fragments are often separated by open savannah, occasionally interrupted by swamps (A). (Photograph taken in Sainte Luce by E. Račevska, April 2018). Closely spaced fragment remnants are sometimes separated by bare sand (B). (Aerial photograph of the satellite remnants North of one of the protected fragments in Sainte Luce (S8), curtesy of SEED Madagascar, September 2019).

3. People, wildlife, and the forest

Biodiversity is an essential part of human cultures. Throughout human history, animals and human-animal interactions have been one of the focal elements of the human world (Manning & Serpell, 2002; Alves, 2012). One of the oldest interactions between humans and wildlife is hunting (Alves, 2012), the purpose of which includes food, clothing, tools, as well as use of wildlife in religious rituals and for medicinal purposes (Alvard et al., 1997; Alves et al., 2009; 2012). However, human relationships with animals extend beyond those based in animals' utilitarian purposes, and animals can be found in mythologies, magic rituals, and belief systems (Allaby, 2010; Alves et al., 2012). Human-animal interactions are often culture-specific, and focused on the locally present wildlife (Alves, 2018). Traditional zoological knowledge is among the main focuses of ethnozoology (Alves, 2018). Many cultures across Africa, Asia and South America consider particular animal species to be sacred, which often has positive implications for these species' conservation (e.g., Colding & Folke, 1997; Jones et al., 2008; Nijman & Nekaris, 2014). Some authors argued that, due to the importance of biodiversity to the subsistence of many human societies relying on the natural resources, meaningful animal conservation strategies are not possible without including the element of human-animal interactions (Alves, 2018).

The importance of investigating people's perceptions of nonhuman primates is their immense importance for conservation. When it comes to the human-nonhuman primate interactions, they are most often believed to be rooted in conflicts over land use, and the studies rarely exceed the topics of predation, crop feeding, pathogen sharing, and anthropogenic impacts on the environment (Fuentes, 2006). Ethnoprimatology (Sponsel, 1997) offers an integrative approach of biological and cultural anthropology, and examines the human-nonhuman primate interface with an inclusion of social, economic, and political histories and contexts (Fuentes & Wolfe, 2002; Fuentes, 2006; Riley, 2006; Fuentes & Hockings, 2010). The perceptions of non-human primates and their treatment vary between cultures to great extents – from being considered sacred and worshipped, to being seen as devious and cunning, or treated as pests (Lee & Priston, 2005). Perceptions can even differ within cultures: it is not uncommon for primates of the same species to be both worshipped in temples and killed on farms due to conflicts over land use. Most socioecological research of human-primate interactions remains at the local level (Nekaris et al., 2013). In areas of human-primate sympatry, primates have historically been perceived as guardians, ancestor spirits, embodied sexuality, wisdom, or torture (Lee & Priston, 2005). Many of those representations are rooted in their morphological similarity to humans (Knight, 1999). Primates have traditionally been hunted for their meat and the use in traditional medicine (Alves et al., 2010). Ethnoprimatological studies consider cultural, ecological, and biological interconnections between humans and primates. One of the approaches include studying local ecological knowledge (LEK) about them. LEK comprises knowledge, practices and beliefs gained through both personal observation and interaction with the local ecosystem shared between members of the same community (Charnley et al., 2007). It is often locally specific (Turvey et al., 2014). LEK is dynamic and may reflect changes in social, economic, and political circumstances (Barbosa, 1996; Wiersum, 1997), as well as changes in biodiversity (Joa et al., 2018).

Tropical forests are also home to a plethora of plant species (Janzen, 1970; Balick et al., 1996), many of which are used by the people inhabiting them. Common uses include food, medicine, construction materials and fuel (Byron & Arnold, 1999; Ingram et al., 2005b; Asprilla-Perea & Díaz-Puente, 2019). Ethnobotanical studies investigate local people's knowledge of plants, as well as their uses and the beliefs surrounding them (Martin, 2010). Anthropogenic activities, such as selective logging, are often responsible for environmental change and biodiversity loss in tropical forests (Gardner et al., 2009; Dent & Wright, 2009; Morris, 2010; Putz et al., 2012). While habitat fragmentation and forest degradation can have detrimental impacts on wildlife, plant species and ecosystem services, they also threaten the survival of people living within these ecosystems and relying on natural resources. When unsustainable forest use becomes a threat to biodiversity, protected areas are often established. While they are an essential part of conserving forest biodiversity (Brechin et al., 2002; Lele et al., 2010), they can create substantial socio-economic costs for people whose livelihoods depend on forest resources (Coad et al., 2008), such as loss of infrastructure, changes in traditional land tenure, restricted use of natural resources, loss of livelihoods, and community displacement. The latter is one of the most controversial aspects of protected area management (West & Brockingon, 2006). Despite it being a highly contested measure, it is estimated that since the 1970s, between 900,000 and 14.4 million people have been displaced as a result of protected areas (Coad et al., 2008). Loss of land and loss of jobs are some of the main risks of displacement, while others include homelessness, marginalisation, food insecurity, increased morbidity and mortality, loss of access to common properties, and social disarticulation (Cernea, 1997).

Some estimates show that there are people living within 56-85 % of protected areas in India, South America and Central Africa (Brockington & Igoe, 2006). Many might be living with resource restriction - a nearly universal feature of protected areas. According to the World Bank, resource restriction is a form of displacement (Coad et al., 2008) which exposes people to the same risks as being physically displaced. In addition to impacting livelihoods, resource restriction can create social tensions, impact local diets or community health (Ferraro, 2002). Protected areas can also create benefits for the local communities, for example, through diversification of income (Twyman, 2001). Ecotourism is a common example. It enables direct generation of revenue, either through selling goods or services to tourists, or through entrance fees to the protected area (Adams & Infield, 2003; Bedunah & Schmidt, 2004; Bajricharya, 2006). Resource restriction does not impact all community members in the same way. As a result, attitudes towards forest protection can be predicted by many sociodemographic variables, such as age, gender, ethnicity, occupation, land ownership, education, and wealth (Infield & Namara, 2001; Allendorf et al., 2006; Kideghesho, 2007). Women and men often differ in their forest-based livelihoods, which can lead to them being differently affected by the different restriction levels associated with different types of forest resources (Sekhar, 1998; Allendorf et al., 2006). Gender-based differences are sometimes also related to land tenure. As traditionally men have land tenure, women might be ignored and receive no compensation when a protected area is established on their land (Sundberg, 2003). Poorer individuals are often more dependent on the forest resources, and therefore more negatively affected by the constraint of their use (Ferraro, 2002). Forest-based livelihoods and the associated higher amount of time spent in the forest are often related to higher knowledge of local wildlife (Boud et al., 2013; Kolb, 2014). However, this might not apply to wildlife inhabiting anthropogenically altered areas, in which most people are likely to encounter them.

4. Red-collared brown lemurs

The red-collared brown lemur (*Eulemur collaris,* É. Geoffroy, 1817), also known as the collared brown lemur or the red-collared lemur, is a species of lemur found only in the southeast of Madagascar, where it inhabits lowland semi-montane humid forests and littoral forests. It is classified as Endangered by the IUCN Red List (Donati et al., 2020). Previously considered a sub-species of the common brown lemur (*Eulemur fulvus*), it was promoted to full species status in 2001 (Groves, 2005). This is a gregarious species, living in multi-male multi-female groups (Donati et al., 2007), ranging between two and 17 individuals. They are sexually dichromatic (Figure 2) and similar in size to a domestic cat, with a mean body mass of 2.18 ± 0.11 kg and mean body length of 48.2 ± 2.1 cm (n=10; Donati, 2002; Donati et al., 2007).

Figure 2. Red-collared brown lemur (*Eulemur collaris*). The species is sexually dichromatic: females (A) have a brownish-grey dorsal and pale grey ventral coat, with creamy or rufous-brown cheeks covered in thick, bushy beard, while females (B) have browner and more rufous dorsal coat, a creamy-grey ventral coat, and a rufous-brown cheeks, less prominent than that of males. Photographs taken by E. Račevska, in Sainte Luce, September 2018.

The species ranges from the Mananara river in the north to Ambatotsirongorongo in the south, and to the Mandrare river in the west (Andriaholinirina et al., 2014) (Figure 3). Some of their habitat is heavily fragmented, to which this species is very sensitive (Eppley et al., 2020). This lemur has been observed crossing open grassland even at distances as far as 2 km (Hyde Roberts et al., 2020). The littoral forest habitat fragmentation has, however, affected their genetic diversity (Bertoncini et al., 2017). The population size is in decline throughout the species' range. The main threats arise from habitat destruction (due to charcoal production, slash-and-burn agriculture, logging and wood harvesting) and fragmentation, local hunting (for food and more occasionally, for the local pet trade), and in the littoral forests, from ilmenite mining (Bollen & Donati, 2006; Donati et al., 2020). Red-collared brown lemurs have few predators in the littoral forests, and are mainly predated by diurnal raptors (Donati et al., 2009), and occasionally by large snakes (Goodman et al., 1993).

Figure 3. Geographical distribution of the red-collared brown lemur (*Eulemur collaris*). (Map reproduced from Donati et al., 2020).

Much like other members of its genus, the red-collared brown lemur is cathemeral, which means that its activity is distributed across the 24-hour cycle, with significant portions of travelling and feeding occurring during both the day and the night (Tattersall, 2006). The hypotheses regarding the reasons behind cathemerality of *Eulemur* species relate to predator avoidance, competition avoidance, thermoregulation or diet quality (Tattersall & Sussman, 1975; Overdorff, 1988; Engqvist & Richard, 1991; Donati et al., 2001; 2007; 2009; 2016; Kappeler & Erkert, 2003; Curtis & Rasmussen, 2006; Colquhoun, 2006). In the case of *E. collaris*, their extended feeding periods seem to be related to a diet rich in fibres (Donati et al., 2007). Red-collared brown lemurs are important seed dispersers in the littoral forests of southeastern Madagascar, where they are the largest currently extant species. Because of their size, they are believed to be an exclusive disperser of several large-seeded tree species (Bollen et al., 2004). It is possible, however, that other, now extinct large frugivorous lemurs, as well as birds, might have also fed on these large fruits (Bollen, 2003).

The difference between Sainte Luce, regarded as the most intact littoral forest in Madagascar (Bollen & Donati, 2006; Rabevohitra et al., 1996; Dumetz, 1999) and Mandena, which has, prior to forest protection, been more degraded (Rabenantoandro et al., 2007), has implications for the ecology of the red-collared brown lemur. Due to the lower habitat quality, Mandena lemurs live in smaller groups to reduce feeding competition, but have larger home ranges (Donati et al., 2011; Campera et al., 2014). They feed on more trees and have longer feeding times than Sainte Luce lemurs (Donati et al., 2011; Campera et al., 2014). While there are more mature leaves in their diet, Mandena lemurs also feed on smaller trees than their Sainte Luce counterparts, which is likely due to the lower availability of larger trees with more abundant resources (Donati et al., 2011). Predation pressures might be higher in Mandena as well, further affecting this lemur's ranging behaviour and resource use (Campera et al., 2014). In turn, these are likely to impact seed dispersal patterns. In the past decades, red-collared brown lemurs have been extensively studied in Sainte Luce and Mandena (Table 1). Besides behavioural observations and home range analyses, population censuses have been carried out in 2011 and 2012 in Sainte Luce by SEED Madagascar (S. Hyde Roberts, personal communication), and yearly in Mandena by TBSE since 2001 (G. Donati, personal communication). In the previous studies, diurnal observations included focal individual follows, while nocturnal observations were done using auditory group sampling (Table 1).

Table 1. Previous research of the red-collared brown lemurs (*Eulemur collaris*) in the littoral forests of Sainte Luce and Mandena.

Researcher	Area	Time of data collection	Methods	Observational hours	Home range analysis
Giuseppe Donati	Sainte Luce	Dec 1999 – Feb 2001	Behavioural observations: diurnal, nocturnal	Diurnal: 948 h Nocturnal: 792h	100 % MCP with feeding trees
	Mandena	May – Dec 2004	Behavioural observations: diurnal	Diurnal: 492h	100 % MCP with feeding trees
TBSE	Mandena	Aug 2000 – present	Behavioural observations: diurnal	Diurnal: 5,509h	-
Andriamandranto M. Ravoahangy	Mandena	2001	Behavioural observations: diurnal	Diurnal: 245h	-
Kelard Ndremifidy	Mandena	May – Aug 2004	Behavioural observations: diurnal	Diurnal: 234h	-
Stacey L. Zander	Mandena	July – Aug 2004	Behavioural observations: diurnal	Diurnal: 87h	-
Kristina Kesch	Mandena	Aug – Nov 2007	Behavioural observations: diurnal	Diurnal: 216h	100 % MCP with feeding trees
Fiona Rowe	Mandena	May – Jul 2009	Behavioural observations: diurnal	Diurnal: 340h	-
Valentina Serra*	Sainte Luce, Mandena	Feb – Jul 2011	Behavioural observations: diurnal, nocturnal	Diurnal: 962 h (Mandena)	At 30-minute intervals 100 % MCP,
Marta Barresi*	Sainte Luce, Mandena	Feb – Jul 2011	Behavioural observations: diurnal, nocturnal	1,118 h (Sainte Luce)	50 %, 95 % Kernel analysis
Marco Campera*	Sainte Luce, Mandena	Mar 2011 – Jan 2012	Behavioural observations: diurnal, nocturnal	Nocturnal: 134 h (Mandena)	Sainte Luce:
Michela Balestri*	Sainte Luce, Mandena	Mar 2001 – Jan 2012	Behavioural observations: diurnal, nocturnal	126 h (Sainte Luce)	2,310 points Mandena: 1,731 points
Murielle Ravaolahy	Sainte Luce, Mandena	Feb – Jun 2011	Behavioural observations: diurnal		
TBSE	Mandena	2001 – present	Population census	-	-
Trang Nguyen	Sainte Luce	May – Jul 2012	Population census	-	-
SEED Madagascar	Sainte Luce	2011, 2012	Population census	-	-

* These researchers collected and analysed data jointly.

Due to their diurnal activity, and conspicuous behaviour, it is fair to assume that the local human communities residing in the proximity of forests inhabited by this lemur would have high recognition of this species, as well as at least basic knowledge of their ecology (i.e., diet type, activity rhythm). However, as of the planning phase of this study, this had not yet been studied. As this is an endangered species, it is important for its conservation action planning strategy to examine the attitudes of the local people towards it, and the practices involving it (i.e., hunting).

5. The Anosy region

Madagascar is one of world's biodiversity hotspots (Myers et al., 2000). As a result, its conservation is considered to be one of the most critical global priorities (Goodman & Benstead, 2005). However, Madagascar’s high population growth, poverty, and unsustainable agriculture have significantly impacted the ecosystems, resulting in deforestation and species' extinction (Green & Sussman, 1990; McConnell et al., 2004). This devastating trend could continue, as the annual population growth is 2.9 % (Vincelette et al., 2007). The Anosy region, located in the south-east of the country is one of the most isolated and economically poorest regions in the country (Vincelette et al., 2007). The local population, belonging to the Antanosy ethnic group, engages mainly in agriculture and fishing for their subsistence (Vincelette et al., 2007). Due to the seasonality of crop productivity and fishing, the local communities are heavily reliant on the forest for sustenance and livelihoods (Ingram et al., 2005; Razafindraibe et al., 2013). Plants are used for everything from medicine to construction and firewood (Lowry, 1999; Vincelette et al., 2003; Ingram et al., 2005b; Razafindraibe et al., 2013). During colonial times, traditional medicine was banned (Dewar & Wright, 1993), resulting in a huge loss of Antanosy traditional knowledge, which was later re-taught to them by the Antandroy people who relied on the Antanosy forests for many plant resources. Due to the isolation of their land in the far south of Madagascar, they did not suffer a similar cultural erosion (Lyon & Hardesty, 2005).

Firewood and charcoal are the primary sources of energy in southeastern Madagascar. While 90% of the rural population relies on firewood, charcoal use is more prevalent among urban populations (i.e., Fort Dauphin) and migrants from the south of Madagascar (i.e., the Antandroy). The establishment of protected areas has restricted forest use, but while this restriction has most likely affected local people's way of life and resource acquirement, no studies have been published. Since 2004, 80 % of the region’s roads are impassable, reducing movements of people and goods, and inflating living costs. The region is home to approximately 807,418 inhabitants (Institut National de la Statistique Madagascar, 2020). According to the 2019 assessment, 75 % of the people in this region were living below the poverty line (World Bank, 2021a), which was 8 % above the national average. Few health facilities are available, and those that do exist often lack staff and equipment. Common diseases include malaria, filarial worms, leprosy, and polio. These difficult living conditions are reflected in a very short life expectancy of 52 years, as compared with the national average for the same year (i.e., 2007), which was 62 years; the current average life expectancy in Madagascar is 67 years, but no information are available for the Anosy region specifically (World Bank 2021b). Only 46 % of the population is literate (Comité Régional pour le Développement de l'Anosy, 2003). The majority of the population is engaged in sustenance agriculture and fishing, but agricultural productivity is seasonal and low. Sisal and rice are dominant crops, but demand for sisal has diminished, and rice productivity is extremely low (Vincelette et al., 2007). Moreover, about 90 % of people do not have access to drinking water. Heavy reliance on forest resource has led to substantial destruction and degradation of the littoral forests over the last 50 years (Dumetz, 1999; QMM, 2001). This habitat is one of Madagascar's most threatened ecosystems (Bollen & Donati, 2005), facing risks in the forms of slash-and-burn agriculture, and charcoal production (Bollen & Donati, 2006). The latter has reportedly intensified since 1995, leading to the complete destruction of some smaller fragments in Mandena, which had not previously been destroyed by excessive anthropogenic pressures, such as charcoal production (G. Donati, personal communication) (Figure 4).

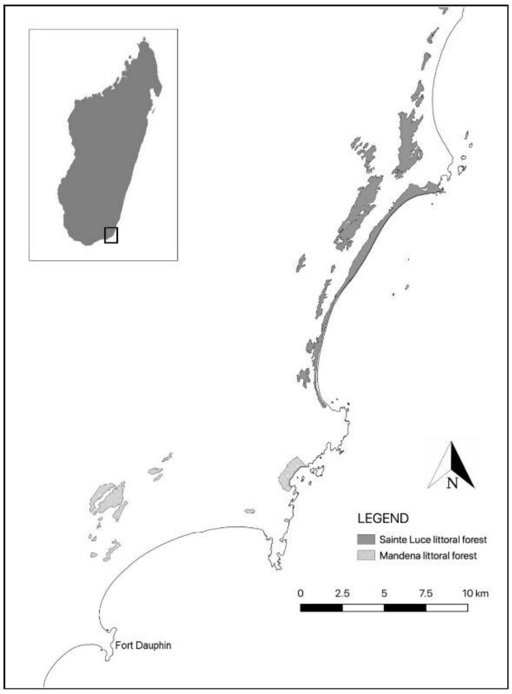


Figure 4. The littoral forests of Sainte Luce and Mandena.

Due to high concentrations of endemism and diverse flora (Dumetz, 1999) and fauna (Ganzhorn, 1998; Ramanamanjato, 2000; Watson et al., 2005), littoral forests of Sainte Luce and Mandena are considered national conservation priorities (Ganzhorn et al., 2001) (Figure 5). The region is also exceptionally rich in minerals. Since 1986, the QMM mining company (*QIT Madagascar Minerals*), owned by the Rio Tinto corporation (80 %) and the Malagasy government (20 %), has become a stakeholder in the area, which it will remain for the following forty years (Rio Tinto, 2017). This is likely to affect 43 villages (Lewis Environmental Consultants, 1992), and the lives of around 6,000 people living in the proximity of the mining zone (QMM, 2001). Primarily interested in the extraction of ilmenite – a titanium ore deposited in the sand below these littoral forests, the QMM has been set to clear out some of the more degraded forest fragments, while simultaneously protecting the other, more pristine ones, and establishing conservation zones. Mandena Conservation Zone (MCZ), comprising two forest fragments (M15 and M16) spreading over 230 ha, was established in 2002. Sainte Luce Conservation Zone was created in 2005, and it includes five forest fragments (S1, S2, S8, S9, S17), covering 747 ha. In addition, a large native species tree nursery was established in MCZ. As endemic species are slow-growing, QMM committed to planting a 100ha forest of fast-growing exotic species each year. Resources were allocated to local capacity building and tourism development. Before the mining began (1989-2007), biodiversity studies were conducted by the QMM Biodiversity Committee to understand the local socio-cultural and economic context associated with the proposed mining project (Vincelette et al., 2007).

Figure 5. Sainte Luce is located close to the Indian ocean, with villages like Manafiafy (A) reaching its shores), villages in Mandena, such as Mangaiky (B) are located more inland. Photographs taken by E. Račevska in July and April 2018, respectively.

When it comes to the local communities' use of the forest resources, however, and especially the related beliefs, traditions, and ecological knowledge, few studies have been published to date, and a lot is still unknown. In 2000, Rasolofoharivelo monitored human activities in three forest fragments in Mandena - M3, M15, M16 (Rasolofoharivelo, 2007). He observed no evidence of hunting, but reported that about 75 people entered the forest each day, with the majority of them arriving from Fort Dauphin for the purpose of charcoal production, cutting between 18 and 25 trees each day. The local people from the nearby villages of Ampasy Nahampoana and Mandromondromontra mainly collected firewood and wood for construction; however, there is no mention of the species collected (with the exception of *Pandanus* sp. leaves). In their 2005 study, Ingram et al. report that 58 % of the forest species are used by the local population for everything from construction materials, medicine, fuel or food (Ingram et al., 2005b). In 2006, Norscia and Borgonini-Tarli published a report on the medicinal use of 22 plant species by the local communities of Sainte Luce to treat conditions from indigestion, cold, headache and diarrhoea to parasitic worms, malaria, or abdominal pains (Norscia & Borgonini-Tarli, 2006). Another survey of medicinal plant knowledge conducted by Lyon and Hardesty in 2002 recorded up to 42 plants used as medicine, with the list comprising both exotic and endemic species (Lyon & Hardesty, 2002). The same year, Hogg et al. surveyed human use of nine palm species native to Madagascar. They found that palms are among the most utilised plants in the area, with a wide array of applications, for example, fishing tackle, lobster traps, medicine, construction of houses and canoes (Hogg et al., 2013). The population growth and the proximity to mining were recognised as risk factors by the authors, as they are likely to lead to a decrease of palm population size and density.

Since the establishment of the protected areas, Sainte Luce and Mandena have likely seen a significant change in its forests' resource availability to the local population. Until this is researched and documented, however, it is only possible to theorise about the extent of impact this may have had on people's daily lives. With that in mind, this project was designed to enable a closer look at the current situation. Due to the red-collared brown lemur’s higher abundance in Sainte Luce than in Mandena (Bollen & Donati, 2006; Donati et al., 2007), and the different degree of these forests’ previous human use, Sainte Luce and Mandena provide an excellent research setting for the ecological questions on which I wanted to focus in this study. In recent years, however, these forests have been undergoing changes in their management and forest resource use. While their impact has been manifold, reflecting in both environmental and social aspects, the relationship between the QMM mining company and the local communities of Mandena (where the mining project began in 2007) and Sainte Luce (where the mining operations will continue in the coming years) (Smith et al., 2012) appears to be complex. For this reason, my study would be incomplete without an inclusion of local communities, and an exploration of how this change may have influenced their culture, traditions, and livelihoods.

6. Study aims and thesis outline

The main aim of this doctoral study has been to understand how forest protection measures, implemented in the two communities living near the littoral forests in the southeast Madagascar, have affected the red-collared brown lemur’s ecology and the lives and livelihoods of the local human population. In my study of lemurs, I primarily focused on this species’ ranging behaviour, diet and seed dispersal. In my study of the local people, I focused on their relationship with the red-collared brown lemurs, their use of plants, and their perception of forest protection and the prompted socio-economic development, as well as the perceived impacts this conservation measure has had on the local livelihoods.

- In Chapter 3, I explore how red-collared brown lemurs' habitat use, activity pattern and diet have changed since the implementation of forest protection measures by comparing them to parameters published in previous studies. Forest protection has likely affected the resource availability, which would have implications for the aspects of red-collared brown lemurs' ecology on which I focus in this chapter. Due to the known differences in this lemur's ecology across seasons and the 24-hour cycle, this chapter includes comparisons across wet and dry season, and day and night. Due to the known past differences in forest degradation levels between Sainte Luce and Mandena, I conduct comparisons between the two study areas.

- In Chapter 4, I analyse the microhabitat characteristics of red-collared brown lemur's defecation locations, as well as consider the spatial and temporal patterns of their defecation. Since this lemur species is uniquely important to forest regeneration as a seed disperser, it is important to investigate and understand the parameters related to its defecation that might have implications for the effectiveness of its seed dispersal. As lemurs' habitat use is non-random and known to vary between seasons and the 24-hour cycle, I compare their defecation patterns across wet and dry seasons, and between day and night. Due to previously reported differences in habitat characteristics of Sainte Luce and Mandena, which have translated into between-site differences in activity patterns, I compare the two areas as well.

- In Chapter 5, I compare the forest regeneration of the fragments inhabited by the red-collared brown lemurs (in Sainte Luce and Mandena), and a fragment from which this species has been extirpated (in Sainte Luce). Red-collared brown lemur is believed to be the only seed dispersers of large-seeded plants in the littoral forests of southeastern Madagascar. This lemur's presence in the forest is therefore likely to have implications on the regeneration of those tree species, leading to an observable difference in their regeneration between the fragments in which this lemur species is present and absent. I focus my comparisons on the total regeneration of seedlings and saplings, and the regeneration of species thought to be exclusively dispersed by the red-collared brown lemur.

- In Chapter 6, I investigate local ecological knowledge (LEK) about the red-collared brown lemur. The themes explored include knowledge about species' diet and activity pattern. Additionally, I examine local people's attitudes towards this species and practices surrounding it (i.e., hunting, eating). Despite numerous studies of the red-collared brown lemur population in the littoral forest, little is known about this species' interaction with the local people. As the success of wildlife conservation efforts is closely tied to particular species' significance to the local human population, understanding the parameters explored in this chapter could have implications for the success of this lemur's conservation. Due to the known differences in livelihood strategies between Sainte Luce and Mandena, some of which could have implications for differences in the level of interaction with and knowledge of red-collared brown lemurs, I also conduct a comparison between Sainte Luce and Mandena.

- In Chapter 7, I explore in detail the local use of forest plant species, either as medicinal plants, building materials or cooking fuel. Many species are endemic to the area, and several are threatened. Moreover, forest protection has brought about resource extraction restriction, which has likely impacted how the local people use the forest fragments (both protected and unprotected). Documenting the cultural importance of the forest flora has become a matter of urgency. While Sainte Luce and Mandena are botanically similar, their past anthropogenic use has been different, which is why my focus is also on comparing the two areas.

- In Chapter 8, I investigate how the people of Sainte Luce and Mandena have adjusted to the forest protection, and how this conservation measure has impacted their lives and livelihoods. While protected areas are an important part of forest biodiversity conservation, they have been reported to have both positive and negative impacts on local people. Understanding the perceptions of different aspects and consequences of forest protection on local livelihoods in a specific context can be beneficial to the longevity of forest protection and success of newly established protected area management. I surveyed local perceptions of forest protection, mining and the QMM mining company, tourism, and an NGO activity (in Sainte Luce).

Although the main topic was sub-divided into chapters focusing primarily on the ecological aspect, and other ones aiming to provide an understanding of the lives of the local people, they are once more joined and reflected upon together in the general discussion. Therein I review and explain this intricate inter-relationship of forest, lemurs and people as indivisible.

CHAPTER 2: General methods

1. Study sites

A. Littoral forest fragments

I conducted the study in two sites in southeastern Madagascar: Mandena Conservation Zone (MCZ; 24°57′S, 47°0′E), and Sainte Luce (SL; 24°45' S, 47°11' E). The nearest urban development to both sites is Fort Dauphin or Tôlanaro (25° 02' S 46°59' E), the capital of the Anosy region, which is one of the economically poorest and most isolated regions in Madagascar (Vincelette et al., 2007). Its population is about 45,000 people. The distance between Fort Dauphin and Mandena is about 10 km, while Sainte Luce is located about 35 km away. Botanical composition of the two sites is similar (Campera et al., 2014), but while Sainte Luce is considered to be the most intact littoral forest not only in the southeastern Madagascar (Bollen & Donati, 2006), but in the entire country (Rabevohitra et al., 1996; Dumetz, 1999), Mandena forest is considered to be more degraded (Rabenantoandro et al., 2007). These fragments of littoral forest on mineralised sandy soil (Vincelette et al., 2007) grow in a narrow band of coastal plain of elevation < 50 m (Ingram & Dawson, 2005). They have a relatively open or non-continuous canopy, typically 6-12 m in height, with few emergent trees of up to 20 m (Bollen & Donati, 2005). The diameter at breast height (DBH) of adult trees does not typically exceed 30-40 cm (Dumetz, 1999).

Sainte Luce comprises 17 forest fragments, five of which (i.e., S1, S2, S8, S9, and S17) have been under protection since 2005 (Figure 1). Red-collared brown lemurs inhabit three of the protected fragments (i.e., S8, S9, S17), and two currently unprotected ones (i.e., S11, and S12) (Hyde Roberts et al., 2020). The majority of my project took place in a protected fragment of S9 (275 ha), but a part of my forest regeneration study was conducted in one of the unprotected forest fragments, namely S7 (198 ha). While the former is the closest fragment to the local villages - which has led to it being heavily exploited by the local communities prior to it becoming protected, the latter is more remote (~2 km away from S9) and harder to reach, as it requires crossing a river on foot (made additionally difficult when the bridge is washed away) or by canoe. Despite this, the local communities' reliance on S7 has increased since S9 became protected (formally in 2002, but this was not officially recognised and adhered to by the local communities until 2015; S. Hyde Roberts, SEED Madagascar, personal communication). The average density of red-collared brown lemurs in S9 is 37 individuals per km^2 (Bollen & Donati, 2006). In addition to them, the fragment is inhabited by three species of nocturnal lemurs - southern woolly lemur (*Avahi meridionalis)*, Thomas's dwarf lemur *(Cheirogaleus thomasi),* and Anosy mouse lemur (*Microcebus tanosi)* (Figure 2). While the nocturnal species are also found in S7, that fragment is no longer inhabited by the red-collared brown lemurs. Sainte Luce forest fragments, which have historically been considered community protected, are now managed by the QIT Madagascar Minerals mining company, who have been granted the mining concession by the Malagasy government. They pay the *FIMPIA* (Association of Managers of Forests of Ambatoatsinana) to monitor and protect the conservation zone (S. Hyde Roberts, SEED Madagascar, personal communication).

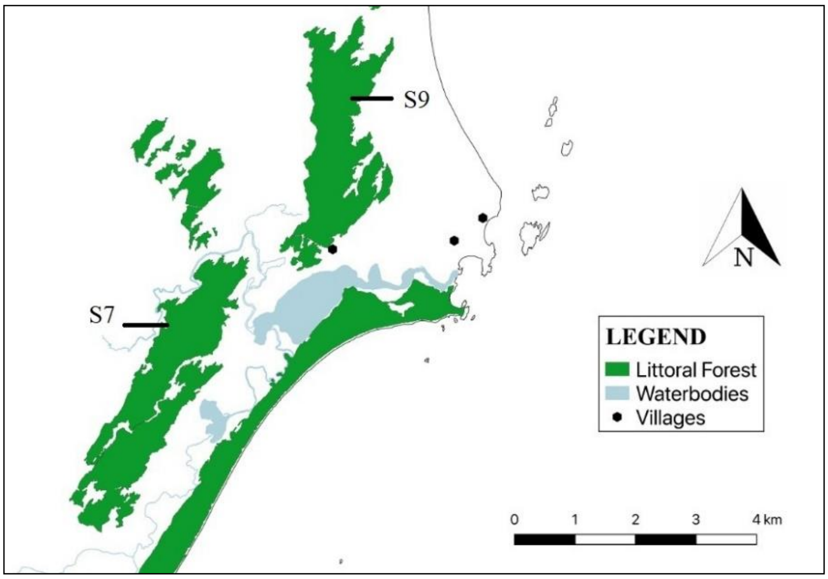


Figure 1. The littoral forest fragments of Sainte Luce included in this study; S9 is currently under protection, while S7 is not. Local villages included in the study are (from left to right) Ambandrika, Ampanasatomboky, and Manafiafy.

Mandena Conservation Zone comprises two fragments - M15 and M16 (230ha), protected since 2003 (Figure 3). While forest protection should have halted collecting endemic tree species for firewood or timber, as well as stopped the hunting, fishing and zebu grazing in the area, all those activities, apart from hunting, have continued (Chapter 8). This suggests they may have decreased and become more covert at best. Red-collared brown lemur groups are present, with an average density of 12 individuals per km^2 (Donati et al., 2007). Besides *E. collaris*, five other species of lemur inhabit MCZ - southern woolly lemur (*Avahi meridionalis),* Ganzhorn's mouse lemur *(Microcebus ganzhorni),* southern bamboo lemur (*Hapalemur meridionalis),* Thomas's dwarf lemur *(Cheirogaleus thomasi)* and greater dwarf lemur (*Cheirogaleus major)* (Figure 2).

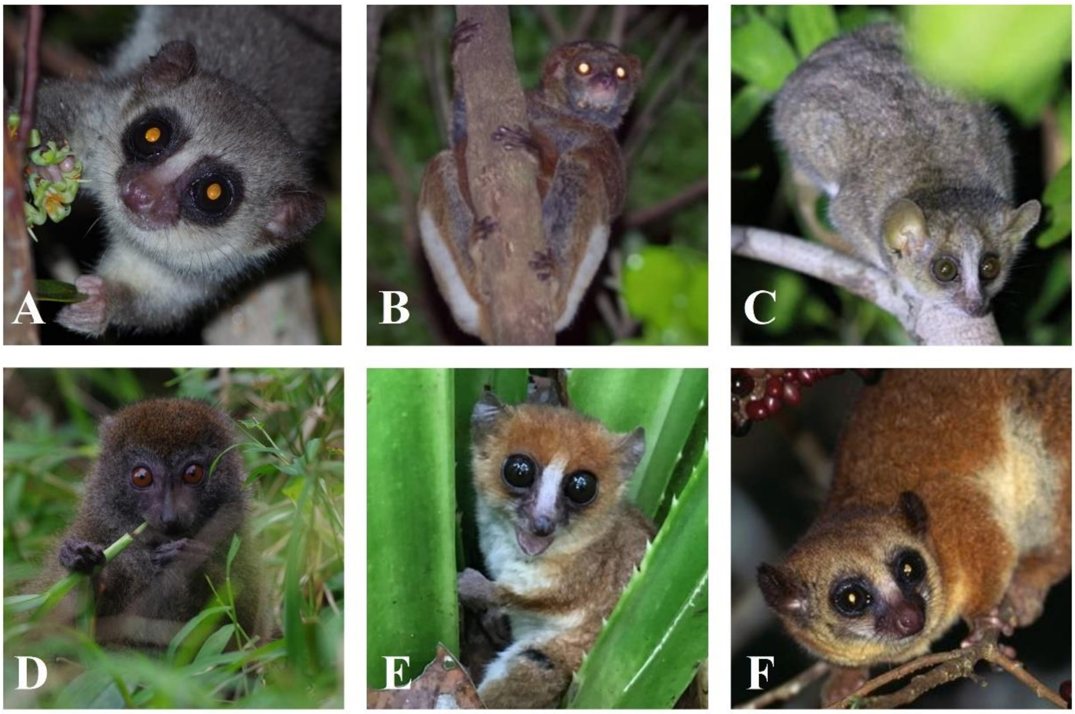


Figure 2. Other lemur species inhabiting the littoral forests of Sainte Luce (A, B, E) and Mandena (A, B, C, D, F): Thomas's dwarf lemur (A), southern woolly lemur (B), Ganzhorn's mouse lemur (C), and southern bamboo lemur (D), Anosy mouse lemur (E), and greater dwarf lemur (F). Photographs A, B, D, and E taken by E. Račevska in Sainte Luce (A, B, E) and Mandena (D) in October 2017, October 2018, August 2017, and September 2018, respectively; photograph C taken by S. Hyde Roberts in Lokaro, in September 2018; photograph F taken by N. Garbutt, time and location unknown).

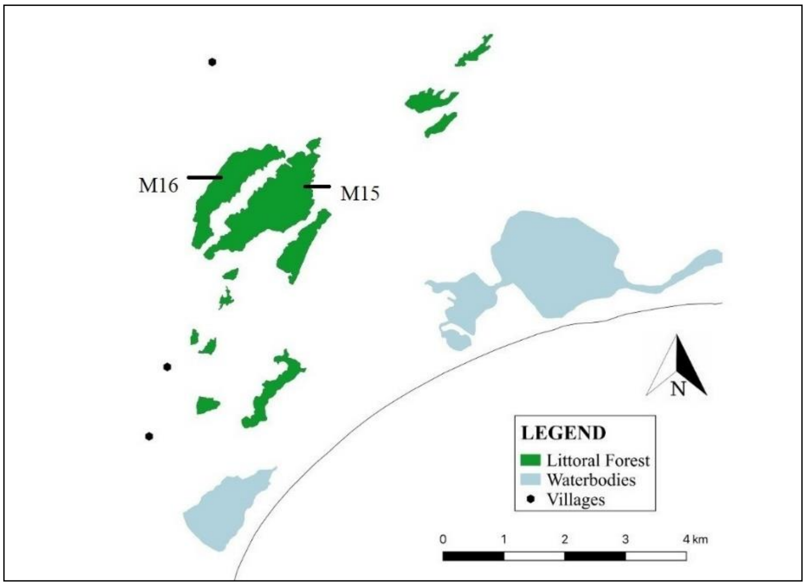


Figure 3. The littoral forest fragments of Mandena. Fragments M15 and M16 form the protected Mandena Conservation Zone. Local villages included in the study are (from top to bottom) Mangaiky, Betaligny and Ampasy Nahampoana.

B. Local communities

As my project encompassed two study sites, I developed my research methodology to include the members of communities living in the proximity of both. The research included three villages in Sainte Luce: Ambandrika (24°46'57.75" S, 47°10'23.99" E), Ampanasatomboky (24°46'48.4" S, 47°11'35.9" E) and Manafiafy (24°46'34.4" S, 47°11'53.5" E), and three villages in Mandena: Ampasy Nahampoana (24°58'51.24" S, 46°58'53.73" E), Betaligny (24°59′28.2" S, 46°58′43.1" E) and Mangaiky (24°56′ 09.0" S, 46°59'20.1" E). They were chosen due to their proximity to the (protected) forest fragments included in the study, and based on recommendations of organisations working in the area (i.e., TBSE in Mandena). Their proximity to the protected areas made them ideal for testing my study hypotheses, which were primarily focused on changes the communities may have faced in the light of forest protection.

One of the central questions of my study was the documentation of how conservation measures have impacted the local livelihoods. Once again, Sainte Luce and Mandena provide an interesting basis for this type of research, due to the differences in their traditional livelihood strategies. Sainte Luce is a fishing community (SEED Madagascar Household Survey, unpublished), whereas the most common livelihood strategies in Mandena have traditionally included agriculture, cattle raising, and timber and non-timber product extraction (Ingram et al., 2005b; Evers & Seagle, 2012; Kraemer, 2012). There is a gender-based division of labour, and while the aforementioned activities are primarily reserved for men, women in both areas typically engage in weaving sedge products (Kraemer, 2012). With regard to formal employment in Sainte Luce, 12 % of households surveyed by SEED Madagascar reported having at least one person formally employed, either by the mining company, a conservation project, an eco-tourism enterprise, or a local fishing company (SEED Madagascar Household Survey, unpublished). In Sainte Luce, the average household comprises 5.3 people, but can range from 1 to 20 people. In terms of population age, 45 % of inhabitants are below 16 years old, while only 4 % are older than 60 (SEED Madagascar Household Survey, unpublished). There were no similar data available for Mandena at the time of the study.

2. Sample description

A. Study animals

In each of the two field sites, I focused my study on two groups of red-collared brown lemurs (please see General Introduction for the species description). To enable and facilitate locating the groups for the close study of their behaviour, one individual from each group was captured and radio collared prior to the beginning of the study (in July and early August 2017). As females are the philopatric sex, the aim was to collar a female in each group; however, in Mandena, the females had already been fitted with radio collars during a previous study (Balestri et al., 2014; Campera et al., 2014), so instead adult males (already stable group members) were collared.

Captures were done by a team comprising an experienced Malagasy blowpipe specialist, my local forest guide, my supervisor (GD) and myself. The active substance used was tiletamine hydrochloride**,** a non-narcotic non-barbiturate injectable anaesthetic, delivered intramuscularly by a hypodermic needle from a near proximity. All lemurs were handled with care during the entire process, which we carried out *in situ*. Immediately after the capture, we took each individual's measurements (Table 1). Radio-collars (Holohil systems Ltd. RI-2D) were tested before being fitted on the lemurs, and again immediately before each individual was released. I stayed with each collared individual until it fully recovered from the anaesthesia and re-joined their group.

Table 1. Biometrical measurements of the radio-collared individuals (N=4).

	Sainte Luce Conservation Zone (S9)		**Mandena Conservation Zone**	
Date	31 July 2017	1 August 2017	2 August 2017	3 August 2017
Animal's sex	Female	Female	Male	Male
Head length	14 cm	15 cm	14.5 cm	14.5 cm
Body length	42 cm	45 cm	44 cm	46.5 cm
Tail length	48 cm	55 cm	50 cm	49 cm
Humerus	9.5 cm	9 cm	8.5 cm	10.5 cm
Radius	10 cm	9.5 cm	10.5 cm	11 cm
Femur	15.5 cm	13 cm	14 cm	16 cm
Tibia	14 cm	14 cm	15 cm	15.5 cm
Hand length	6 cm	7 cm	6.5 cm	7 cm
Foot length	9 cm	10 cm	10 cm	10.5 cm
Canine length	0.9 cm	1.1 cm	1.3 cm	1.1 cm

Sainte Luce groups were labelled A and C, and Mandena groups B and D. I only collected data from adults (Table 2). For diurnal observations, focal individuals were rotated daily. I distinguished individual lemurs by differences in colouration (e.g., a darker stripe along the dorsal coat, differences in the prominence of facial markings), tail shape (e.g., fur missing, differences in fluffiness), and the presence of radio collars (placed in this or a previous study). I was not able to find Group D after October 2017, which led to their exclusion from the study.

Figure 4. Radio-collared individuals: two adult females (Sainte Luce; A, C) and two adult males (Mandena; B, D). The letters correspond to the groups to which each of the radio-collared individual belongs. All photographs taken by E. Račevska in August and September 2017.

Table 2. Group compositions of all four lemur groups originally included in the study.

		Adult females	Adult males	Subadult females	Subadult males	Total group size
Sainte Luce	Group A	2	3	2	0	7
	Group C	4	3	1	1	9
Mandena	Group B	2	4	1	1	8
	Group D	1	1	0	1	3

B. Human participants

The sample comprised 60 participants, 10 from each village included in the study. They were selected using quota sampling (Newing, 2010). Men and women were equally represented in the sample, and their age varied between 24 and 90; however, many people in this area are not sure of their exact age (T. H. Longosoa, SEED Madagascar, personal communication), so these values may not be accurate (especially in the case of the older participants). Age distribution of the participants in the Mandena was positively skewed (0.947, SE=0.427), failing the Shapiro-Wilk test of normality (W(30)=0.918, p=0.024), and moderately negatively skewed in the Sainte Luce area (0.450, SE=0.427), (W(30)=0.906, p=0.012). For this reason, I decided to use Median as the central tendency when carrying out analyses including participants' age. Participants' age in the Mandena area varied between 24 and 90, with the Median of 39.0 years (IQR=24.0), while in the Sainte Luce area it varied between 28 and 80, with the Median of 44.5 years (IQR=30.0). A Mann-Whitney test indicated that participants from Sainte Luce did not differ in their age from participants from Mandena (U=332.00, p=0.081), but they tended to be older.

3. Data collection

Behavioural observations of red-collared brown lemurs

Observational data of my study species was the basis of the part of my research concerning red-collared brown lemur diet (more specifically, its seasonal and daily variation). I collected all behavioural data myself between August 2017 and August 2018 (Table 3), during diurnal and nocturnal observations. Diurnal observations were conducted using Instantaneous Sampling (Altmann, 1974) at five-minute intervals of a focal individual, rotated daily to ensure that all individuals are equally sampled. During nocturnal observations, I used the Auditory Group Sampling method (Andrews & Birkinshaw, 1998; Donati et al., 2007), recording the general activity of an entire group, also at five-minute intervals. Using two different methods might have implications for the results: auditory group sampling can be less effective in detecting feeding on certain food items (i.e., leaves, flowers, nectar) (Andrews & Birkinshaw, 1998). My study design included more diurnal than nocturnal observations, and the groups followed in this study were well habituated, allowing following from a relatively close proximity (and as a result, a good view of the focal animal during the day). Therefore, in order to not sacrifice the precision in documenting lemurs' food intake, instead of entirely relying on the auditory group sampling (as in Andrews & Birkinshaw, 1998), I opted to use a combination of the two methods (as in Donati et al., 2007). The ethogram I used is in General Appendix. Due to the focus on this chapter largely being on the seed dispersal, I gave the most attention to feeding behaviour and variables relating to tree species consumed (i.e., species, food item) (Donati et al., 2011b). Detailed methods and analyses are explained in Chapter 3.

Patterns of defecation and microhabitat analysis of defecation locations

Characteristics of microhabitats in which the seeds are dropped can have big implications for seed survival and seedling recruitment (Schupp, 1988; Forget, 1997; Wenny, 2000; Gross-Camp & Kaplin 2005; Russo 2005). In this study, I focused on examining two microhabitat characteristics: canopy closure and forest density. I measured forest density using the point-centre quartile method (Bower et al., 1998), while canopy closure measures were obtained using a convex spherical densitometer (Strickler, 1959). Additionally, I examined the spatial and temporal patterns of defecation, focusing on the proximity of defecation locations to the most recent previous resting and feeding tree (spatial patterns), and the temporal proximity of defecating to resting and feeding (temporal patterns). I collected all data myself between August 2017 and August 2018 (Table 2). Detailed methods and analyses used are described in Chapter 4.

Forest regeneration

One of the key aspects of this thesis was research of the effects of red-collared brown lemur presence on the regeneration of the forest. This process is dependent on seed dispersal, but impacted by anthropogenic disturbances, such as logging or hunting. Large-bodied frugivores and the plants they disperse are at a particular risk (McEuen & Curran, 2004; Lahann, 2007). In the littoral forests of Sainte Luce and Mandena, the red-collared brown lemur is the only disperser of plants whose seeds are larger than 12.5 mm in diameter (Bollen et al., 2004; Bollen & Donati, 2006). It has been extirpated from several forest fragments in Sainte Luce (Bollen & Donati, 2005; Donati et al., 2007), but it is difficult to know exactly when this occurred. However, the species remains present in several protected fragments in both Sainte Luce (e.g., S9) and Mandena (i.e., Mandena Conservation Zone). This created an opportunity to examine the effects of this lemur's presence on forest regeneration, and specifically the species believed to only be dispersed by this lemur.

To enable a quantification of this relationship, I collected botanical data between August and October 2018 (Table 3), in three forest fragments – two where this lemur is present, albeit at a different abundance (i.e., S9 in Sainte Luce, and MCZ in Mandena), and one from where it has been extirpated (i.e., S7 fragment in Sainte Luce). I designed this study in this way as I expected that this species' presence will have implications for forest regeneration, due to it being a likely sole disperser of many native species with seeds larger than 12.5 mm (Bollen et al., 2004; Bollen & Donati, 2006). This study primarily focused on the comparison in forest regeneration and species diversity between the fragments in which red-collared brown lemur is present / absent. I collected all data myself between August 2017 and October 2018. For the detailed methods and analyses, please refer to Chapter 5.

Interviews with the human participants

I collected data between April and October 2018 (Table 3). As I did not live in the focal villages from which my participants were selected, I visited them with my translators. Ampasy Nahampoana, Betaligny, Mangaiky and Ambandrika were visited twice (i.e., interviews were conducted over two-day periods), while I visited Ampanasatomboky three times, and Manafiafy once. I planned to recruit participants using systematic random sampling (Newing, 2010). However, as many people worked during the day and were away from their homes (especially men), I adjusted my approach and used availability sampling (Newing, 2010). Specifically, I used quota sampling (Newing, 2010) to ensure equal representation of women and men in the sample. I used a qualitative approach based on semi-structured interviews (Bernard, 2017). This method allows flexibility in its implementation, which ensures that participants are able to add more information than what was asked, and which they find important. Furthermore, it provides the ability to accommodate participants' concerns, should they arise while discussing some of the more sensitive aspects of their lives. It also allows the researchers to establish a rapport with the participants, as well as debrief them if the data collection process becomes uncomfortable or distressing. Finally, this approach enables further exploration of more complex issues and explore contradictions in participants' answers. Because the conservation measures are likely to have impacted people's day to day living, and potentially their livelihoods, I found this approach to be more appropriate than a quantitative one, which would have resulted in fewer nuances of the gained information, as well as a potential disregard for any participants' concerns (Fylan, 2005). As I was also interested in the hunting practices, and attitudes to powerful stakeholders in the area (i.e., the mining company), I made sure that my research methodology was discretionary. More details are given in Chapters 6-8.

Each of the chapters focuses on a different aspect of the local population's use of and relationship with the forest and wildlife – i.e., local ecological knowledge about the red-collared brown lemur, the use of forest plant species, and the impact of forest protection on people's lives and livelihoods. I collected data using semi-structured interviews (the Interview guide I used is in the General Appendix). I interviewed 60 adults (30 women and 30 men) inhabiting six villages located in the vicinity of the protected forests of Sainte Luce and Mandena (I surveyed three villages in each area). Each participant was interviewed once, and the interviews took place in participants' homes. All interviews were conducted in the local (Antanosy) dialect of Malagasy, with help from one of my local translators (N=3), which were either recommended by my local collaborators (i.e., SEED Madagascar) (N=2), or had been previously employed by other researchers from Oxford Brookes University who had worked in Mandena (N=1). One of SEED Madagascar's translators worked with me in Sainte Luce and Mandena, while the other, along with the third, independently hired translator, only worked with me in Mandena. The arrangements were made with the translators' availability in mind: SEED Madagascar's translators were involved in other aspects of the NGO's work, while the third translator worked with another Oxford Brookes University researcher at the same time. In the interview section where participants were asked to explain their perception of the foreigners' presence in their area, participants' answers often focused on the tourist projects operating locally, and in Sainte Luce, on SEED Madagascar. While this allowed me to analyse the gained information in a way that was not anticipated or planned, it created a conflict because the translator working with me was employed by SEED Madagascar. I discuss the implications of this in the discussion of Chapter 8.

All three translators spoke English, but before the data collection started, I had a meeting with each of them during which I explained the study purpose and the Interview guide in great detail. This was done to ensure that they understood all of the questions, and this allowed me to reframe them in a culturally sensitive way. Moreover, the meetings gave me a chance to explain exactly what information I was looking, so that the translators could help me obtain it from the participants in a culturally sensitive manner. All translators signed a confidentiality agreement prior to the beginning of the study, wherein it was stated that any of the information gathered during the course of the study would not be discussed with any third parties. Before starting the interviews in each village, my translators and I met with the village chief to introduce ourselves, explain the purpose of the study and ask for permission to collect data in their village; all contacted village chiefs gave their permission. Once the data collection began, the translators helped with the introduction to the potential interviewees. They explained to them the purpose of the study, as well as what would be asked of them if they agreed to participate. At this time, I used the Participant Information Sheet 2 (General Appendix) as guidance.

If a person agreed to participate, I noted their age, gender and the name of their village as identifying factors. I did not ask for participants' signatures due to low levels of literacy in the area (Comité Regional pour le Développement de l'Anosy, 2003). I interviewed a single respondent per household to ensure independence of responses (Nash et al., 2016). Participants' anonymity was of outmost importance to me, due to the potentially sensitive information that might be revealed in the study (i.e., hunting habits, attitudes towards the mining company). I emphasised the anonymous nature of the study and data confidentiality, also making sure that my participants understood they did not have to answer any question that they did not want to answer, without disclosing the reason. I obtained separate consent for the interviews to be audio recorded, the purpose of which was, as we also explained to each participant, to ensure a higher accuracy when documenting their responses. After the interview, each recording was transcribed and translated with the help of a translator. The interviews lasted between 30 and 90 minutes. Longer surveys are sometimes associated with shorter and less detailed answers to the questions asked towards the ending (Galesic & Bosnjak, 2009), and a fatigue effect, defined as a decline in participants' performance due to a prolonged or demanding research tasks, generally attributed to the participants becoming tired of bored (APA Dictionary of Psychology, 2020). To decrease the chance of this happening, I took several precautions. I explained the importance of the study to the participants, and thanked them for their participation. I kept the questions clear, concise, and as short as possible. I also varied the way in which they were asked. For example, some were simple and only required a yes or no answer, while others required an explanation (e.g., use of medicinal plants to prepare medicines). Between the different themes, I introduced pauses consisting of a more casual conversation. Introducing pauses reduces the risk of a decrease in the quality of participants answers (Schatz et al., 2012). Participants' boredom can also influence their answers (Schatz et al., 2012). However, the diversity of the discussed topics in this study might have been beneficial in this matter, as I did not find the participants to rush through the themes and questions introduced at the ending of the interview. Due to ethical considerations, participants were not offered monetary compensation, but were thanked for their help and treated to refreshment at the end of the interview.

Table 3. Timeline of data collection.

Activity	Date	Area
Focal animal captures	30 – 31 July 2017	Sainte Luce
	1 – 2 August 2017	Mandena
Lemur group follows	8 August – 30 November 2017	Sainte Luce
(Chapter 3)	9 March – 9 April 2018	
	26 July – 16 August 2018	
	21 August – 9 November 2017	Mandena
	27 March – 19 April 2018	
	19 July – 24 August 2018	
Mapping lemur defecation sites	18 August – 1 December 2017	Sainte Luce
(Chapter 4)	16 March – 8 April 2018	
	1 – 17 August 2018	
	30 August – 9 November 2017	Mandena
	3 – 19 April 2018	
	24 July – 25 August 2018	
Mapping forest regeneration	18 August – 30 September 2018	Sainte Luce
(Chapter 5)	19 – 24 September 2018	Mandena
Interviews with local people	18 August – 6 September 2018	Sainte Luce
(Chapter 6-8)	29 July – 3 October 2018	Mandena

5. Data analyses

Research methods and data analyses were selected based on previous studies. Home range sizes were analysed in Ranges 9 (Anatrack Ltd.). I used two types of home range analysis – the fixed kernel (FK) and the minimum convex polygon (MCP). The two approaches can provide very different results (Boyle et al., 2009; Pebsworth et al., 2012). The MCP method assumes that the entire area within a home range is used equally, which is why even a single point may substantially extend the home range size (Gregory, 2016). This approach also includes the areas that may not be utilised at all, such as large water bodies (White & Garrot, 1990), which often leads to an overestimation of home range sizes (Franzreb, 2006). On the other hand, the FK method removes the limitation associated with sample sizes, and is often considered to be more accurate than the MCP method (Powell, 2000; Pimley et al., 2005), although not everyone agrees (Hemson et al., 2005; Moorcroft & Lewis, 2006). I have used both methods to enable comparisons of my findings to those of previous studies of the same lemur populations, which typically opted for one or the other (please see Table 1 in General Introduction). All other data were in SPSS 26.0 (IBM, 2018). Analyses were chosen based on the characteristics of the data and research questions. Models were chosen based on data type and fit (Table 4). In the remaining three chapters, the main focus is on the narrative. In some cases, mainly non-parametrical tests are used to compare the participants from Sainte Luce and Mandena, and test gender- and age-related differences.

Table 4. Models used in the thesis, and the criteria used for their selection.

	Research question	Analysis type	Selection criteria
Chapter 3	Comparing activity (counts of active behaviour per observation session) between the two areas, seasons, and day phases	Generalized Linear Model with Poisson distribution and log link function	Data type (i.e., counts)
	Comparing feeding behaviour (counts of feeding) between the two areas, seasons, and day phases	Generalized Linear Model with Poisson distribution and log link function	Data type (i.e., counts)
	Comparing the proportions of different food items in the lemurs' diet	Generalized Linear Model with Poisson distribution and log link function	Data type (i.e., counts)
	Comparing dietary diversity between the two areas, seasons, and day phases	Generalized Linear Model with Poisson distribution and log link function	Data type (i.e., counts)
Chapter 4	Comparing canopy closure and forest density of defecation locations of lemurs inhabiting the two areas	Generalized Linear Model with gamma error distribution and log link function	Data type (i.e., positive-only data, with positively skewed errors)
	Comparing canopy closure and forest density of lemur defecation locations and random locations	Generalized Linear Model with gamma error distribution and log link function	Data type (i.e., positive-only data, with positively skewed errors)

	Comparing canopy closure and forest density in lemur defecation locations between the two areas and seasons	Generalized Linear Model with gamma error distribution and log link function	Data type (i.e., positive-only data, with positively skewed errors)
	Modelling spatial and temporal distribution of defecation, in relation to resting and feeding times and locations	Generalized Linear Model with gamma error distribution and log link function	Data type (i.e., positive-only data, with positively skewed errors)
Chapter 5	Comparing total regeneration of fragments in which *E. collaris* is present and absent	Generalized Linear Model with a negative binomial distribution	Akaike information criteria (AIC): the model with the smallest AIC was selected
	Comparing the regeneration of species dispersed exclusively by *E. collaris* in fragments in which *E. collaris* is present and absent	Generalized Linear Model with a negative binomial distribution	Akaike information criteria (AIC): the model with the smallest AIC was selected
	Comparing the total forest regeneration in lemur defecation locations and random locations in fragments in which *E. collaris* is present and absent	Generalized Linear Model with a negative binomial distribution.	Akaike information criteria (AIC): the model with the smallest AIC was selected
	Comparing the regeneration of species dispersed exclusively by *E. collaris* in lemur defecation locations and random locations	Generalized Linear Model with a negative binomial distribution	Akaike information criteria (AIC): the model with the smallest AIC was selected

4. Project collaborators

The project was conducted under the collaboration between the Department of Animal Biology at the University of Antananarivo and the Department of Social Sciences at the Oxford Brookes University. While in the field, I received logistical support of the following people and institutions:

1. The Department of Animal Biology of the University of Antananarivo, Madagascar,
2. SEED Madagascar (*Sustainable Environment, Education & Development in Madagascar*),
3. TBSE (*Tropical Biodiversity and Social Enterprise*),
4. QMM (*QIT Madagascar Minerals*).

5. Ethics statement

Ethical approval was granted by the Oxford Brookes University Research Ethics Committee (UREC Registration No: 171103). Research protocols were approved, and permits acquired by the University of Antananarivo, the Directeur Regional de l'Environmeneted de l'Ecologie et des Forets in Fort Dauphin, and Ministere de l'Environement, de l'Ecologie et des Forets in Antananarivo (Autorisation de recherche n. 181/17/MEEF/SG/DGF/DSAP/SCB.Re, and Autorisation de recherche n. 174/18/MEEF/SG/DGF/DSAP/SCB.Re).

CHAPTER 3

Living with forest protection: habitat use and diet of red-collared brown lemurs (*Eulemur collaris*) in the protected littoral forests of Sainte Luce and Mandena, southeastern Madagascar

Introduction

Protected areas are an essential part of conservation in many low- and middle-income countries (Brechin et al., 2002; Lele et al., 2010; Ervin, 2013; Singh et al., 2013), and many studies focus on evaluating the effectiveness of their management (Hockings et al., 2000; Leverington et al., 2010). As this conservation measure is expected to safeguard the protected species from illegal extraction while also preserving their habitat, it is equally (if not more) important to investigate the effects of forest protection on the wild fauna (e.g., Mduma et al., 1999; Carrillo et al., 2000; Cuarón, 2000; Kawanishi & Sunquist, 2004; Beaudrot et al., 2016; Kamilar & Beaudrot, 2018; Donati et al., 2020b), and flora (Andam et al., 2008; Gaveau et al., 2009; Pfeifer et al., 2012). Wildlife population trends are variable, and while most of the monitored mammal and bird populations remain stable, more seem to experience a decline than an increase in their numbers (Beaudrot et al., 2016). However, the effectiveness of restriction enforcement is important. Lower hunting restrictions are related to a decrease of mammal abundance, especially in the case of preferentially hunted species (Carrillo et al., 2000). If only primates are considered, a global assessment (Kamilar & Beaudrot, 2018) showed that none of the monitored populations increased. While most remained stable, several experienced a significant decline. As they were not hunted, authors believe that this was due to the prior anthropogenic disturbance. The time of assessment might be important – although animals might shift to a protected forest quickly after their previous habitat was destroyed (which can artificially increase their densities), their numbers can subsequently decrease due to insufficient resources (Kamilar & Beaudrot, 2018). In addition to monitoring population sizes, understanding how the animals have been affected by conservation measures can be helped by examining aspects of their ecology, such as activity pattern, home range use, or diet.

Temporal organisation is one of the most influential aspects of animal behaviour, shown to affect everything from physiology and organisms' internal processes to species' survival (Daan & Aschoff, 1982). Because activity patterns evolve under ecological pressures, they are affected by external factors, such as food quality and availability, habitat characteristics, and weather (Curtis et al., 1999; Halle & Stensteth, 2000; Lambert & Rothman, 2015). Many of these factors are influenced by seasonality. One of the traits most affected by seasonality is diet. Diet also impacts animals' fitness, which is why it is reflected in the species-level adaptations (Lambert & Rothman, 2015). One of the common strategies for coping with the adverse effects of either temporal or spatial variation in resource variability is dietary flexibility (Hemingway & Bynum, 2005). In periods of food scarcity, it is not unusual for animal species typically considered frugivores to shift to a predominantly folivorous diet (e.g., MacKinnon, 1977; Terborgh & Stern, 1987; Chapman, 1987; 1988; Hill, 1997; Lambert et al., 2004; Irwin et al., 2014; Terborgh, 2014). The same dietary transition can occur as a response to anthropogenic habitat alterations (e.g., Riley, 2007; Nowak & Lee, 2013), which are a well-known stressor for numerous vertebrates worldwide (Marra & Holberton, 1998; Homan et al., 2003; Jachowski et al., 2012; Johnstone et al., 2012). Non-human primates (hereafter primates) are no exception (Chapman et al., 2006; Martínez-Mota et al., 2007; Rangel-Negrin et al., 2009; Dunn et al., 2013; Estrada et al., 2017), especially the canopy-dwelling frugivores (Isaac & Cowlishaw, 2004; Godfrey & Irwin, 2007).

While most animal species are either diurnal or nocturnal, several exploit both niches, with portions of their activity spread out evenly across the 24-hour cycle. This is called cathemerality (Tattersall, 1987). Cathemerality is believed to be influenced by seasonal variations in food abundance and quality (Enquist & Richard, 1991; Pereira et al., 1999; Wright, 1999). When food resources are scarce, the adaptive value of cathemerality manifests in allowing the species to continue feeding over the 24-hour cycle, therefore enhancing the nutritional value provided in the lower-quality food (Engqvist & Richard, 1991; Mutchler, 1999; Tarnaud, 2006). While it is common in mammals, cathemerality is present in only a handful of primates (Curtis & Rasmussen, 2006). The relationship between activity pattern and diet was confirmed in lemurs (Engquist & Richard, 1991; Tarnaud, 2006; Donati et al., 2009), as well as anthropoid primates (Dasilva, 1992; Milton, 1998; Hill & Dunbar, 2002; Nagy-Reis & Setz, 2017). While some primates respond to changes in resource availability by decreasing of increasing their dietary diversity, others change their ranging and behaviour. Energy minimizers (Schoener, 1971) switch to alternative, more abundant sources, and conserve energy during foraging. Energy maximisers (Schoener, 1971) spend more time and energy foraging, and maintain their energy intake across seasons. Small-bodied mammals, and particularly frugivores, are more susceptible to seasonal fluctuations in resources (Lindstedt & Boyce, 1985). Common brown lemurs (*Eulemur fulvus*) were found to increase nocturnal activity in the dry season, as a result of poor food quality (Tarnaud, 2006), and spend more time resting during the day. Lower activity enables energy conservation, and more time spent digesting fibre-rich food (such as leaves) (Chivers & Hladik, 1980). Similarly, titi monkeys (*Callicebus nigrifrons*) were found to travel less in periods of food scarcity (Nagy-Reis & Setz, 2017). Seasonality of resource abundance leads not only to morphological and physiological adaptations, but also to behavioural ones (van Schaik et al., 1993). For instance, howler monkeys (*Alouatta* spp.) show a variety of behaviours associated with energy conservation – for instance, high selectivity in feeding, goal-directed travel between food sources, long periods of inactivity, postures that conserve body heat, and avoidance of sudden movements (Milton, 1998).

Madagascar is a prime example of irregular and unpredictable seasonality (Wright, 1999; Dewar & Richard, 2007), which can be especially challenging for the frugivores. The environmental variability affects forest phenology, leading to a lower diversity and density of fruiting plants, as well as irregular and unpredictable fruit production (Meyers & Wright, 1993; Hemingway, 1996; Goodman & Ganzhorn, 1997; Bollen & Donati, 2005; Wright et al., 2005). Combined with the increasing pressure of anthropogenic changes to the habitat, periods of resource scarcity can negatively impact the survival of numerous wildlife species (Wright, 1999; Veilledent, 2017). An adaptation that is beneficial in terms of coping with resource scarcity, while simultaneously diminishing resource competition (Kappeler & Erkert, 2003) is cathemerality. In Madagascar, five extant lemur genera exhibit this adaptation – *Eulemur, Prolemur, Lemur*, *Hapalemur* and *Varecia* (van Schaik & Kappeler, 1996; Wright, 1999; Curtis & Rasmussen, 2002; 2006; Schwitzer et al., 2007b; Donati et al., 2007; 2009; 2013; 2016; LaFleur et al., 2014; Eppley et al., 2015), and to some extent *Avahi* (Campera et al., 2019), albeit there is inter-specific variation within the genera (Colquhoun, 1993; Curtis & Zaramondy, 1998; Rasmussen, 1999; Donati et al., 1999; Curtis & Rasmussen, 2006; Tarnaud, 2006; Fernadez-Duque & Erkert, 2006).

The red-collared brown lemur (*Eulemur collaris*) is a good model for examining the effects of forest protection due to its ecology. This species has relatively large and flexible home ranges (Overdorff, 1993; Volampeno et al., 2011; Donati et al., 2011; Sato, 2013; Campera et al., 2014), which help them cope with fluctuating fruit availability and fruiting pattern. As these large home ranges can alleviate the effects of habitat degradation (Curtis & Zaramody, 1998; Schwitzer et al., 2007; Donati et al., 2011; Kelley, 2013), a change in their size would signal a change in the quality of the habitat. Since this species has also been shown to cope with scarce resources by minimizing energy expenditure by prolonging resting (Campera et al., 2014) - a tendency not uncommon in the primate order (e.g., Clutton-Brock, 1977; Oates, 1987; Yamagiwa & Mwanza, 1994), a change in their activity budgets would signal a change in resource availability.

The red-collared brown lemur is predominantly frugivorous throughout the year (Donati et al., 2007; 2011), showing no major shift in its diet type regardless of the season. Its dietary breadth includes over 120 plant species spanning over 45 families (Donati et al., 2007). Due to its body size, this lemur is particularly important for seed dispersal (Bollen et al., 2004; Bollen & Donati, 2006). Seasonal fluctuation in the proportion of fruit, or specific fruiting species in the diet may have implications for their regeneration through the differences of success of their seedling establishment (for a similar case in *E. rufifrons*, see Ganzhorn et al., 1999). As this lemur is also cathemeral (Donati et al., 2007; 2016), differences in activity and diet associated with day phase could also impact the seedlings' establishment success, as a result of a variation in seed predation associated with the time of day (i.e., activity pattern of seed predators; Ewer, 1971; Ramanamanjato & Ganzhorn, 2001).

The littoral forests of Sainte Luce and Mandena in the southeast of Madagascar, where this species is the largest of the extant lemur species, are fragmented and as a result of intense past human pressure, heavily disrupted. Historic differences in the levels of anthropogenic pressures of Sainte Luce and Mandena make these two areas interesting for a comparison: prior to forest protection, Sainte Luce was the most intact littoral forest in Madagascar (Bollen & Donati, 2006; Rabevohitra et al., 1996; Dumetz, 1999), while Mandena was more heavily degraded (Rabenantoandro, et al, 2007). However, the establishment of the protected areas in both Sainte Luce (in 2005) and Mandena (in 2002) has likely affected their forest structure and density, as protected fragments typically experience a decreased level of forest degradation, as well as an increase in plant regeneration (Hartshorn, 1978; Denslow, 1995). One of the ways in which this is examined is through the NDVI (Normalized difference Vegetation Index), a satellite-based measure of photosynthetic activity (Myneni et al., 1995) that is used as a proxy for leaf cover and forest regeneration. In Mandena, the average NDVI has increased significantly between 2001 and 2018 (Donati et al., 2020b), showing that the vegetation has improved since the establishment of the Mandena Conservation Zone. In addition to the likely resource availability increase, the same protection measures also brought about an attenuation (if not the complete cessation) of hunting, leaving the diurnal birds of prey as this species only predator (Donati et al., 2009). All of these factors are likely to have impacted lemur activity budgets and habitat use, previously shown to differ between Sainte Luce and Mandena (Donati et al., 2011; Campera et al., 2014), possibly eliminating the difference between lemurs inhabiting the two forests in these aspects.

In this project, I examine the current red-collared brown lemur's habitat use, activity budget, and diet, as well as establish whether these two aspects of its ecology have been affected by the forest protection measures (and if so, how). This study is designed in a way that will allow for a direct comparison with previous works (e.g., Donati et al., 2007; 2011; 2020; Campera et al., 2014), while simultaneously providing an assessment of the current situation. I address the following questions:

1. Have home range sizes of the red-collared brown lemurs in Sainte Luce and Mandena changed since the protected areas were implemented?
2. Has the lemurs' activity pattern changed since the establishment of the protected areas?
3. Has the lemurs' diet changed, in terms of the percentage of feeding in their activity budgets, and the percentages of different food items in their diet?
4. Has this lemurs' dietary diversity changed since forest protection measures were implemented? Does it show seasonal variability, or variation between day phases (i.e., diurnal and nocturnal activity)?

Based on the previous findings, I offer the following hypotheses and predictions:

H1: In degraded habitats, red-collared brown lemurs have large and fragmented home ranges (Donati et al., 2011; Campera et al., 2014). Habitat improvement observed in MCZ since becoming protected (Donati et al., 2020) will be related to smaller and less fragmented home ranges of red-collared brown lemurs inhabiting MCZ.

Prediction: Home ranges of red-collared brown lemurs inhabiting MCZ have changed since forest protection: they will be smaller and less fragmented than previously reported.

H2. Activity patterns and diet are related: higher diurnality of red-collared brown lemurs is related to higher quality diet (Donati et al., 2007). When food quality is low, during the day and at night lemurs spend equal times feeding, as well as being active (Engqvist & Richard, 1991; Donati et al., 2007).

Prediction: Activity patterns of red-collared brown lemurs in MCZ have changed, due to habitat quality improvement. Activity patterns of lemurs in MCZ and S9 will not differ. Lemurs from both fragments will be more active during the day than at night, and more active in the dry than in the wet season.

H3. Littoral forest phenology cycles and fruit production peaks affect time spent feeding and the percentage of fruit in red-collared brown lemurs' diet, but the species remains mainly frugivorous year-round (Donati et al., 2007; Campera et al., 2014).

Prediction: If littoral forest phenology and fruit production peaks (which occur in the wet season) affect lemurs' diet and feeding proportion, then lemurs will consume more fruit during the wet season (the period of abundance) and their percentage of feeding in the activity budget will be larger in the dry season (the lean period). Due to the habitat improvement in MCZ, there will be no difference between the lemurs inhabiting S9 and MCZ. Red-collared brown lemurs in S9 and MCZ will be frugivorous throughout the year.

H4. Dietary diversity of red-collared brown lemurs in different seasons is related to habitat quality, littoral forest phenology cycles and activity patterns (Donati et al., 2007). As MCZ habitat quality has improved since becoming protected (Donati et al., 2020), dietary diversity of red-collared brown lemurs inhabiting MCZ and S9 should not differ.

Prediction: Red-collared brown lemurs will feed on a higher number of tree species during the period of abundance (wet season) than in the lean period (dry season). Dietary diversity of red-collared brown lemurs inhabiting S9 and MCZ will not differ. Red-collared brown lemurs will feed on a higher number of tree species during the day than at night.

Methods

Data collection

The study was conducted between August 2017 and August 2018 and resulted in 511 observational hours. It took place in two protected littoral forest fragments, one in the Sainte Luce (i.e., S9, 24°45′S, 47°11′E), and one in Mandena (i.e., joined M15 + M16 fragment, forming Mandena Conservation Zone (MCZ), 24°57′S, 47°0′E). Located in the Anosy region, these littoral forests are characterised by a tropical wet climate. In Sainte Luce, the average monthly temperature is 23°C, with around 2,480 mm of average annual rainfall (Bollen & Donati, 2005). The average monthly temperature of Mandena is 23°C, with an average annual rainfall of 1,600 mm (Ramanamanjato & Ganzhorn, 2001). The two forests are of similar botanical composition (Rabenantoandro et al., 2007).

Climate data were collected long term at one of the field sites (i.e., Sainte Luce) (collected by Sam Hyde Roberts, SEED Madagascar). Months with a total rainfall of 100 mm or above were defined as wet months (Morellato et al., 2000; Donati et al., 2007). This seasonality pattern was in line with those recorded over several years in previous studies (Donati et al., 2007). For this reason, I expect that resource availability pattern, which is more likely to affect the lemurs than climate itself, was also likely similar to the previously reported one (Campera et al., 2014). The period of abundance (i.e., the wet season) therefore included months between November and April, while the lean period (i.e., the dry season) included data collected between May and October.

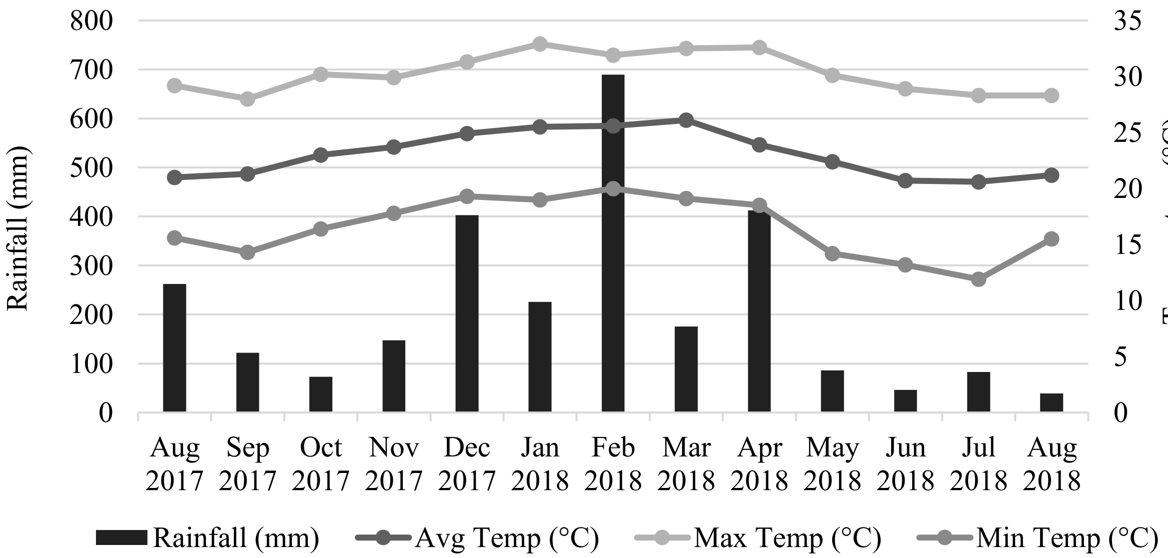


Figure 1. Rainfall and temperature in Sainte Luce from August 2017 to August 2018 (Data collected by Sam Hyde Roberts, at SEED Madagascar's field station).

A. Behavioural observations

This study included behavioural observations of four groups of red-collared brown lemurs, two in Sainte Luce (i.e., S9 forest fragment), and two in Mandena (i.e., M15+M16 forest fragments, making up the Mandena Conservation Zone). To facilitate locating the lemur groups selected for observation, one individual in each group was fitted with a radio collar (the procedure is described in detail in the *General Methods*). The research design initially included two diurnal observations per group, and one nocturnal observation per study site per month. Diurnal data are generally regarded as more useful than nocturnal data in the studies of brown lemurs, as diurnal observations allow for a lot more detailed data collection. However, I was not able to track one of the groups in Mandena (i.e., Group D) from October 2017 onwards, possibly as a result of radio collar issues. For this reason, data were thereafter only collected for the remaining three lemur groups (i.e., groups A, B, and C). I also often had issues with locating Group A (possibly also as a result of radio collar issues). This is why data from this group is slightly less represented (Table 1).

I collected behavioural data during diurnal and nocturnal observations between August 2017 and November 2017. Only diurnal data were collected in March-April 2018, and July-August 2018. Nocturnal data collection was suspended due to local social developments (i.e., tomb robbery and the theft of human remains), which resulted in a police curfew. Gaps in data collection periods were caused by unfavourable weather conditions (i.e., heavy rainfall), and personal health issues. The latter, along with issues with guides, and scheduling conflicts led to a decrease in the monthly follows (Table 1). A total of 511 hours of observations were included in the analyses. Both the diurnal and the nocturnal observations generally lasted 12 hours, except in situations of difficult weather conditions (i.e., heavy rainfall) which prompted observations to be cut short, or in situations in which I encountered staff issues (i.e., when a guide was not able to work through the entire night follow). Behavioural data collection differed between night and day. During the diurnal follows, I used Focal-animal Instantaneous Sampling (Altmann, 1974) at five-minute intervals. Focal adults were rotated daily, to ensure equal sampling of all adult members (males and females) of each group. During nocturnal follows, I followed the Auditory Group Sampling method (Andrews & Birkinshaw, 1998; Donati et al., 2007), which consisted of recording the general activity of the group at five-minute intervals based on their auditory output; additionally, visual cues were used whenever possible. Feeding was recorded if I heard chewing noises, or observed fragments of food items falling to the ground (Andrews & Birkinshaw, 1998; Sato et al., 2014). Diurnal observations included all the observations between sunrise and sunset, as well as during the astronomical twilights (data taken from www.timeanddate.com), or until the time when the sun is at 18° below the horizon (at this latitude, this is around 75 minutes). This was done to ensure that only true night hours are included in nocturnal activity (Donati & Borgognini-Tarli, 2006; Donati et al., 2016).

Table 1. Number of observational hours collected from each lemur group per month.

		Aug 2017	Sep 2017	Oct 2017	Nov 2017	Mar 2018	Apr 2018	Jul 2018	Aug 2018
Sainte Luce	Group A	29	24	24	18	6	4.5	-	-
	Group C	36	30	36	36.5	11.5	12.5	12	12
Mandena	Group B	36	18	36	36	16	24	12	12
	Group D	11	18	-	-	-	-	-	-

B. Diet

Variables of interest included plant species and food item (i.e., fruit, nectar (flowers), young leaves, mature leaves, and invertebrates). Young and mature leaves were distinguished based on their colour, shape, and size. While flowers and nectar are different items, I do not distinguish between them in this study because I was not able to make this distinction during the observation. Each feeding tree location was recorded using a handheld GPS tracker (*Garmin 64s*), while a flag with a unique code was placed around the trunk, to facilitate recognition of repeated uses of the same feeding trees. After the study was completed, all the flags were removed from the forest. The species of feeding plants were identified *in situ* with the help of a local forest guide, using their local vernacular names.

Statistical analysis

For the home range analysis, I collected spatial data every 30 minutes using a handheld GPS tracker (*Garmin 64s*). I conducted home range analysis using Ranges 9 (Anatrack Ltd). I estimated the annual home ranges via minimum convex polygons (MCPs) using all available location points. Additionally, I used 95 % and 50 % fixed kernels (FK) with the smoothing selected by least-squares cross-validation (LSCV) (Seaman et al., 1999). Smoothing parameter (h) was set at 0.8. Incremental analysis (IAA) was performed to determine whether annual ranges (i.e., 100 % MCP, and 95 % FK) show evidence of stability (Campera et al., 2014).

I analysed activity budgets using all available data for the groups A, B, and C. To avoid temporal autocorrelation, the proportions of activity were calculated separately for each observation sessions longer than 3 hours (N=50). As nocturnal data were only collected for two groups (i.e., Group C in Sainte Luce, and Group B in Mandena), only those two groups' data were included in the analyses of day phase patterns. Median is used throughout as central tendency measures, reported with the interquartile range (Q3 – Q1).

Throughout the models, variables for which I had the data for all levels of interest (i.e., wet and dry season, day and night, Sainte Luce and Mandena), and which were tied to my hypotheses and tested in the model were chosen as fixed factors. Lemur groups were chosen as random factors – there are many lemur groups in each fragment, but I only followed a few of them, which can be considered randomly selected among the many that exist. I used a Generalized Linear Mixed Model with Poisson distribution and log link function to calculate the effect of seasons and day phases on activity, using counts of active behaviour (i.e., all but resting) in each observational session as the dependent variable, and season (i.e., wet, dry), day phase (i.e., day, night), and area (i.e., Sainte Luce, Mandena) as fixed factors, while I used lemur groups (i.e., Group A, B, C) as a random factor, and log-transformed total counts in each observation session as the offset variable. To calculate differences in feeding between the two areas, seasons, and day phases I used a Generalized Linear Model with Poisson distribution in which feeding counts were entered as the response variable, season (i.e., wet, dry), day phase (i.e., day, night), and area (i.e., Sainte Luce, Mandena) as fixed factors, lemur groups (i.e., Group A, B, C) as a random factor, and log-transformed total counts in each observation session as the offset variable. To compare the proportions of different food items in lemurs' diet, I used Generalized Linear Model with Poisson distribution, in which food item was the response variable, season (i.e., wet, dry), day phase (i.e., day, night), and area (i.e., Sainte Luce, Mandena) were the fixed factors, and lemur group (i.e., Group A, B, C) the random factor. The log-transformed total count of feeding in each observation session was used as the offset variable. Observation sessions with no recorded feeding were excluded from this analysis.

Dietary diversity, measured as the number of plant species in the diet, was also compared across the two areas, two seasons, and between day and night using Generalized Linear Model with Poisson distribution. Area (i.e., Sainte Luce, Mandena), season (i.e., wet, dry), and day phase (i.e., day, night) were entered as fixed factors, lemur group (i.e., Group A, B, C) as the random factor, and the log-transformed total count of feeding in each observation session as the offset variable. Species for which I was unable to obtain a scientific name were excluded from analysis (three in Sainte Luce, one in Mandena), but their vernacular names and details of their consumption (seasons, day phases) are included in the tables for future reference. The reason for their exclusion was the inability to confirm that they are distinct species, as sometimes different vernacular names are used for the same species. The present study may therefore present a slightly more conservative result. Sorenson's similarity coefficients between different sub-categories (i.e., wet and dry season, day and night) were calculated using the following formula

$$C_S = \frac{2C}{S_1 + S_2}$$

where C are the species in common, S_1 are species in the first subset, and S_2 the species in the second one. All data were analysed in SPSS 26.0 (IBM, 2018).

Results

A. Home ranges

The number of spatial data points for the home range analysis differed between the three groups. For Group A, there were 100 data points (33 collected in the wet season, and 67 in the dry season), at which point the area in the incremental plot was still increasing (likely due to the difficulties of locating this group, which led to fewer observations) (Figure A1, Appendix I). For Group B, there were 207 spatial data points (94 in the wet season, and 113 for the dry season), and 100 % was reached at 140 (Figure A2, Appendix I). For Group C, there were 182 data points (81 in the wet season, and 101 in the dry season), and the 100 % was reached around 135 points (Figure A3, Appendix I). According to MCP analysis, Group B in Mandena has the largest home range(Table 2, Figure 2). According to the 95 % FK, Group C has the smallest home range, while the other two groups have similar home range sizes.

Table 2. Home range comparison between the three groups of red-collared brown lemurs (*Eulemur collaris*) in the two study sites included in this study.

				Annual home range size (ha)			
	No. of months	No. of GPS locations	No. of individuals	95 % MCP	100 % MCP	95 % FK	50 % FK
Sainte Luce							
Group A	8	100	7	13.023	16.344	16.277	3.369
Group C	8	135	9	17.346	19.899	13.533	3.439
Mandena							
Group B	8	207	8	21.458	37.330	17.907	3.925

* For Group A, the asymptote has not been reached.

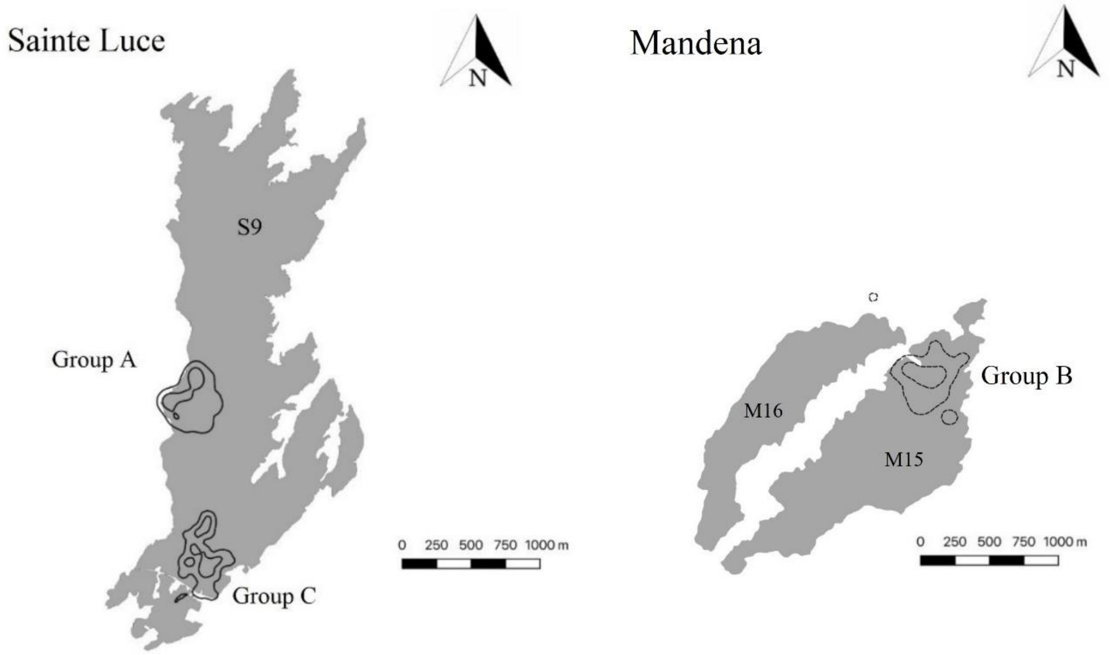


Figure 2. Annual home ranges and core areas of the three red-collared brown lemur (*Eulemur collaris*) groups included in this study, two in Sainte Luce (i.e., S9 fragment, 275 ha) (left-hand side) and one in Mandena (i.e., M15+M16, 230 ha) (right-hand side). Location data were collected between August 2017 and August 2018. Depicted are the 95 % (inner ring) and 50 % (outer ring) FK analysis. For Group A, the asymptote has not been reached.

B. Activity budgets

Lemurs on average spent 31.38 % (IQR=24.59) of activity during observation sessions in active behaviours (N=50). The overall model was significant (χ^2=17.779, df=3, p<0.001). Percentages of time spent in active behaviours did not differ between Sainte Luce (31.72 % (IQR=35.17), N=31) and Mandena (31.03 % (IQR=15.17), N=19) (B=0.039, SE=0.047, p=0.399) (Figure 3a).

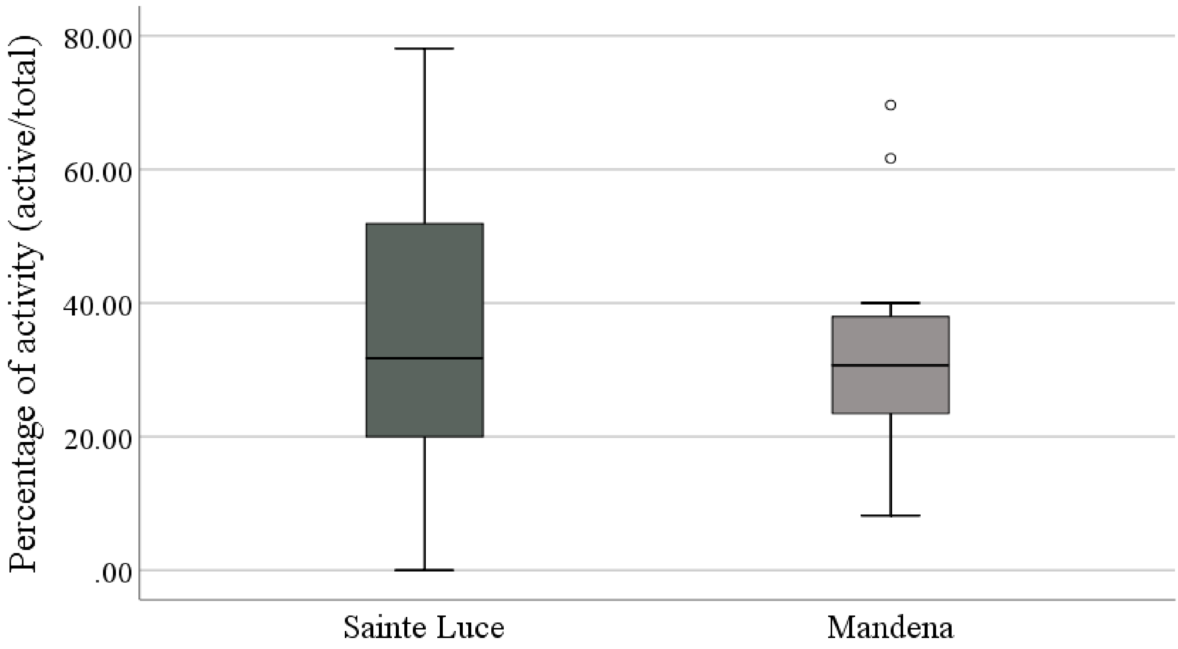


Figure 3a. Percentage of active behaviour of red-collared brown lemur (*Eulemur collaris*) between Sainte Luce (N=31) and Mandena (N=19).

Lemurs spent 35.86 % (IQR=36.71) (N=26) of time in active behaviours during the wet season, and 30.68 % (IQR=12.83) (N=24) in the dry season, but the percentage of active behaviours in their activity budgets did not show seasonal variation (B=0.063, SE=0.046, p=0.173) (Figure 3b). Finally, lemurs spent significantly more time being active during the day (31.72 % (IQR=21.74), N=39) than at night (13.69 % (IQR=38.22), N=11) (B=0.241, SE=0.061, p<0.001) (Figure 3c).

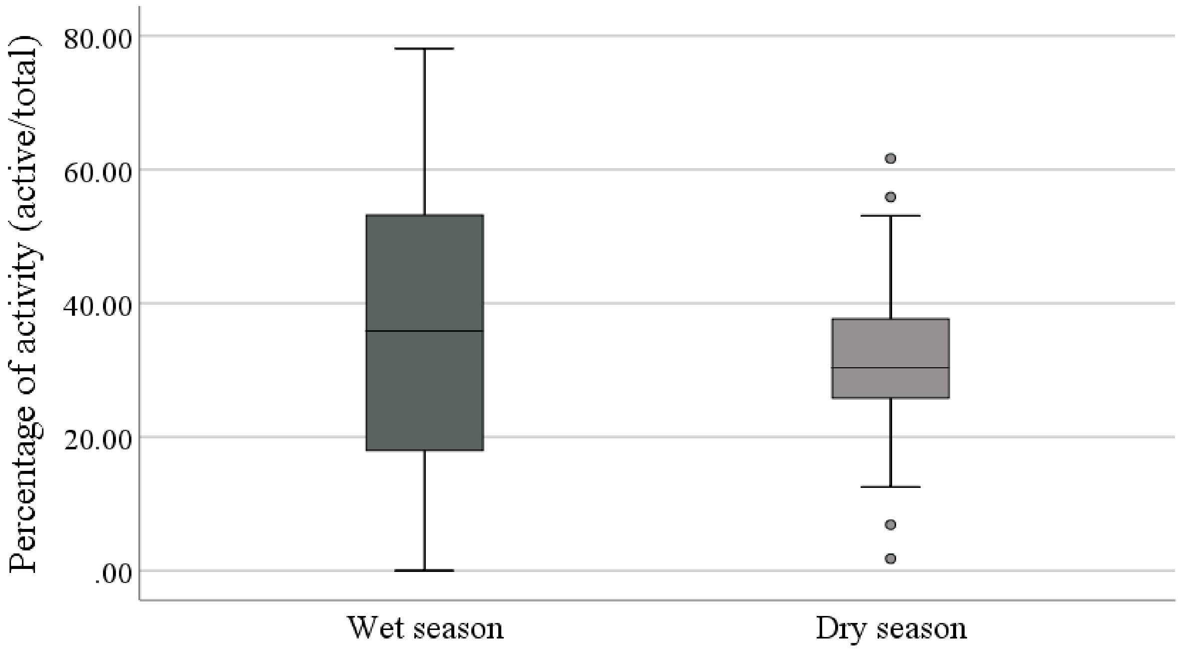


Figure 3b. A comparison of percentage of active behaviour of red-collared brown lemurs (*Eulemur collaris*) across two sites during the wet (N=26) and dry (N=24) seasons.

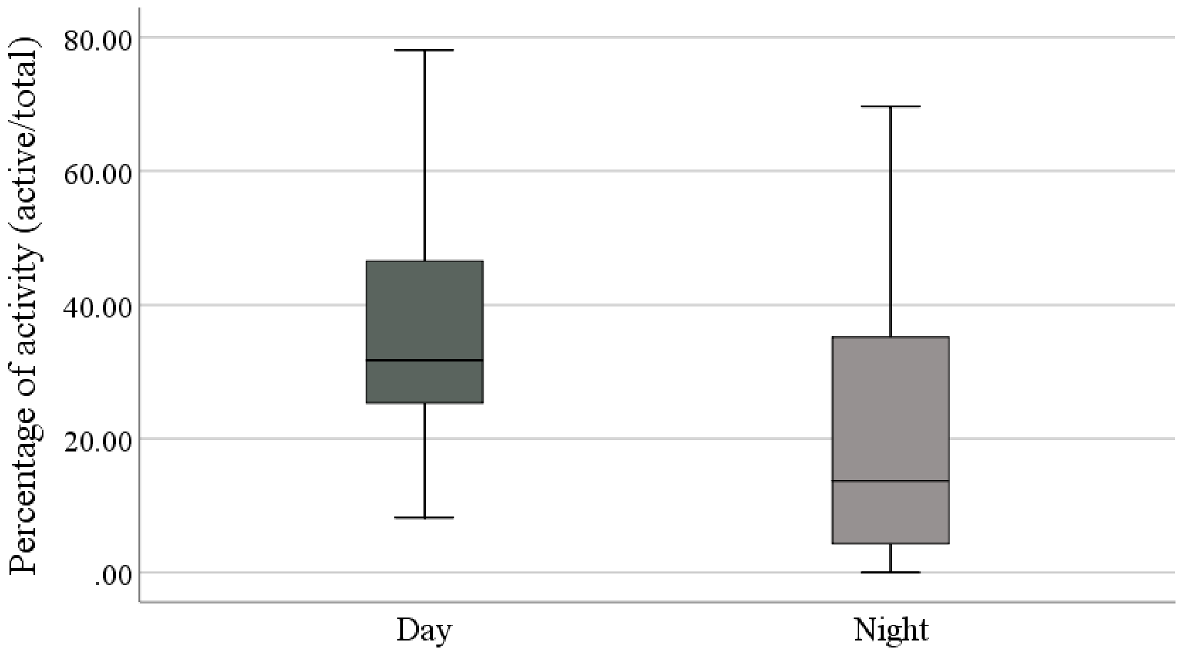


Figure 3c. A comparison of percentage of active behaviour of red-collared brown lemurs (*Eulemur collaris*) across two sites during the day (N=39) and at night (N=11).

C. Diet

Although their diet showed variation between Sainte Luce and Mandena, wet and dry season and across the 24 hours, red-collared brown lemurs were predominantly frugivorous throughout the year. Other prominent food items included nectar, young and mature leaves, and invertebrates (i.e., spiders, grasshoppers). On average, lemurs spent 9.50 % (IQR=11.0) (N=50) feeding, 10.0 % (IQR=13.0) in Sainte Luce (N=31) and 9.0 % (IQR=11.0) in Mandena (N=19). During the day (N=39), lemurs fed 10.0 % (IQR=10.0) of time, and at night (N=11), they fed 10.0 % (IQR=21.0) of time.

The overall model of feeding proportion was not significant, but showed a strong tendency (χ^2=7.134, df=3, p=0.068). There was no significant difference in feeding between the two areas (B=0.101, SE=0.079, p=0.204, $N_{Sainte\ Luce}$=31, $N_{Mandena}$=19), but the lemurs spent more time feeding in the dry season than in the wet season (B=-0.159, SE=0.078, p=0.041, N_{wet}=26, N_{dry}=24). The difference in feeding between day and night was also not significant (B=-0.140, SE=0.093, p=0.130, N_{day}=39, N_{night}=11) (Table 2). The overall model of fruit consumption was not significant (χ^2=3.868, df=3, p=0.276). There was no difference in fruit consumption between Sainte Luce and Mandena, between the two seasons, and between day and the night (Tables 3 and A1, Appendix I). The overall model of nectar consumption was significant (χ^2=121.129, df=3, p<0.001). Sainte Luce lemurs consumed more nectar than Mandena lemurs. Nectar was also more often consumed in the dry season (i.e., the lean period) than in the wet season (i.e., the abundance period), and at night than during the day. The overall model of consumption of young leaves was significant (χ^2=20.799, df=3, p<0.001) (Tables 3 and A1, Appendix). Young leaves were also represented more in the diet of Sainte Luce lemurs than in the diet of Mandena lemurs, but there were no seasonal differences or differences between day and night, although there was a trend towards more young leaves being consumed in the wet than in the dry season, and during the day than at night (Tables 3 and A1, Appendix). The overall model of the consumption of mature leaves was significant (χ^2=9.158, df=3, p=0.027). Mandena lemurs consumed more mature leaves than Sainte Luce lemurs, but there were no seasonal differences or differences between day and night (Tables 3 and A1, Appendix). As invertebrates were consumed in only two observational sessions, and both times by the same lemur group (i.e., Group B) in Mandena during the day (but once in each season), these data were not modelled (Table A1, Appendix I).

Table 3. Comparisons of percentages of fruit, young leaves, and mature leaves in the lemur diet across two sites. Significant results are presented in **bold**.

		B	SE	p	N_1	N_2
Fruit	Sainte Luce vs Mandena	-0.111	.110	0.311	26	18
	Wet vs dry season	0.169	.110	0.124	22	22
	Day vs night	-0.093	.149	0.149	38	6
Nectar	**Sainte Luce vs Mandena**	**1.117**	**0.161**	**0.000**	**26**	**18**
	Wet vs dry season	**-0.806**	**0.142**	**0.000**	**22**	**22**
	Day vs night	**-1.191**	**0.147**	**0.000**	**38**	**6**
Young leaves	**Sainte Luce vs Mandena**	**1.098**	**0.420**	**0.009**	**26**	**18**
	Wet vs dry season	0.632	0.335	0.059	22	22
	Day vs night	1.846	1.015	0.069	38	6
Mature leaves	**Sainte Luce vs Mandena**	**-0.936**	**0.461**	**0.042**	**26**	**18**
	Wet vs dry season	-0.845	0.491	0.085	22	22
	Day vs night	-0.396	0.565	0.483	38	6

Dietary diversity

During the duration of the study, red-collared brown lemurs fed on a total of 38 tree species in Sainte Luce belonging to 24 families (Table A4, Appendix I), 31 in the wet season (belonging to 17 plant families), and 19 in the dry season (belonging to 15 plant families), showing higher diversity during the wet months (Table 4). Of those 36 species, lemurs consumed fruit of 28 species. The overlap between seasons was 11 species (belonging to 10 families), and Sorenson's similarity coefficient between these lemurs' diet in the wet and in the dry season was 0.449.

During the day, Sainte Luce lemurs overall fed on 35 species (29 species in the wet season, and 18 in the dry), and during the night, they were recorded feeding on six (four in the wet season, and two in the dry) (Table 4). During daytime, the lemurs fed on 32 unique species (i.e., species that they only ate during the day and that were not observed in their diet at night), whereas only one species was recorded in their diet solely at night (i.e., *Bembicia uniflora*, or bemalemy (Table A2, Appendix I)). The overlap between diurnal and nocturnal species was five (belonging to four families). Sorenson's similarity coefficient between species found in these lemurs' diurnal and nocturnal diet was 0.244.

Table 4. Numbers of tree species in the diet of the red-collared brown lemurs (*Eulemur collaris*) in Sainte Luce and Mandena.

	Sainte Luce			Mandena		
	Day	Night	Total	Day	Night	Total
Wet season	29	4	31	11	4	13
Dry season	18	2	19	19	3	19
Total	35	6	38	23	5	24

In Mandena, red-collared brown lemurs fed on 24 tree species belonging to 19 families (Table A3, Appendix I), 13 in the wet season (belonging to 10 families), and 19 (belonging to 16 families) in the dry. Of the 24 species, lemurs consumed fruit of 17 species. The overlap between wet and dry seasons was eight species (belonging to eight families). Sorenson's similarity coefficient between the species red-collared brown lemurs fed in the wet and in the dry season was 0.5.

During the day, Mandena lemurs fed on 24 species (11 species in the wet season, and 19 in the dry), and during the night, they were recorded feeding on five (four in the wet season, and three in the dry) (Table 5). During daytime, the lemurs fed on 20 unique species, while one species was recorded in their diet solely at night (i.e., *Grisollea* sp., or zambo) (Table A3, Appendix I). The overlap between day and night was four species, and Sorenson's similarity coefficient between species found in the diurnal and nocturnal diet was 0.286.

The overall model of dietary diversity was significant (χ^2=11.169, df=3, p=0.011). Sainte Luce and Mandena lemurs did not significantly differ in the average number of plant species consumed per observation session (B=-0.099, SE=0.175, p=0.572, $N_{Sainte\ Luce}$=26, $N_{Mandena}$=18). More plants were consumed during the wet than in the dry season (B=0.404, SE=0.169, p=0.017, N_{wet}=22, N_{dry}=22) and during the day than at night (B=0.662, SE=0.279, p=0.018, N_{day}=38, N_{night}=6) (Table 5). During the course of the study, 13 species in Sainte Luce and 16 species in Mandena with over 1 % share in the diet accounted for the total of 89.85 % and 96.22 % of their diet, respectively (Table A4, Appendix I). In the dry season, seven species with over 1 % share in the diet accounted for 94.91 % of Sainte Luce lemurs' diet, while in the wet season, 23 species accounted for 96.39 % of the diet, with the most common one being mampay (*Cynometra cloiselii*) during both seasons. In Mandena, 14 species with a 1 % of higher share in the diet accounted for 96.99 % of diet in the dry season, with the most prominent being fandra (*Pandanus madagascariensis*) (Figure 4). In the wet season, 10 species accounted for 97.05 % of the diet, and the most prominent one was meramaintso (*Sarcolaena multiflora*) (Table A4, Appendix I).

Table 5. Average numbers of species consumed per observation session in Sainte Luce (N=26) and Mandena (N=18), wet (N=22) and dry (N=22) seasons, and day (N=38) and night (N=6).

	Sainte Luce	Mandena	Wet season	Dry season	Day	Night	Total
M	2.65	2.74	3.10	2.29	2.98	1.36	2.68
SD	2.176	1.982	2.242	1.883	2.097	1.502	2.087

Figure 4. Dietary diversity of red-collared brown lemur (*Eulemur collaris*): a female feeding on *Pandanus madagascariensis* fruit (A), and a male feeding on *Intsia bijuga* nectar (B). Photographs taken by E. Račevska in Mandena, September 2017 (A), and Sainte Luce, September 2018 (B).

Discussion

The findings of this study indicate that home range sizes of Mandena lemurs are smaller and less fragmented than previously reported. The lemurs inhabiting the two areas did not differ in their activity percentages: although I found no seasonal variation, both Sainte Luce and Mandena lemurs were more active during the day than at night. Sainte Luce and Mandena lemurs were largely frugivorous year-round, but they ate more fruit during the wet than in the dry season, and spent more time feeding during the dry than in the wet season. Their diet was also more diverse in the period of wet than in the dry season, and during the day than at night.

<u>Behavioural observations</u>

In this chapter, I used two types of home range analysis – the fixed kernel (FK) and the minimum convex polygon (MCP). They can often give very different results (Boyle et al., 2009; Pebsworth et al., 2012), as was the case in this study. Specifically, in the case of Group B, the MCP method has predicted a much larger home range size than did the FK method. This is likely due to the fact that the MCP method assumes that the entire area within a home range is used equally (Gregory, 2016). As the GPS points for Group B outnumber those for the other two groups and its territory includes a large swamp, it is quite possible that these could be the reasons why the estimate of this group's home range size is much larger when calculated using the MCP method than the FK method. The FK method, which removes the limitations associated with sample sizes, resulted in much more comparable home range sizes, and I will focus my discussion on them.

Home ranges of red-collared brown lemurs were larger in Mandena than in Sainte Luce, similar to the results of previous studies (Campera et al., 2014), although this difference was now very small. If home range sizes are compared based on their 95 % FK, previously reported home range sizes for lemur groups in Mandena were 83.25 ha and 37.52 ha (Campera et al., 2014), while in the current study, Mandena group's home range was 16.27 ha. When Sainte Luce groups are concerned, lemur groups' home ranges were previously 17.10 ha and 14.70 ha (Campera et al., 2014), while in the current study, their sizes were 13.53 ha and 17.91 ha; however, it is important to remember that Group A's home range is likely underestimated, and more data points are needed for its accurate estimate. It is evident that the home ranges' size difference is larger in Mandena than in Sainte Luce. In the past, the reason for the discrepancy between the two littoral forests could have been attributed to the distinction between them. Before the forest protection measures were implemented, Mandena had experienced stronger anthropogenic pressures, leading to it being more heavily disturbed. Forest degradation is accompanied by a decreased availability of food sources, which had likely prompted the lemurs to extend their search for food (i.e., feeding trees) into other areas, thus increasing their home ranges. A similar finding was documented in this species before (Donati et al., 2011; Campera et al., 2014), as well as in other *Eulemur* species (Schwitzer et al., 2007; 2011), and lemurs of different dietary types (Martinez, 2008; Irwin, 2008). However, according to the recent NDVI data (Donati et al., 2020b), the regeneration of the Mandena Conservation Zone has seen a significant increase over the past two decades. This suggests that the previous degradation has at least in part been compensated by the new growth. The finding that Group A's incremental plot area was still increasing suggests that more data points are needed to correctly estimate the size of this group's home range.

Lemurs of the *Eulemur* genus are flexible in their ranging patterns, which are affected by the characteristics of their habitats, such as food and water availability (Scholz & Kappeler, 2004). Home ranges of *E. collaris* and *E. rufus* (red brown lemur) are typically much larger, ranging from 57 ha (Vasey, 1997) to over 100 ha (Overdorff et al., 1999). This is likely a result of lower fruit abundance and its unpredictable availability (Bollen & Donati, 2005; Wright et al., 2005). On the other hand, home range sizes of *E. rufifrons* (red-fronted brown lemur) tend to be smaller, varying from 2.8 to 18.2 ha (Colquhoun, 1993; Curtis & Zaramody, 1998; Bayart & Simmen, 2005; Volampeno et al. 2011). Red-fronted lemurs were found to increase their home ranges during the times of seasonal water scarcity (Scholz & Kappeler, 2004), as a result of multiple commutes to the water hole, or even a temporary move closer to the water source in periods of more severe water scarcity. This type of habitat shifting was also observed in other *Eulemur* species (Overdorff, 1993; Sato et al., 2013; Campera et al., 2014).

While it was not possible to confirm whether my Sainte Luce lemur groups were the same ones discussed in previous studies, Group B in Mandena is likely the group *MAN-C,* followed by researchers for several years (Campera et al., 2014; Balestri et al., 2014; Donati et al., 2016; 2020). The other Mandena group (i.e., Group D), initially observed in the more intact part of Mandena Conservation Zone, is most likely the group *MAN-AB* from the previously referenced studies. However, this group had dispersed away from the study area before sufficient data were collected for a meaningful comparison to be made. The current data show that the annual home range of Group B was much smaller than was previously estimated (Campera et al., 2014). Furthermore, contrary to the previous findings, this group's home range no longer extended to other forest fragments, or non-forested areas outside the M15 fragment. As group sizes were similar to those in the previous study, it is unlikely that this decrease of home range would have resulted from a decrease in individual numbers (as smaller groups usually occupy smaller home ranges; Barton et al., 1992). This finding may suggest that the resource availability in the Mandena Conservation Zone may have increased over the past years. This is supported by the increase in the NDVI over the past decades (Donati et al., 2020b), indicating the improvement in habitat quality. The annual range of Group B was still somewhat fragmented, but to a much lesser degree than was described in Campera et al. (2014), and with fewer core areas, none of which were outside the Mandena Conservation Zone (specifically, the M15 forest fragment). As widely spaced, scarce food resources typically lead to an increase in the number and size of core areas in other herbivorous animals (Lurz et al., 2000; Richard et al., 2011; Pasch & Koprowski, 2011), the opposite finding further supports the conclusion that habitat characteristics of Mandena Conservation Zone may have changed in a way that increased food availability.

Seasonality of resource abundance and distribution, as well as climatic variables (i.e., temperature, rainfall) often contribute to changes in primate activity patterns (Overdorff et al., 1997). Prolonged resting is a common primate strategy for coping with low resource abundance (Clutton-Brock, 1977; Oates, 1987; Yamagiwa & Mwanza, 1994; Guo et al., 2007; Campera et al., 2014), while in some cases, it is associated with lower energy expenditure (Korstjens et al., 2006; 2010; Asensio et al., 2009; Dunbar et al., 2009; Masi et al., 2009; Sato, 2012b), or thermoregulation (Stelzner, 1988; Morland, 1993; Hill et al., 2004; Hill, 2006; Hanya et al., 2007; Campos & Fedigan, 2009; Kosheleff & Anderson, 2009; Donati et al., 2011b). It is possible that my data collection took place during an unusually abundant lean season, making it more similar to the abundance season, and thus eliminating the seasonal differences in the activity budgets.

In the present study, red-collared brown lemurs were more active during the day than at night. This is in line with my prediction, as well as the results of previous studies of *Eulemur* sp., such as the red brown lemur (Kappeler & Erkert, 2003), or the red-fronted brown lemur (Overdorff, 1996), while the opposite was the case in the red-bellied lemur (*E. rubriventer*) (Overdorff, 1996). As higher activity often relates to longer time spent feeding, it may seem surprising that in this study feeding duration showed no difference between day and night. This is in contrast with previous research conducted on this lemur (Donati et al., 2007), which revealed that it fed for longer during the day in the hot wet season. Red-collared brown lemurs were also found to prolong their feeding periods into the night as a result of lower food quality (Donati et al., 2011), while the increase in diurnal feeding was revealed to coincide with the peak of ripe fruit availability (Donati et al., 2007). Extending feeding into the night is more common in periods of lower fruit abundance (Engqvist & Richard, 1991; Mutchler, 1999; Tarnaud, 2006) (and similarly, in this study, lemurs also fed longer during the lean period, when fruit was less represented in their diet than in the period of abundance (see below). The reason for this might be that lemurs got enough nutrients during their nocturnal feeding. The percentage of fruit in their nocturnal diet was similar to its diurnal percentage, and the percentage of nectar higher, while the food sources typically associated with lower quality (i.e., leaves) were less represented in their nocturnal diet.

Activity pattern, and particularly percentages of feeding and feeding times show seasonal variation and variation across the 24-hour cycle in several *Eulemur* sp. For example, black lemurs (*E. macaco*) were found to feed more in the night-time during the wet season (Andrews & Birkinshaw, 1998). Red-bellied lemur (*E. rubriventer*) and the red-fronted brown lemur (*E. rufifrons*) occurring sympatrically changed their feeding times in the periods of food scarcity, as they rely on the same keystone species (Overdorff, 1996). The same strategy was also observed in crowned lemur (*E. coronatus*) and Sanford's lemur (*E. sanfordi*) (Freed, 1995). Red-collared brown lemurs are sympatric with several species of nocturnal lemurs (*Microcebus tanosi*, *Avahi meridionalis, Cheirogaleus thomasi* in Sainte Luce, and *Microcebus ganzhorni, Avahi meridionalis*, and *Cheirogaleus major* in Mandena), and one species of cathemeral lemur (*Hapalemur meridionalis* in Mandena). However, due to their differences in both activity patterns and diet, it is unlikely that brown lemurs would switch their feeding times as a result of resource competition.

<u>Diet</u>

To understand how a species is utilising the available food sources, the percentage of feeding in the activity budget can be a useful proxy, as well as serve as an indication of habitat quality – the higher the quality of a feeding patch, the longer an animal is likely to feed in it (Whiten, 1988; Nakagawa, 1990; Nakagawa, 2009). In this study, lemurs did not consume more fruit in the wet season than in the dry season, which contradicts my prediction. However, lemurs spent less time feeding during the wet than the dry season. Although the lemurs remained frugivorous in the lean period (i.e., dry season), they consumed significantly more nectar during this time. This coincided with longer feeding times, similar to previous studies of this and other primate species (Donati et al., 2007; 2011; Fan et al., 2008).

While seasonal differences in diet are easily understandable from the relationship between seasonality and resource abundance, the differences between day and night, found only in the case of nectar consumption, could be explained by the fact that in certain species, nectar is only secreted at night (e.g., Andrews & Birkinshaw, 1998). This is, for example, the case for *Brexia madagascariensis* (Birkinshaw, 2002), one of the species whose nectar lemurs fed on extensively. Previous studies of *Eulemur* sp. showed that common brown lemurs (*E. fulvus*) fed on the nectar of this species in the early morning. Combined with the food processing type (i.e., not damaging to the flower structure), this prompted the hypothesis about this lemur's role in pollination of this plant species (Birkinshaw, 2002). Previous research showed that consuming food items with higher fibre content (associated with lower-quality sources, such as leaves) is related to a more balanced distribution of activity across the 24 hours in red-collared brown lemur (Donati, 2009) and the common brown lemur (Tarnaud, 2006). Contrarily, the mongoose lemur does not show a similar variation in cathemeral activity in response to changes in nutritional intake (Curtis et al., 1999). Higher proportions of leaves in the diet are also correlated to longer resting periods (Korstjens et al., 2006; 2010; Dunbar et al., 2009), due to leaves' longer processing times. As there was no significant difference in consumption of leaves in relation to season or day phase in this study, this correlation may be the reason for lemurs being more active during the day than at night.

There could be other reasons for this difference that were not assessed in this study, such as characteristics of feeding trees. Trees of larger crown sizes are typically more abundant in food sources, which is likely to result in longer feeding times (Andrews & Birkinshaw, 1998). Assessing tree characteristics (e.g., crown size, DBH, tree height and lemur height while feeding), and comparing them across the 24-hour cycle could provide an explanation of whether the differences in diet are related to the nutritional content or something else. Some of the possibilities are predator avoidance (Overdorff, 1988; Goodman, 1994; Curtis et al., 1999; Curtis & Rasmussen, 2002; Rasmussen, 2005; Donati et al., 2007) or thermoregulation (Clutton-Brock, 1973; Donati et al., 2011b).

The red-collared brown lemur is a primarily frugivorous species (Donati et al., 2007; Sato et al., 2016), which was also confirmed in this study. Previous literature showed that fruit in this lemur's diet accounts for 74.0 ± 12.81 % food in Sainte Luce (Donati et al., 2007), and 75 % (quartiles 64-71 %) in Mandena (Donati et al., 2020b), which is higher than in the present study. On the other hand, the percentage of nectar in the diet is much higher in this study than in the previously published ones. One of the reasons that this pattern appeared during the dry season was the flowering of *Brexia madagascariensis* in Mandena, which accounted for long feeding sessions, similar to those reported by Campera et al. (2014). Similarly, a high percentage of nectar in the diet was prompted by the availability of *Cynometra cloiselii* in Sainte Luce. It is clear that the fruiting patterns are not the only determinants of red-collared brown lemur's diet composition, and that other phenological aspects may have powerful roles as well. Moreover, due to weather conditions, lemurs were not followed during January and February, at which time fruit availability in the littoral forest peaks (Donati et al., 2007), so it is possible that some fruiting events that took place are not represented in the data. Sainte Luce and Mandena lemurs differed in their diet, but measuring aspects of habitat quality, such as forest productivity and resource abundance, extends beyond the focus of this study, so it is not clear whether these differences are related to seasonality of resource availability.

In accordance with my prediction, dietary diversity was larger during the wet season, when red-collared brown lemurs fed on more species than during the dry season. Red-collared brown lemurs fed on a total of 38 species in Sainte Luce, and 24 in Mandena, which is fewer than was found in previous studies (Donati et al., 2007; 2020). In Sainte Luce, only four of the species previously found to be important food sources were among those accounting for >1 % of the diet in the present study (Donati et al., 2007).This number was even lower in Mandena, and the same was true of only two species (Donati et al., 2020b). While this is very little, this finding is not completely unusual, as it is expected for the most represented species to fluctuate in the level of their usage between years (Donati et al., 2020b). This is due to the irregular seasonality (Wright, 1999; Dewar & Richard, 2007), which results in unpredictable food availability. The seasonal overlap was moderate, indicating that about half of the species are present in these lemurs' diet across both seasons. However, in many cases, different parts of the plants are consumed during the different seasons, or their relative percentages differ (a certain degree of similarity between seasons is expected, of course, as plant phenology does not completely correlate to the calendar months).

More species and more unique tree species were recorded in the lemurs' diet during the day than at night, both of which findings are in line with those from previous studies of this species (Donati et al., 2007) and of other cathemeral lemur species (Andrews & Birkinshaw, 1998). Numbers of diurnal and nocturnal plant species in the diet were lower than in the previous studies (Donati et al., 2007), as was the dietary similarity between day and night. While the majority of species were present in the diurnal portion of the feeding bouts, the number of unique species that were included only in the nocturnal feeding was minimal. Lower diversity of nocturnal diet can be related to the differences in the way that lemurs use their habitat during the day and night, which can be motivated by their predator avoidance strategy (Donati et al., 2007). Previous studies found that *Eulemur* sp., which are mainly predated by diurnal birds of prey (e.g., *Polyboroides radiatus*, *Accipiter henstii*, *Buteo brachipterus*) preferentially feed on emergent trees and in higher canopy at night, and in lower canopy during the day (Overdorff, 1988; Andrews & Birkinshaw, 1998; Curtis et al., 1999; Donati et al., 1999; 2007; Curtis & Rasmussen, 2002; Rasmussen, 2005). However, tree height and lemur feeding height were not included in the model in the present study, so this question should be revisited in the future to understand whether changes in feeding are related to resource abundance, predation, or something else. Finally, it is also possible that the lower number of species recorded in this study is a result of a shorter data collection period as compared with other studies, whereby important peaks of fruit and other food item availability may have gone undocumented.

Conclusion

Despite the once large differences between Sainte Luce and Mandena, which had previously manifested in ecological differences of red-collared brown lemur populations inhabiting them, this study showed that several aspects of this lemur's ecology (i.e., ranging behaviour, activity, feeding, dietary diversity) in Sainte Luce and Mandena have become less different since the forest fragments that they inhabit became protected. The lemurs were more active during the day than at night, but there was no seasonal variation in their activity. They remained largely frugivorous throughout the year, but consumed more fruit in the wet than in the dry season. Dietary diversity was lower than in previous studies, which could be an artefact of the study period. As the forests continue to regenerate without the anthropogenic pressures that they historically endured, habitat use of the red-collared brown lemurs inhabiting them may continue to change. These research questions should therefore be revisited to truly understand the impacts of forest protection measures on this lemur's ecology. The findings of this study are also applicable to other primate species inhabiting fragmented forests or protected areas established in areas that had in the past experienced significant anthropogenic pressures. As the forests regenerate, the resource availability increases, which then might reflect in the primates' activity, ranging behaviour and diet. To better understand this relationship, other variables, such as predation (including hunting pressures), should be examined.

CHAPTER 4

Spatial and temporal patterns of seed dispersal by red-collared brown lemurs (*Eulemur collaris*) in the littoral forests of Sainte Luce and Mandena, southeastern Madagascar

Introduction

Frugivorous vertebrates are the most prevalent vertebrate group in the tropics (Gautier-Hion et al., 1985). Zoochory (Vittoz et al., 2007) is the most common seed dispersal type in the tropical forests (McKey, 1975; Charles-Dominique et al., 1981; Howe & Smallwood, 1982; Janson, 1983; Gautier-Hion et al., 1985; Jordano, 1992). It is responsible for the dispersal of 95 % of the species (Terborgh et al., 2002). According to the Janzen-Connell hypothesis, seed dispersal away from the parent tree is crucial to the success of seedling establishment (Janzen, 1970; Connell, 1971; Howe & Smallwood, 1982). Seed shadow, or the frequency distribution of dispersal distances, can vary in response dispersers' characteristics. These include their home range size, movement pattern, and gut passage time (Fuzessy et al., 2017). Seed handling type also has implications for seed dispersal distances: while spat out seeds will typically only move a few metres away from the parent tree, those that were defecated can be moved hundreds of meters (e.g., Garber, 1986; Zhang & Wang, 1995; Stevenson, 2000; Wehncke et al., 2003). Dispersal distances can also be affected by the location in which the seeds are dropped. This brings importance to seed dispersers' use of habitat.

Non-random habitat use, such as animals preferentially selecting specific feeding and resting locations can affect dispersal distances and seed survival (Julliot, 1997; Chapman & Russo, 2007; González-Zamora et al., 2015). Repeated use of trees as sleep sites can result in seed aggregation in specific locations, therefore affecting the seedling establishment. Some animal species were found to use latrines, which is defined as a repeated use of specific sites for defecation or urination, that are recognised from excretory waste accumulated on arboreal, terrestrial, or subterranean substrates (Irwin et al., 2004). They are fairly common in mammals such as ungulates, carnivores, and primates (Dröscher & Kappeler, 2014), but there are several hypotheses about their function. European badgers (*Meles meles*) use latrines as territory defence, and immature juveniles rarely use them (Brown et al., 2009). Contrarily, in species like white-footed sportive lemur (*Lepilemur leucopus*), latrines occur within core areas of their home ranges, and are used by all group members, suggesting they might play a role in social bonding (Dröscher & Kappeler, 2014). Latrines have also been hypothesised to help with social bonding of ungulates (Apio et al., 2006). They might also facilitate intra-group recognition of solitary foragers (Dröscher & Kappeler, 2014). Latrine frequency of meerkats (*Suricata suricatta*) was found to increase in the presence of prospecting males (Jordan et al., 2007), likely due to the perceived intruder pressures. Latrine behaviour may also have implications for seed dispersal, as it results in clumped distribution of seeds. In Geoffroy's spider monkey (*Ateles geoffroyi*), sleep tree fidelity was found to be positively related to seed abundance and seed species diversity, but most likely as a result of sleeping sites being located in the areas with higher density of this primate's feeding trees (González-Zamora et al., 2015). Depending on the seed species composition, this could either contribute to higher floristic heterogeneity in these areas (Julliot, 1997) or leave the seeds vulnerable to a range of abiotic and biotic factors in species with density-dependent seedling mortality. Howler monkeys (*Alouatta* spp.) commonly defecate almost simultaneously after resting, near their resting areas (Julliot, 1996b; Gilbert, 1997). This often results in large aggregations of seeds (de Figueiredo, 1993). Latrine trees and resting trees do not always overlap, for example in sportive lemurs (*Lepilemur leucopus*) (Dröscher & Kappeler, 2014), but this might be related to sleeping site selection and ownership (Rasoloharijaona et al., 2003). Understanding why certain sites are chosen for distinct purposes might benefit from examining their microhabitat characteristics.

Microhabitats in which seeds are deposited may have huge implications for their survival (Wenny, 2000; Gross-Camp & Kaplin 2005; Russo 2005). In situations where animals feed, rest and defecate from the same tree, seeds are likely to be dispersed below or very close to their parent tree, which likely reduces seedlings' germination success (Overdorff & Strait, 1998; Gross-Camp, 2009). Seed dispersal pattern is also influenced by activity budgets. In many animal species, temporal distribution of behaviour is both non-random and non-uniform (Milner & Harris, 1999; Ding & Zhao 2004; Henkel et al., 2004; Porter, 2004; Westcott et al., 2005). Many frugivores have a distinct pattern of feeding, travelling and other behaviours (Heithaus & Fleming, 1978; Smythe, 1978; Charles-Dominique, 1991; Westcott & Smith 1994; Katugaha et al., 1999; Poulsen et al., 2001). Behavioural patterns affect the location where the seeds are dropped. Seeds can be deposited at much longer (or shorter) distances due to the distribution of periods of movement and inactivity throughout the day (Westcott et al., 2005). Activity patterns could have repercussions in seed distributions being clumped or scattered, which will affect the survival of seeds, as well as recruitment of seedlings (Schupp et al., 2002; Muller-Landau & Hardesty, 2005). If gut retention is short, even shorter periods of resting may affect dispersal distances (González-Zamora et al., 2015). Behavioural patterns are affected by seasonality (e.g., Stevenson, 2000; Culot et al., 2010) due to the change in resource availability (Overdorff et al., 1997) or climate (Sato, 2012b). As a result, the spatial and temporal distribution of seed dispersal are also affected (Janzen, 1970; Howe, 1989; Schupp et al., 2002; Westcott et al., 2005; Russo et al., 2006).

Dispersal distances are also affected by the time of day at which the fruit was consumed (Westcott et al., 2005; Russo et al., 2006). Some studies showed that fruit is most often consumed in the morning (Garber, 1986; Porter, 2004). This is important because the time at which fruit is consumed will affect both when and where the seeds are dropped. These patterns will also depend on the gut passage times of a particular disperser species (Link & Di Fiore, 2006). In frugivores, gut passage time tends to be fast because of their typically short and simple digestive tracts (Campbell et al., 2004; Sato, 2012).

Some of the most important vertebrate seed dispersers are non-human primates (hereafter "primates") (Chapman, 1995; Wallace & Painter, 2002; Culot et al., 2010; Lambert, 2011; Valenta et al., 2018). Their seed dispersal efforts have been well-documented across the tropics and subtropics (e.g., Wrangham et al., 1994; Chapman & Chapman, 1996; Lucas & Corlett, 1998; McConkey, 2000; Stevenson, 2000). For the most part, primates disperse seeds through endozoochory, although spitting seeds is common among Ceropithecinae (Kaplin & Moermond, 1998; Lambert, 1999). One of the main benefits of primate seed dispersal are the large dispersal distances associated with many of these taxa's large body sizes (Noma & Yumoto, 1997; Kitamura et al., 2002). However, there is a growing body of evidence of how primate activity budgets, especially regarding their seasonal variation, relate to the effectiveness of their seed dispersal. For example, brown woolly monkeys (*Lagothrix lagotricha*) spend less time resting and more time travelling and feeding during periods of fruit abundance (Stevenson, 2000). As a result, their dispersal distances increase. Common brown lemurs (*Eulemur fulvus*) prolong their daily resting during the dry season (Sato, 2012; 2018), which also results in shorter daily path lengths (Sato, 2018). The same study revealed that during the dry season, nocturnal dispersal distances were short. Dispersal distances were longer during the wet season, as a result of the lemurs' increased travelling, to maximize fruit intake during the period of abundance (Sato, 2018).

Seasonality also affects the frugivorous vertebrates, which are key seed dispersers in the littoral forests of southeast Madagascar (Howe & Smallwood, 1982; Bollen et al., 2004). Many forest fragments in Sainte Luce and Mandena are also heavily fragmented (Rabenantoandro et al., 2007). This is known to present challenges for both the frugivores and their seed dispersal (Cordeiro & Howe, 2003; Kirika et al., 2008; Cordeiro et al., 2009; Lehouck et al., 2009; Uriarte et al., 2011), and large-seeded plants are especially vulnerable (McEuen & Curran, 2004; Cramer et al., 2007). Mandena was historically much more degraded and incurred a higher degree of anthropogenic disturbance than Sainte Luce, which was considered the most intact littoral forest in Madagascar (Rabevohitra et al., 1996; Dumetz, 1999; Bollen & Donati, 2006). Since the early 2000s, protected areas were established in both Sainte Luce (in 2002) and Mandena (in 2005). The protected fragments are home to several frugivorous lemurs, the largest of which is the red-collared brown lemur (*Eulemur collaris*). Due to its body size, this predominantly frugivorous lemur (Donati et al., 2007) is likely to disperse seeds far away from the parent trees of the fruits it eats. There are no published studies on this species' dispersal distances, but *Eulemur* sp. in southeastern rainforests were found to disperse around 40 % of all consumed seeds further than 100 m away from the parent tree (Razafindratsima et al., 2014); however, dispersal distances over 500 m were very rare (Razafindratsima et al., 2014). *Eulemur* sp. gut passage times vary between 1.5 and 3.2 hours (Overdorff & Rasmussen, 1995) to over 7h, depending on the fibre in their diet (Campbell et al., 2004). This species is primarily predated by diurnal raptors (Donati et al., 2009), which might be reflected in them preferentially choosing areas of closed canopy and high forest density for resting, to minimise predation risk. Due to its size, the red-collared brown lemur is likely the exclusive disperser of many large-seeded plant species (Bollen et al., 2004), the seeds of which are too large to *survive* swallowing and digestion intact if consumed by other, smaller species. Other frugivores include the Malagasy green pigeon (*Treron australis*), Madagascan blue pigeon (*Alectroenas madagascariensis*), Malagasy bulbul (*Hypsipetes madagascariensis*), and Madagascan flying fox (*Pteropus rufus*). Fruit is also eaten by the omnivorous black rat (*Rattus rattus*), Thomas's dwarf lemur (*Cheirogaleus thomasi*), greater dwarf lemur (*C. major*, now likely only present in Mandena), and frugivorous/omnivorous Anosy mouse lemur (*Microcebus tanosi*, only present in Sainte Luce) and Ganzhorn's mouse lemur (*M. ganzhorni*, only present in Mandena) (Bollen et al., 2004; Lahann, 2007; Ganzhorn et al., 2000; Donati et al., 2020c). There is no evidence to confirm the co-evolution between red-collared brown lemur and the fruiting plant species of which it is the only disperser in the littoral forests (Bollen et al., 2004). Since this lemur shows seasonal variation in activity (Donati et al., 2011; 2011b), as well as across the 24-hours (Donati et al., 2007; 2009) due to its cathemerality (Tattersall, 1987), its seed dispersal pattern is also expected to differ between seasons, and between day and night.

In this study, I explore the microhabitat characteristics of the red-collared brown lemur's defecation locations, as well as the spatial or temporal patterns of this species' defecation. Because of the historical difference in the anthropogenic pressures exerted on Mandena and Sainte Luce, I am also interested in a comparison between the lemur groups inhabiting the two areas. Within this context, I address the following research questions:

1. How do the canopy closure and forest density in defecation locations compare to those of randomly chosen locations within the same habitat?
2. Is there a pattern in the spatial and temporal distribution of the red-collared brown lemur's defecation locations, particularly in relation to resting and feeding? Is there seasonal variation, or variation across the 24-hour cycle in spatial or temporal patterns of defecation?

I offer the following hypotheses and predictions:

H1: Defecation locations of red-collared brown lemurs differ from random locations in their microhabitat characteristics because defecation locations occur close to these lemurs' resting locations. Because red-collared brown lemurs are primarily predated by diurnal raptors (Goodman et al., 1993;

Donati et al., 2007; 2007b), they rest and defecate in areas with more closed canopy and higher forest density during the day than at night.

Prediction: Canopy will be more closed and the forest denser in defecation locations. Defecation locations with closed canopy and high forest density will be more common during the day than at night. Canopy will be more closed, and forest denser in the home range of lemur group located in a more intact area of the forest (i.e., Group A) than in the home ranges of the other two groups.

H2.A Red-collared brown lemurs defecate following resting (Overdorff & Strait, 1998). Defecation patterns follow the variation in resting patterns across seasons.

Prediction: Red-collared brown lemurs will defecate sooner after resting than after feeding. Although the species typically rests more in the dry season, no such seasonal difference was observed in this study (Chapter 3). There will be no seasonal differences in how soon after resting lemurs defecate. There will be no differences between the three lemur groups in this respect.

H2.B Seasonal variation in red-collared brown lemurs' diet affects their defecation patterns. When the lemurs consume more fibre-rich foods (i.e., in the dry season and at night – Donati et al., 2007), they defecate sooner after feeding and closer to feeding trees than when their diet contains less fibre.

Prediction: Previous studies showed red-collared brown lemurs consume more fibre-rich foods in the dry season and at night, but this was not confirmed in this study (Chapter 3). The lemurs' defecation patterns will show no pattern in relation to feeding times and locations. The three lemur groups will not differ in this respect.

H2.C Aerial predation (Goodman et al., 1993; Donati et al., 2007; 2007b) affects red-collared brown lemurs' resting site selection, and in turn their defecation patterns.

Prediction: Because red-collared brown lemurs are mostly predated by diurnal raptors, they will defecate closer to their most recent resting tree and sooner after resting during the day than at night. As predation risk is higher in the dry season, due to less leaf cover, lemurs will defecate sooner after resting and closer to the resting trees in the dry season. There will be no differences between the three lemur groups in this respect.

Methods

Characterisation of red-collared brown lemurs' defecation locations

I marked and characterised the defecation locations of four red-collared lemur groups, which I followed between August 2017 and August 2018 (Chapter 3). I collected microhabitat characteristics data on a total of 143 defecation locations: 81 in Sainte Luce and 62 in Mandena. All defecation locations' coordinates were recorded with a handheld GPS tracker (*Garmin 64s*), and marked using a bright orange flag (Figure 1) to facilitate their finding at the end of each month, when all the locations were revisited for collection of microhabitat characteristics data – i.e., canopy closure, and forest density. After data collection was finished, I removed all flags from the forest. Canopy closure was measured using a convex spherical densitometer, with a cross-shaped grid of 24 quarter-inch squares delineating the plot overhead, and a built-in levelling bubble (*Forestry Suppliers Spherical Crown Densiometer, Convex Model A*). I followed the procedure detailed on the instrument. The measurements were taken in the experimental location by holding the densitometer about 15 inches in front of my body at an elbow height. Four equispaced dots were assumed in each square of the grid (i.e., one in each square), and those equivalent to quarter-square canopy openings were systematically counted. As the formula provided on the densitometer requires, the total was multiplied by 1.04 to obtain the percent of overhead area not occupied by canopy (i.e., canopy closure; Lemmon, 1956; Korhonen et al., 2006). Assuming that each dot represents one percent of the over-story, the difference between this number and 100 was used as an estimation of the density (in %). Four readings were made per location - facing North, East, South, and West, and the average recorded (Strickler, 1959). Forest density was measured using a point-centre quartile method (PCQ; Brower et al., 1998). Defecation point was taken as the centre of the plot, and from there, distances to the nearest adult tree, defined as trees with a DBH ≥ 5 cm, were measured (Atzeni, unpublished manuscript; Campera et al., 2014). This DBH was chosen because of the slow growth of trees in the littoral forests, determined by the thin layer of topsoil over sand, so in this ecosystem, trees with DBH ≥ 5 cm are considered adults (Rabenantoandro, unpublished manuscript). Forest density per hectare was calculated using the following formula:

$$Density\ (all\ species) = \frac{1}{Mean\ point - to - plant\ distance^2}$$

To enable a comparison between microhabitat characteristics of the defecation locations and the random locations, I took the same measures in 30 random locations within each lemur group's home range, in both study sites. In this approach, I used grids, which I set up in a random location within each lemur group's habitat. Random locations were selected across two habitat types - forest, and swamp edge, and set at ~ 15 m apart (Atzeni, unpublished data), in a 3 x 5 grid shape. Adult trees were not shared between locations, so none of them were measured twice. As I was also interested in seasonal comparisons, I divided the months into wet and dry, following the previous literature (Donati et al., 2007).

Spatial and temporal patterns of defecation behaviour

Between August 2017 and August 2018, I documented defecation locations across the four lemur groups that I followed in Sainte Luce and Mandena (N=143). As I was only able to follow three groups (excluding Group D in Mandena), only three groups defecation points were entered into analyses concerning spatial and temporal patterns of defecation. For the spatial analysis of defecation sites' distribution, I measured the distance between each defecation point and the most recent feeding, and resting trees (in metres), using Garmin BaseCamp. For the temporal analysis, I measured the time between defecation and the most recent feeding and resting bouts (in minutes). Feeding was recorded after the focal individual (or the group, in the case of nocturnal observations) used the tree for more than five seconds (Donati et al., 2007; 2011b). For behaviour to be considered resting, the focal individual (or the group) had to be inactive (i.e., not moving, or vocalising) for at least two data points (taken at five-minute intervals). When the focal individual (or the group, during the night) stayed at the same resting location over multiple measurement points, I used the first GPS point to minimize measurement errors.

For analyses concerning only the defecation locations (i.e., comparing microhabitat characteristics across seasons and day and night, as well as examining spatial and temporal patterns of defecation), I used all defecation locations in my database. Temporal proximity to feeding (i.e., time since the most recent feeding activity) was available for 18 defecation locations of Group A, 60 defecation locations of Group B, and 66 defecation locations of Group C. Temporal proximity to resting (i.e., time since the most recent resting activity) was available for 19 defecation locations of Group A, 62 defecation locations of Group B, and 59 defecation locations of Group C. Spatial proximity to feeding (i.e., distance from the most recently used feeding tree) was calculated for 13 defecation locations of Group A, 45 defecation locations of Group B, and 41 defecation location of Group C. Spatial proximity to resting (i.e., distance from the most recently used resting tree) was calculated for 15 defecation locations of Group A, 40 defecation locations of Group B, and 35 defecation location of Group C. The total number of locations was limited by equipment issues (i.e., radio-collar malfunction), which prevented me from finding the lemurs on several occasions, most often as a result of bad weather (i.e., rainfall). Terrain characteristics, namely the presence of swamps, also led to some lemur defecation locations not being documented.

Statistical analysis

Before exploring temporal patterns of defecations, I adjusted my data so that the astronomical twilights (before sunrise and after sunset, until the time when the sun is at 18° below the horizon (at this latitude, this is around 75 minutes) were added to diurnal observations, to include only true night hours in nocturnal activity (Donati & Borgognini-Tarli, 2006; Donati et al., 2016) (data taken from www.timeanddate.com). Median was used as a central tendency measure of canopy closure and forest density, accompanied with interquartile range (IQR) (Q3 – Q1). I used a Generalized Linear Model with gamma error distribution and log link function to test for differences in the canopy closure and forest density between the three lemur groups (A, B, C), and between their defecation locations and random locations. In each model, lemur group and microhabitat type were treated as fixed factors, while canopy closure and forest density were the response variables (analysed separately). Lemur groups were compared *post hoc* using pairwise comparisons.

For seasonal and between-area comparisons of canopy closure and forest density of defecation locations, I also used a Generalized Linear Model with gamma error distribution and log link function. Season (wet, dry), day phase (day, night), and lemur groups (A, B, C) were treated as fixed factors, while canopy closure and forest density were the response variables (analysed separately). Lemur groups were compared *post hoc* using pairwise comparisons.

Finally, I used a Generalized Linear Mixed Model with gamma error distribution and log link function to test for seasonal, between-site and day phase differences in spatial and temporal distribution of defecation, in relation to lemur feeding and resting. Season (wet, dry), lemur group (A, B, C) and day phase (day, night) were introduced as fixed factors, while the spatial pattern (i.e., distance to the most recent feeding and resting tree, separately) and temporal pattern (i.e., time passed since the most recent feeding and resting bout, separately) were the response variables. Lemur groups were compared *post hoc* using pairwise comparisons. All data were analysed in SPSS 26.0 (IBM, 2018).

Results

A microhabitat comparison of defecation and random locations

Canopy closure did not differ between the three lemur groups and two types of locations (Tables 1 and 3, Figure 1). The overall model was not significant (χ^2=0.672, df=3, p=0.880). The canopy closure in the home range of Group A (M=97.56, SE=0.932) was not different from that in the home range of Group B (M=97.01, SE=0.625) (ΔM=0.55, SE=1.108, df=1, p=0.617), or Group C (M=96.90, SE=0.726) (ΔM=0.66, SE=1.159, df=1, p=0.569), and Groups B and C also did not significantly differ in this respect (ΔM=0.10, SE=0.916, df=1, p=0.909). Canopy closure of defecation locations (M=96.94, SE=0.513) did not significantly differ from canopy closure of random locations (M=97.38, SE=0.758).

Table 1. A comparison of canopy closure in defecation locations and random locations in the home range of the three groups.

	Estimate	SE	df	p
Intercept	4.578	0.010	1	**<0.001**
Group C vs Group A	-0.007	0.012	1	0.569
Group B vs Group A	-0.006	0.011	1	0.616
Random vs Defecation	0.005	0.009	1	0.622

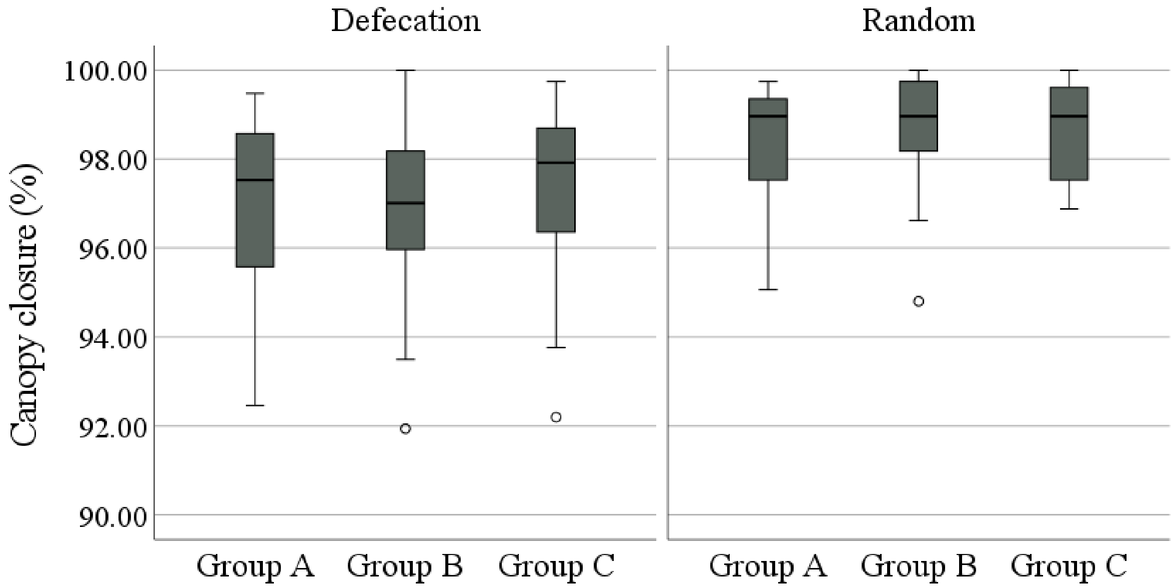


Figure 1. A comparison of canopy closure between defecation locations (N_A=24; N_B=60, N_C=57) and randomly selected locations (N_A=15; N_B=30, N_C=15) in each of the lemur groups' home range.

Contrarily, forest density differed between the three lemur groups, and the two types of locations (Tables 2 and 3, Figure 2). The overall model was significant (χ^2=318.605, df=3, p<0.001). Forest density in the home range of Group A (M=0.077, SE=0.008) did not differ from that in the home range of Group B (M=0.083, SE=0.006) (ΔM=-0.007, SE=0.011, df=1, p=0.512), but it was significantly higher than the forest density in the home range of Group C (M=0.049, SE=0.004) (ΔM=0.027, SE=0.009, df=1, p=0.005). Forest density was also higher in the home range of Group B than in the home range of Group C (ΔM=-0,034, SE=0.007, df=1, p<0.001). Finally, forest density was higher in the random locations (M=0.241, SE=0.022) than in the defecation locations (M=0.019, SE=0.001).

Table 2. A comparison of forest density in defecation locations and random locations in the home range of the three groups.

	Estimate	SE	df	p
Intercept	-3.833	0.119	1	**<0.001**
Group C vs Group A	-0.426	0.138	1	**0.002**
Group B vs Group A	0.086	0.133	1	0.518
Random vs Defecation	2.525	0.107	1	**<0.001**

Table 3. A comparison of average canopy closure and forest density of the three red-collared brown lemur (*Eulemur collaris*) groups' defecation locations and random locations.

			Minimum	Maximum	Median	IQR	N
Group A	**Canopy closure**	Defecation site	92	99	97.53	3	24
		Random site	95	100	98.96	2	15
	Forest density	Defecation site	0.000	0.076	0.015	0.013	24
		Random site	0.107	0.838	0.163	0.269	15
Group B	**Canopy closure**	Defecation site	85	100	97.01	2	60
		Random site	48	100	98.96	2	30
	Forest density	Defecation site	0.000	0.080	0.020	0.027	60
		Random site	0.034	0.627	0.234	0.022	30
Group C	**Canopy closure**	Defecation site	61	100	97.92	2	15
		Random site	82	100	98.96	3	15
	Forest density	Defecation site	0.002	0.049	0.010	0.012	57
		Random site	0.059	0.494	0.175	0.213	15

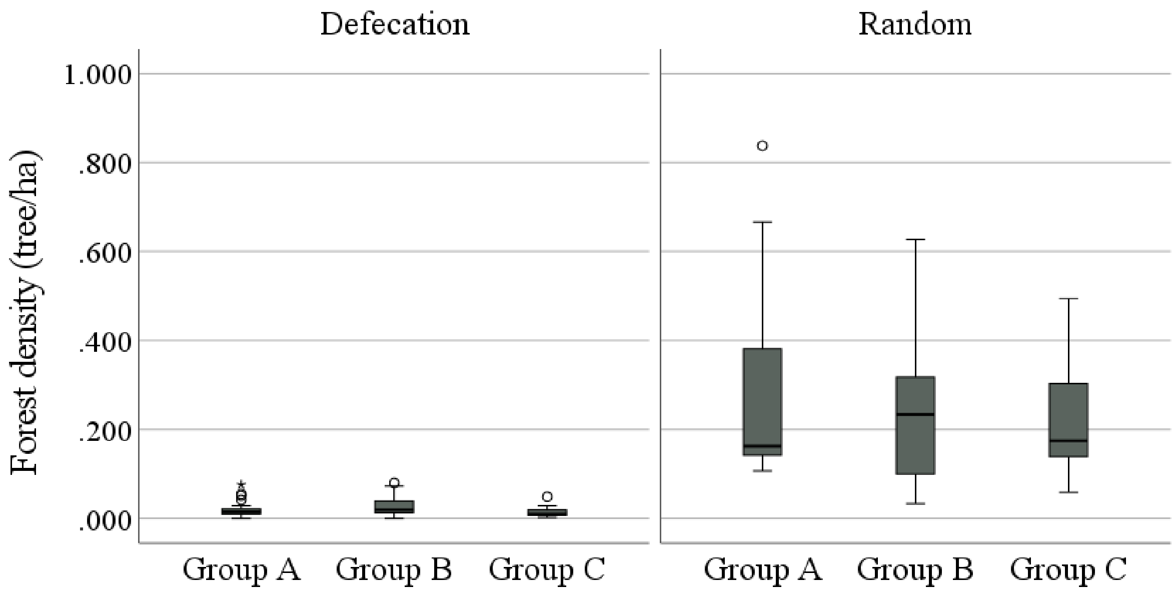


Figure 2. A comparison of forest density between defecation locations (N_A=24; N_B=60, N_C=57) and randomly selected locations (N_A=15; N_B=30, N_C=15) in each of the lemur groups' home range.

<u>Characterisation of red-collared brown lemurs' defecation locations</u>

Lemur groups did not differ in the canopy closure of their defecation locations (Group A: M=97.04, SE=1.027; Group B: M=96.90, SE=0.690; Group C: M=96.73, SE=0.733) (Table 4, Figure 3a). The overall model of canopy closure differences in the defecation locations of the three lemur groups across two seasons was non-significant (χ^2=0.663, df=4, p=0.956). There was no statistically significant difference between Groups A and B (ΔM=0.14, SE=0.995, df=1, p=0.892), Groups A and C (ΔM=0.30, SE=0.995, df=1, p=0.761) or Groups B and C (ΔM=0.17, SE=0.753, df=1, p=0.823). The difference in canopy closure between the wet season (M=96.63, SE=0.686) and the dry season (M=97.15, SE=0.770) was not significant either. The difference between the canopy closure of defecation locations selected during the day (M=96.95, SE=0.393) and at night (M=96.83, SE=1.172) was also not significant.

Table 4. Comparison of canopy closure of defecation locations of lemurs from the three groups, across seasons and day phases.

	Estimate	SE	df	p
Intercept	4.578	0.009	1	**<0.001**
Group C vs Group A	-0.003	0.010	1	0.760
Group B vs Group A	-0.001	0.010	1	0.892
Season	-0.005	0.010	1	0.459
Day phase	-0.001	0.012	1	0.922

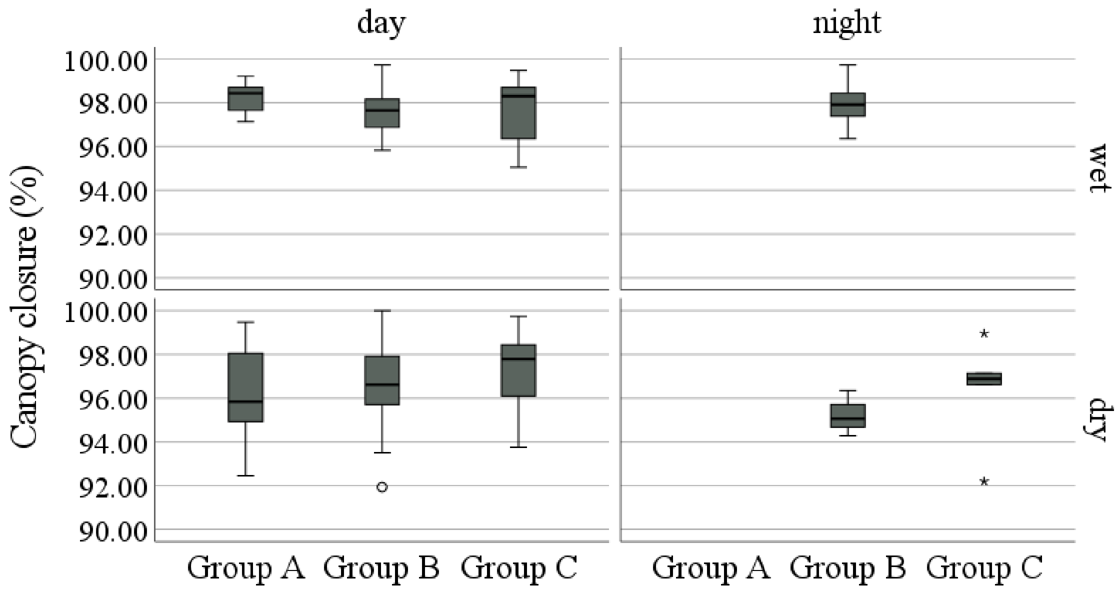


Figure 3a. Canopy closure of defecation locations of lemurs in Groups A (N=24), Group B (N=60) and Group C (N=57).

The forest density of lemur defecation locations differed (Table 5, Figure 3b). The overall model was significant (χ^2=26.681, df=4, p=0.000). Forest density of defecation locations of Group C (M=0.0146, SE=0.002) was lower than that of Group A (M=0.024, SE=0.004) (ΔM=-0.009, SE=0.004, df=1, p=0.016) and Group B (M=0.028, SE=0.004) (ΔM=-0.014, SE=0.003, df=1, p<0.001). The difference in forest density between defecation locations of Groups A and B was not significant (ΔM=0.005, SE=0.004, df=1, p=0.277). Forest density of defecation locations was not significantly different between the dry season (M=0.021, SE=0.002) and the wet season (M=0.022, SE=0.003). Forest density was also not different between day (M=0.018, SE=0.001) and night (M=0.025, SE=0.005).

Table 5. Comparison of forest density in defecation locations of lemurs from the three groups, across seasons and day phases.

	B	SE	df	p
Intercept	-3.849	0.162	1	**<0.001**
Group C vs Group A	-0.494	0.171	1	**0.004**
Group B vs Group A	0.177	0.169	1	0.297
Season	-0.044	0.121	1	0.716
Day phase	0.281	0.205	1	0.170

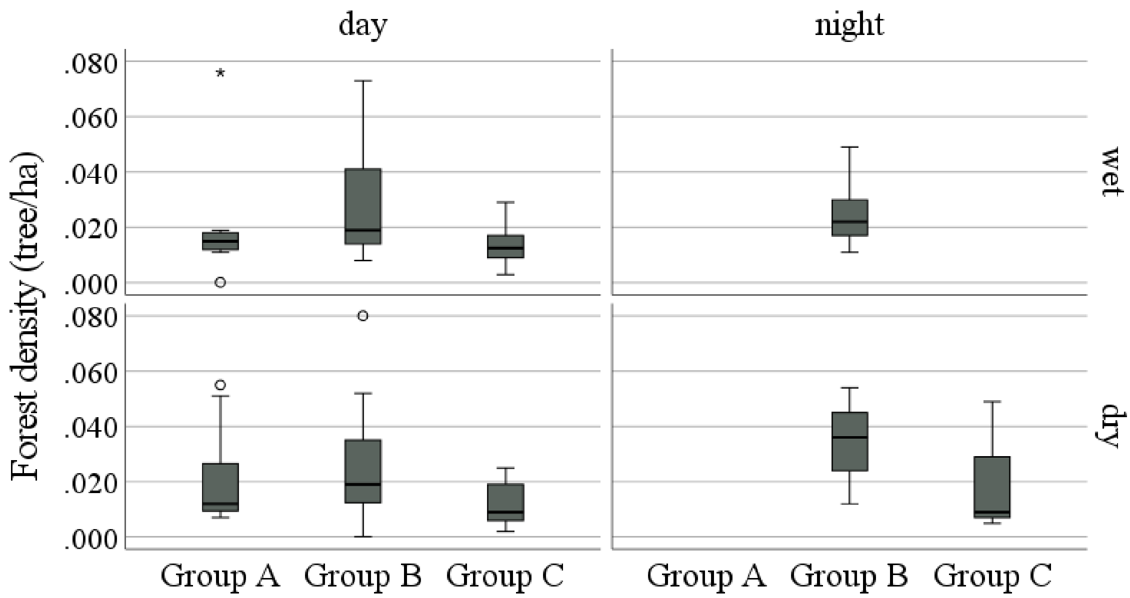


Figure 3b. Forest density of defecation locations of lemurs in Groups A (N=24), Group B (N=60) and Group C (N=57).

Spatial and temporal patterns of defecation behaviour

Lemur groups differed in terms of distance from the most recent feeding tree to the defecation location (Table 6, Figure 4a), and the overall model was significant (χ^2=19.441, df=4, p=0.001). However, although model parameters indicate that lemurs of Group C defecated closer to the most recent feeding tree (M=28.84, SE=5.474) than lemurs of Group A (M=78.11, SE=25.409), the pairwise comparison was not significant (ΔM=49.27, SE=25.223, df=1, p=0.051). Lemurs of Group B defecated closer to the most recent feeding tree (M=25.15, SE=5.128) than lemurs of Group A (ΔM=52.96, SE=24.412, df=1, p=0.030), but the difference between Group B and Group C was not significant (ΔM=3.69, SE=6.254, df=1, p=0.555). Lemurs also defecated closer to the feeding trees in the wet season

(M=30.30, SE=6.624) than in the dry season (M=48.69, SE=9.487), but the difference was not significant. There was also no significant difference between day (M=51.99, SE=6.659) and night (M=28.37, SE=8.512).

Table 6. A comparison of the distance between the most recently used feeding tree and defecation location of the three lemur groups, across seasons and day phases.

	Estimate	**SE**	**df**	**p**
Intercept	4.424	0.297	1	**<0.001**
Group C vs Group A	-0.995	0.353	1	**0.005**
Group B vs Group A	-1.133	0.330	1	**0.001**
Season	0.474	0.234	1	**0.042**
Day phase	-0.606	0.310	1	0.050

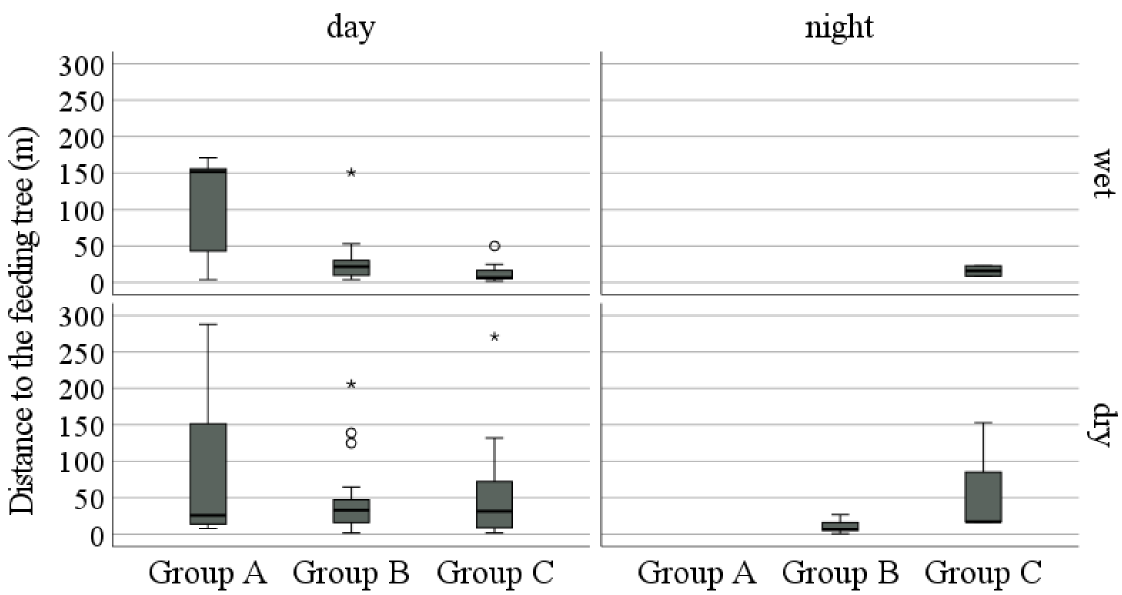


Figure 4a. A comparison of average distances from the defecation location to the most recent feeding tree in Group A (N=13), Group B (N=45) and Group C (N=41), between seasons (N=99) and day phases (N=99).

Lemur groups differed in terms of distance from the most recent resting tree to the defecation location (Table 7, Figure 4b), and the overall model of comparisons between the three lemur groups was significant (χ^2=9.031, df=4, p<0.001). Lemurs of Group C defecated closer to their most recent resting tree (M=48.94, SE=11.672) than lemurs of Group A (M=130.92, SE=48.415), but the pairwise comparison was not significant (ΔM=81.98, SE=46.434, df=1, p=0.077). Lemurs of Group B defecated closer to their most recent resting tree (M=52.40, SE=11.865) than lemurs of Group A, but this difference was also not significant (ΔM=78.52, SE=46.292, df=1, p=0.090). There were no significant differences between wet (M=79.06, SE=22.833) and dry (M=61.10, SE=12.103) seasons, or between night (M=89.59, SE=31.222) and day (M=53.92, SE=8.280).

Table 7. A comparison of the distance between the most recently used resting tree and defecation location of the three lemur groups, across seasons and day phases.

	Estimate	**SE**	**df**	**p**
Intercept	4.750	0.378	1	**<0.001**
Group C vs Group A	-0.984	0.378	1	**0.009**
Group B vs Group A	-0.916	0.372	1	**0.014**
Season	-0.258	0.281	1	0.359
Day phase	0.508	0.352	1	0.149

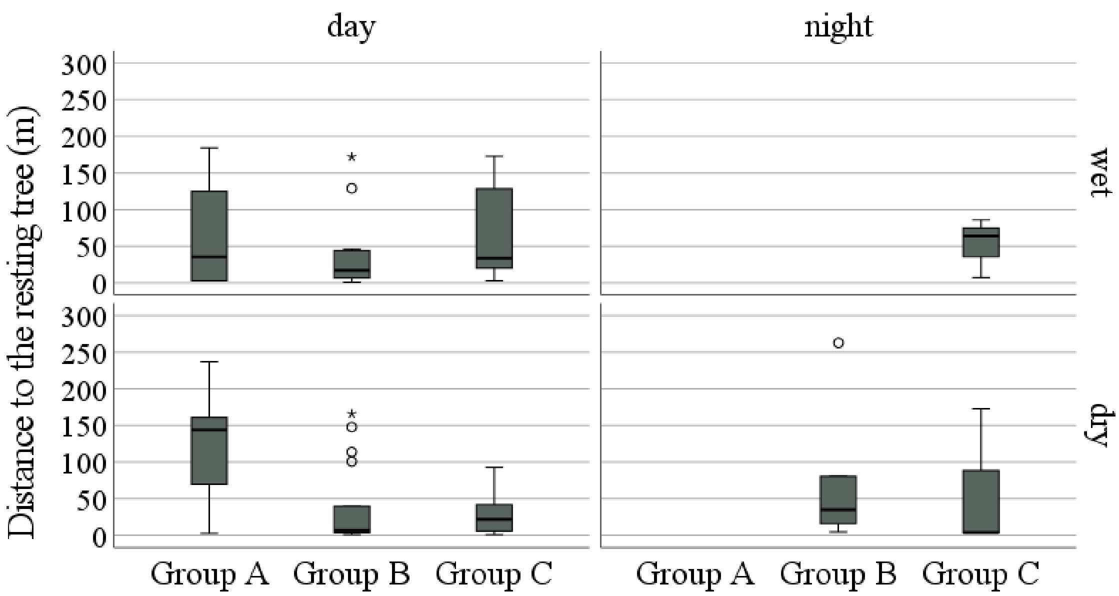


Figure 4b. A comparison of average distances from the defecation location to the most recent resting tree in Group A (N=15), Group B (N=40) and Group C (N=35), between seasons (N=90) and day phases (N=90).

The three lemur groups did not differ in the time passed between the most recent feeding and defecation (Table 8, Figure 5a). The overall model of comparisons between the three lemur groups was not significant (χ^2=4.301, df=4, p=0.367). The results showed no difference between Group A (M=100.84, SE=33.22) and Group B (M=96.38, SE=19.13) (ΔM=4.47, SE=32.939, df=1, p=0.892) or Group C (M=75.79, SE=16.493) (ΔM=25.05, SE=32.118, df=1, p=0.435). Groups B and C were also not significantly different in this respect (ΔM=20.59, SE=19.358, df=1, p=0.288). There was no significant difference between time passed between feeding and defecation in the wet season (M=95.79, SE=24.524) and the dry season (M=81.74, SE=15.603). There was also no significant difference between day (M=105.50, SE=13.211) and night (M=77.31, SE=25.480).

Table 8. A comparison of time passed between the most recent feeding and defecation of the three lemur groups, across seasons and day phases.

	Estimate	SE	df	p
Intercept	4.869	0.307	1	**<0.001**
Group C vs Group A	-0.286	0.333	1	0.351
Group B vs Group A	-0.045	0.329	1	0.891
Season	-0.199	0.231	1	0.387
Day phase	-0.311	0.329	1	0.345

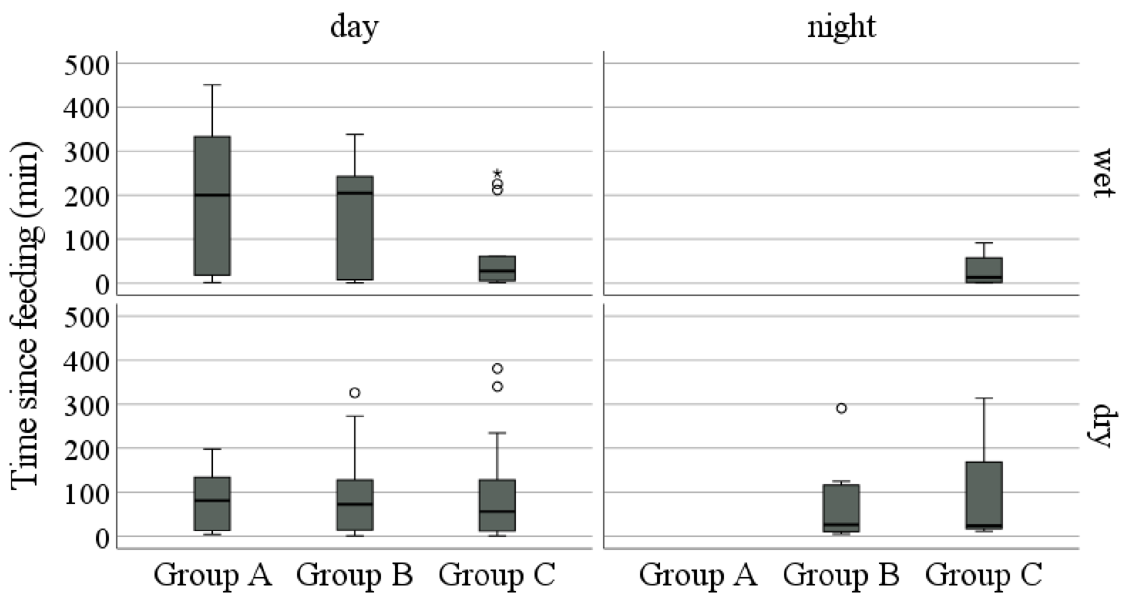


Figure 5a. A comparison of average times between feeding and defecating of Group A (N=18), Group B (N=60) and Group C (N=66), between seasons (N=144) and day phases (N=144).

The three lemur groups differed in the time passed between resting and defecating (Table 9, Figure 5b), and the overall model of comparisons between the three lemur groups was significant (χ^2=27.918, df=4, p<0.01). According to pairwise comparisons, the time between resting and defecating was longer for Group C (M=86.14, SE=20.193) than Group A (M=24.56, SE=8.125) (ΔM=61.58, SE=19.025, df=1, p=0.001), and longer for Group B (M=48.70, SE=9.330) than for Group A

(ΔM=24.15, SE=10.966, df=1, p=0.028). The time between resting and defecating was longer at night (M=88.77, SE=29.705) than during the day (M=24.76, SE=3.142), but there was no difference between wet season (M=48.17, SE=11.760) and dry season (M=45.62, SE=8.872).

Table 9. A comparison of time passed between resting and defecation of the three lemur groups, across seasons and day phases.

	Estimate	**SE**	**df**	**p**
Intercept	2.590	0.2993	1	**<0.001**
Group C vs Group A	1.255	0.3340	1	**<0.001**
Group B vs Group A	0.685	0.3446	1	**0.047**
Season	-0.054	0.2331	1	0.815
Day phase	1.227	0.3401	1	**<0.001**

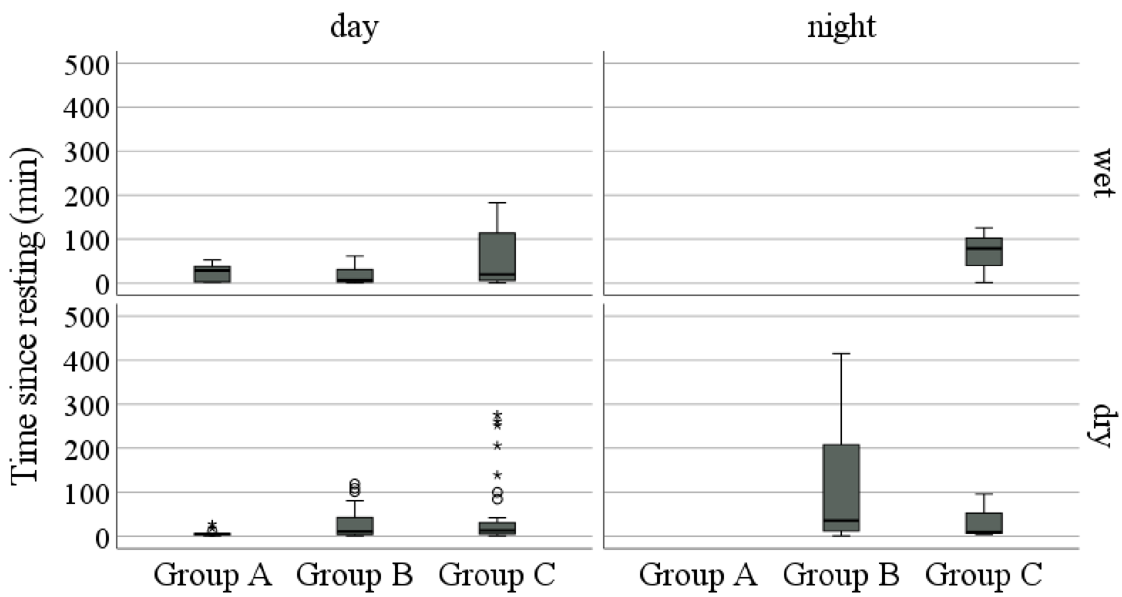


Figure 5b. A comparison of average times between resting and defecating of Group A (N=19), Group B (N=62) and Group C (N=59), between seasons (N=140) and day phases (N=140).

Discussion

The findings of this study showed that canopy closure did not differ between the three lemur group's home ranges, nor between defecation and random locations. However, forest density differed between the three lemur group's home ranges, and was higher in random locations than in the defecation locations. When only defecation locations were analysed, I did not reveal any differences between the three lemur groups in canopy closure. There were also no seasonal differences, or differences relating to day and night. On the other hand, lemur groups' defecation locations differed in the forest density, but there were no seasonal or day phase differences. Red-collared brown lemurs defecated sooner after resting, especially in the dry season and during the day. When feeding was considered, however, I found no seasonal differences, or differences between day and night. The three lemur groups differed in spatial and temporal patterns of their defecation.

Characterisation of red-collared brown lemurs' defecation locations

My results show that red-collared brown lemurs defecate in areas with relatively closed canopy (i.e., average canopy closure of over 97 %), but there is no difference between defecation locations and randomly selected locations. Canopy closure is important for seed dispersal due to its repercussions for the associated light levels breaking through to the ground. However, depending on the tree species, high canopy closure can both increase and decrease seed survival and seedling establishment (Denslow, 1995; Wenny, 2000b; Valenta & Fedigan, 2010; Gross-Camp & Kaplin, 2011). Seed dispersal type also plays an important role (Schupp et al., 1989): seeds dispersed by large-bodied animals (such as red-collared brown lemurs) usually have a better chance of survival beneath the more closed canopy. This is due to higher seed predator concentration near canopy gaps, and in some cases, their lower susceptibility to pathogens (Brokaw, 1985: Sork, 1987).

Canopy closure can be increased by a small number of large-crowned trees, or a large number of small-crowned trees, so its relation to forest density can be positive and negative, as well as non-significant. While canopy closure did not show significant between-area variation, forest density was higher in the home range of the Mandena lemurs (i.e., Group B). It was also higher in the random locations, used for control. I cannot confirm, however, that these randomly chosen locations were not also the red-collared brown lemurs' defecation locations that simply have not been observed as such in this study. To understand why the lemurs defecated in areas of lower forest density, it might be useful to consider the factors of forest phenology, human presence in the forest, the proximity of lemur groups' home range locations to human settlements, and the local human-lemur dynamic, all of which are likely to impact lemurs' behaviour. While Group A's home range is located further inside the forest fragment (in Sainte Luce), home ranges of Group C (in Sainte Luce) and Group B (in Mandena) are comparatively closer to the villages. Forest density was lower in the home range of Group C lemurs than in the home range of Group A and Group B lemurs. A possible reason might be an overall higher forest density in the home ranges of Groups A and B, but this finding could also be related to the habituation of Group C lemurs to the local human population. While red-collared brown lemurs used to be hunted in both Sainte Luce and Mandena, this practice ended with the forest protection measures (Chapter 6). This might mean that lemurs feel less threatened in areas of lower forest density, or closer to human settlements, and do not gravitate towards denser parts of their habitat. Lemurs of Group C would often travel alongside the road, as well as cross into the TBSE and SEED Madagascar camps. Similarly, they often travelled on the ground, and did not seem to be afraid of humans (this is not surprising, as this group is habituated, and has featured in several studies), which supports my argument.

While the home range of Group B is close to the forest edge and the TBSE research station in Mandena, and is in this way similar to Group C, recent NDVI data show high forest regeneration of Mandena Conservation Zone (Donati et al., 2020). This could be the cause of the higher forest density in Group B's home range. However, similar forest regeneration data are not available for Sainte Luce, so I cannot confirm that this is the reason for the difference. Moreover, anthropogenic disturbance might be higher in Mandena than it is in Sainte Luce, thus prompting the lemurs to spend more time in denser areas of their home range. People from the nearby villages were present in the forest on most of my diurnal follows. The purpose of their presence in the Mandena Conservation Zone largely focused on fishing, cattle (zebu) grazing or moving the cattle through the protected fragment to graze in a different area. Many of them also used the main forest path to move more quickly between the villages, or on their way to work at the QMM mine. It is therefore possible that lemurs of Group B, in whose home range forest density was higher than in Group C, spend more time in the denser parts of their home range to avoid anthropogenic disturbance. It is also possible that lemurs spend more time in denser parts of the forest if these areas are richer in food (Balko & Brian Underwood, 2005) However, forest density and phenology were not the focus of the present study, so these hypotheses should be revisited in the future.

Apart from people, lemurs have other natural predators, whose prevalence, as well as incidence of their predation is likely to influence their behaviour. Fossa (*Cryptoprocta ferox*), a known predator of red-collared brown lemurs and other *Eulemur* species (Goodman, 2003b; Hawkins, 2003) has been observed in Sainte Luce in the past (Lewis Environmental Consultants, 1992). Its predation on red-collared brown lemurs was also documented in Mandena in 2004, following a translocation of several groups from degraded fragments into at the time newly established conservation zone (i.e., M15+M16) (Donati et al., 2007b). However, after these predation cases, fossas were captured and relocated to the Tsitongambarika humid forest (about 25 km north of Mandena) (Donati et al., 2007b). To my knowledge, this predator has not been observed in Sainte Luce in the recent years. However, as Mandena is much closer to Tsitongambarika, it would be possible for fossas to travel to Mandena (although they were not observed by me or my team in the Mandena Conservation Zone during the duration of this study). The presence of fossas could lead to lemurs spending more time (and subsequently defecating) in denser parts of their habitat to avoid predation. Apart from fossas, the diurnal birds of prey, such as Madagascar harrier-hawk (*Polyboroides radiatus*), Henst's goshawk

(*Accipiter henstii*), or Madagascar buzzard (*Buteo brachipterus*) (Donati et al., 2007; 2007b) also predate on the red-collared brown lemurs in these forests (in addition to an occasional large snake predation; Goodman et al., 1993). However, without knowing their predation levels in Sainte Luce and Mandena, and parts of each forest fragment in which these predators might be more abundant, it is difficult to hypothesise these species' influence on lemur behaviour, or use this as an argument when comparing the three lemur groups. I sometimes observed lemurs defecating in locations in which the seeds are unlikely to germinate – namely, in the swamp. Knowing the exact proportion of defecation (especially of seeds) in such locations can be helpful in projecting forest generation and relating it to red-collared brown lemurs. Moreover, it is possible that other characteristics of defecation locations may be more important, such as their proximity to other important locations: resting or feeding trees.

<u>Spatial and temporal patterns of defecation behaviour</u>

According to the results of this study, red-collared brown lemurs' defecation is related to the temporal patterns of their resting, but not feeding. Defecation more closely following resting is not surprising as resting and defecation are closely related in many primate species. For example, red brown lemur (*Eulemur rufus)* and red-fronted brown lemur (*E. rubriventer*) often slept in feeding trees, and defecated closely after waking up (Overdorff & Strait, 1998), resulting in clumped seed distributions and reduced germination success. Seed densities were also revealed to be particularly high beneath (reused) sleeping sites of spider monkeys (*Ateles paniscus*) (Russo & Augspurger, 2004; Russo et al., 2006). Tamarins (*Saguinus fuscicollis* and *S. mystax*) also dispersed significantly more seeds within their resting areas (Lazo et al., 2011), resulting in higher concentration of seedlings in these locations.

Defecation pattern showed seasonal variation, and variation between day and night, but not completely in accordance with my predictions I expected that lemurs would defecate closer to their resting trees in periods of prolonged resting. Although this usually happens in the dry season (Donati et al., 2011b), most likely as a result of lemurs' energy saving strategy (also evident from this species' shorter daily path lengths during the dry season (Campera et al., 2014), and possibly larger home ranges), this was not the case at the time of this study, when I found no seasonal variation in activity (Chapter 3). This might be the reason why I detected no significant relationship between resting locations and defecation locations: lemurs were neither more nor less likely to defecate closer to their most recent resting location in either season.

While I found no significant difference between the three lemur groups in the proximity of their defecation locations to their most recently used resting locations, I found a difference in the defecation locations' proximity to the most recently used feeding trees. Specifically, lemurs of Group B defecated closer to their most recently used feeding trees than lemurs of Group A. This finding could be related to differences in the diet, as Mandena lemurs consumed more leaves (Chapter 3). Leaves are richer in fibre, which is likely to affect gut passage times (i.e., prolong them) (Campbell et al., 2004). However, if this were the case, I would have expected to also find a significant difference between Groups B and C, which did not occur. Moreover, nutritional contents of the different food items were not examined in this study, but since the improvement of the Mandena Conservation Zone habitat (Donati et al., 2020b), it may be useful to reassess in the future. As Groups A and B did not differ in how soon after feeding they defecated, the spatial difference between them could potentially also be linked to their preferential use of habitat. Group B might be spending more time in particular areas within their home range that are rich in food, and as a result, also defecate closer to feeding trees. To examine this, future studies should focus on comparing different lemur groups' daily path lengths, and preferential use of habitat (i.e., staying close to important places, such as feeding and resting trees, water sources, etc.).

Defecation was more likely to follow resting during the day. In the current study, the lemurs were more active during the day (Chapter 3), but dietary preferences also play a significant role, as they affect gut passage time (Tsuji et al., 2010). Although I found no significant relationships between defecation and feeding times, it is possible that defecation patterns were affected by the different times at which particular food items were consumed (Westcott et al., 2005; Russo et al., 2006). A distribution of different food items' (i.e., fruit, nectar, mature/young leaves, invertebrates) consumption across the 24-hour cycle would, in relation to these items' different nutritional contents, provide a framework for understanding the variation of defection patterns across the 24-hour cycle, and should therefore be included in the analyses of the future studies. Previous research showed that the longest dispersal distances were associated with seeds (fruit) consumed early in the morning (Stevenson, 2000; Westcott et al., 2005; Russo et al., 2006). Moreover, there may be differences in how fast the lemurs move at different times of the day, which may be a better predictor of defecation pattern than the mere passage of time since feeding (or resting) (Russo et al., 2006). However, to fully understand this relationship, it will be necessary to include dispersal distances (i.e., from the parent tree to the primary dispersal location) in the model.

The importance of examining the relationship between feeding and defecation has important implications for understanding the red-collared brown lemur's seed dispersal efficiency. By documenting the fruit species consumed at different times of day, and considering *Eulemur* sp. gut passage times (e.g., Overdorff & Rasmussen, 1995; Campbell et al., 2004), it should be possible to predict when their seeds will be dropped, and where, thus allowing prediction of plant species-specific dispersal distances (Westcott et al., 2005; Russo et al., 2006). However, while gut passage times are useful, to a degree, in predicting dispersal patterns, they lack information relating to behavioural patterns, which can affect temporal and spatial patterns of seed dispersal. Misunderstanding spatial variance of seed deposition is likely to lead to biased predictions regarding the dynamics of seedling recruitment (Chesson et al., 2005), or the effects of seed dispersers' extirpation (Wright et al., 2000). Additional factors are likely to influence this lemur's seed dispersal, that were not included in the current study's design. For example, on multiple occasions I observed several individuals from the same group sequentially defecating from the same tree, and in the same location. Such defecation pattern is something that is likely to impact seed distribution, and (provided seed predation is included in the model), allow predicting seedlings' survival and recruitment (Schupp et al., 2002; Muller-Landau & Hardesty, 2005), and should therefore receive research attention.

This study provided valuable information regarding red-collared brown lemur's defecation-related behaviours, and the characterisation of its defecation locations, but there is not enough evidence to argue for the existence of latrine behaviour in this species. Common in mammals, this behaviour is rare among primates; nevertheless, it has been observed in three lemur genera: *Cheirogalues* (Ganzhorn & Kappeler, 1996), *Lepilemur* (Irwin et al., 2004; Dröscher & Kappeler, 2014), and *Hapalemur* (Irwin et al., 2004; Eppley & Donati, 2010; Eppley et al., 2015). Latrine behaviour is believed to be a means of olfactory communication (Brown & MacDonald, 1985; Gorman & Trowbridge, 1989), but there are several hypotheses about its function. There include advertising sexual cycle (Woodroffe et al., 1990), intragroup spacing for resource use (Kruuk, 1992), intergroup resource defence (Krishnamani & Mahaney, 2000), territoriality, and predator avoidance (Boonstra et al., 1996; Viitala et al., 1995). However, latrine behaviour is typically not the main focus of primate studies, and no specific hypotheses regarding its function have yet been offered (Irwin et al., 2004). Confirming any of these hypotheses would require a focus on different aspects of behaviour that precedes defecation, as well as a consideration of defecation locations' microhabitat parameters.

Conclusion and recommendations

This study revealed that red-collared brown lemurs defecate in areas of lower forest density, but canopy closure does not appear to play an important role. I found seasonal differences in spatial and temporal patterns of red-collared brown lemur defecation. While my results indicate differences in defecation patterns over the 24-hour cycle, nocturnal data points are few, and this aspect of their seed dispersal ecology needs further examination. The results of this study answer several questions regarding the defecation patterns of red-collared brown lemur, but the scientific understanding of this subject could still be improved by examining a few additional aspects of this lemur's defecation behaviour. I offer the following guidelines for further studies:

1. Documenting the proportion of animals defecating in the same location sequentially. Individuals' age and sex classes should be recorded, and the order of defecation. If the species most often defecates between resting and feeding, the order may reflect group hierarchy.

Brown lemurs do not show female social dominance (Pereira et al., 1990; Overdorff, 1996; Ostner & Kappeler, 1999; Johnson, 2006; Petty & Drea, 2015), but there is some evidence pointing toward a linear hierarchy (Palagi & Norscia, 2011). Because of this, I would not expect to see any robust sex differences, but there may be differences arising from individuals' different hierarchical positions. If higher ranked individuals eat sooner, they could also be defecating sooner (if gut passage is similar between individuals). Examining sequential defecation is important because even in an absence of latrine behaviour, clumping may have a negative impact on seed survival if its mortality is density dependent (Forget, 1993). This would also provide a good setting to study secondary dispersal or seed predation.

2. For the study of temporal patterns of defecation, more specific categories should be examined – for example, social behaviour. If defecation is a means of olfactory communication (Brown & MacDonald, 1985; Gorman & Trowbridge, 1989), it would be interesting to investigate when lemurs defecate in relation to, for example, social grooming, as well as whether these patterns change in relation to life history traits, sex, and reproduction status.

3. Spatial data on lemurs' use of their habitat should continue to be collected over the 24-hour cycle, as calculation of home range overlap between day and night could reveal spatial patterns important to understanding this lemur's seed dispersal.

4. Microhabitat analysis of defecation locations should be extended to more landscape variables, such as slope or elevation, proved to influence seedling establishment significantly (Gross-Camp & Kaplin, 2011).Seasonality-dependent environmental variables, such as soil moisture, should also be included. Differentiating between defecations that included seed depositions (opposed to defecations of other food stuffs) would enable a more fine-grained analysis of the repercussions of defecation location characteristics on seed dispersal effectiveness. As home range use shows seasonal variation (Campera et al., 2014), it is possible that seeds of particular species of fruiting trees are more likely to be dispersed in some areas than others. In the long term, this dispersal pattern could have implications for forest composition.

5. Lemurs' height and branch position should be noted, to provide further insight into potential preferential selection of defecation locations and to determine the presence and functions of latrines (if their existence is confirmed). Previous studies showed that these lemurs' feeding tree selection varies across the 24-hour cycle, and that they choose lower canopy trees during the day, and upper canopy or emergent trees during the night to avoid diurnal predation (Curtis & Rasmussen, 2002; Rasmussen, 2005; Donati et al., 2007). A comprehensive study which would also include measures of resting tree heights (and specific heights at which the lemurs

rest during the day and at night) would help develop evidence-based hypotheses that could lead to more substantial conclusions. The proportion of defecations which are unlikely to result in germination due to the unfavourable environment (e.g., a swamp, or a middle of the transect/road, from which they are very likely to be removed) should be calculated as well. This could have important implications for understanding the role of defecation (and possibly latrine behaviour, if confirmed) in chemical (olfactory) communication.

6. Seed predation should be investigated, especially in relation to the seed predator type (i.e., comparing different predator groups, as well as the native and invasive species) and population densities, as well as their relationship to the area (comparing Sainte Luce and Mandena) and different types of habitat within the same area (e.g., forest edge, swamp edge, interior forest). It is already known that the native and invasive species of rodents - namely the Webb's tuft-tail rat (*Eliurus webbi*), and the black rat (*Rattus rattus*) are present in the littoral forests, where they seem to predate on seeds regardless of the fruit type, pulp type and seed protection (Bollen & Elsacker, 2002). Their preferences for seeds of different plant species should be examined too, as it may have implications for the species' relative regeneration. Finally, experiments comparing the predation rates of viable, intact seeds and of lemur-digested seeds belonging to the same plant species should be conducted to understand the possible protective role of red-collared brown lemur digestion from seed predation.

CHAPTER 5

The role of red-collared brown lemurs (*Eulemur collaris*) in forest regeneration of littoral forests of Sainte Luce and Mandena, southeastern Madagascar

Introduction

Seed dispersal is among the most essential ecological processes, and one that affects all aspects of vegetation dynamic. In the tropical forests, frugivorous vertebrates are crucial seed dispersers of numerous tree species (Howe & Smallwood, 1982; Howe, 1984; Gautier-Hion et al., 1985). The composition of the frugivores' community, as well as the abundance of particular frugivores strongly affects the dispersal success of many tropical plant species (Terborgh et al., 2008). For example, when the abundance of large frugivorous vertebrates decreases, it is reflected in reduced seed dispersal (Wright et al., 2000; Want et al., 2006), decreased seedling recruitment (Cordeiro & Howe, 2001; 2003), shorter dispersal distances (Wyatt & Silman, 2004), and lower relative abundance of plant species (Dirzo & Miranda, 1991; Asquith et al., 1999; Wright et al., 2007). It can also lead to an increased invertebrate seed predation due to the lack of vertebrate seed predators (Andresen & Laurance, 2007).

Adult trees attract animals, resulting in both positive (e.g., pollination, seed dispersal) and negative (e.g., seed predation, herbivory, pathogens) outcomes, the balance of which is related to the success of tree species' reproduction. According to the Janzen-Connell hypothesis (Janzen, 1970; Connell, 1971), the negative outcomes are distance-dependent, and their presence often diminishes with an increase of distance from the reproductive adult trees. This means that seedling recruitment will be more successful if the seeds are dispersed farther away. Large-seeded plants tend to be dispersed by large vertebrates, such as frugivorous non-human primates (hereafter "primates") (Andresen, 1999; Peres & van Roosmalen, 2002; Poulsen et al., 2001). Primates have a potential to disperse seeds several hundreds of meters (Lambert & Chapman, 2005; Albert et al., 2014; Haurez et al., 2015), but while large-bodied primates, such as non-human apes, are known for their long-distance seed dispersal (over 500m away from the likely parent tree), such long-distance dispersal appears to be rare in comparably smaller species, like lemurs (Spehn & Ganzhorn, 2000; Moses & Semple, 2011; Razafindratsima et al., 2014). This is possibly the result of their smaller home-range sizes and shorter day-range lengths (Crowley et al., 2011). These constrain their dispersal distances and can in some cases lead to the dispersal of seeds directly beneath (or in close proximity of) the parent tree.

Anthropogenic disturbances, such as forest fragmentation, selective logging or hunting affect the interactions between plants and animals (Wright, 2007; Jordano et al., 2011), such as animal-mediated seed dispersal (Cordeiro & Howe, 2003; Kirika et al., 2008; Cordeiro et al., 2009; Lehouck et al., 2009; Uriarte et al., 2011). This is especially the risk for the large-seeded plants that are likely to only be dispersed by larger-bodied frugivorous species (McEuen & Curran, 2004; Lahann, 2007). Such animal species are often the ones incurring the largest impact from human pressures, such as hunting (Lehman & Wright, 2000; Wright, 2003; Lehman et al., 2006; Cramer et al., 2007; Terborgh et al., 2008; Golden, 2009; Vanthomme et al., 2010; Linder & Oates, 2011). One of the consequences of overhunting is the impoverished community of seed dispersers and seed predators, often referred to as the "empty forest syndrome" (Redford, 1992; Forget & Jansen, 2007; Stoner et al., 2007; Terborgh et al., 2008; Fa & Brown, 2009). This can lead to diminished seedling recruitment and forest regeneration (Forget & Jansen, 2007; Muller-Landau, 2007; Brodie et al., 2009), even if only a few taxa are removed (Ganzhorn et al., 1999; Terborgh et al., 2008). Large-seeded plants are also often associated with shorter dispersal distances and fewer fruits (Hedge et al., 1991). Interestingly, however, they also generally have higher seedling recruitment rates (Turnbull et al., 1999).

Madagascar provides an excellent context for investigating forest regeneration and its relationship with the changes in frugivore community for several reasons. Firstly, the forests in Madagascar have high diversity of botanical species, many of which are reliant on frugivorous vertebrates for their seed dispersal (Bollen et al., 2004; Razafindratsima, 2014). Secondly, many frugivore guilds that are present and abundant in other tropical islands, such as frugivorous birds, are impoverished in many ecosystems across Madagascar (Haawkins & Goodman, 2003; Bollen, 2004). While there are 30 species of bats in Madagascar, only three are known to be frugivorous (MacKinnon et al., 2003). Thirdly, frugivores that could have been important for seed dispersal, such as large-bodied lemurs, have gone extinct (Godfrey et al., 2004; Yoder & Nowack, 2006; Razafindratsima et al., 2013). Larger lemurs typically feed on the fruits of larger-seeded plants (Bollen et al., 2004; Lahann, 2007; although there are exceptions - e.g., Overdorff, 1993b; Dew & Wright, 1998). This has left the large-seeded plants particularly vulnerable – they are, due to the size of their fruit and seeds, inaccessible to smaller animals and therefore inappropriate for their dispersal.

While extirpation of larger primates may result in an increased abundance of medium-sized primate species (Peres & Dolman, 2000), they are unlikely to consume the fruits of large-seeded plants (Lahann, 2007), as their seeds are simply too large for them (Dew & Wright, 1998). Nocturnal lemurs of smaller body sizes therefore cannot replace the larger-bodied diurnal (or cathemeral) lemurs (Wright et al., 2011). Over time, the lack of large-bodied dispersers should be reflected in the forest composition, especially when it comes to seedlings and saplings (already established adult trees will not be affected, or will be gone as a result of different processes, such as selective logging). The negative consequences of large-bodied lemurs' local extirpation for seedling recruitment has been shown in western Madagascar, where the local extirpation of red-fronted brown lemur (*Eulemur* *rufifrons*) has resulted in low recruitment of species believed to be exclusively dispersed by this lemur (Ganzhorn et al., 1999).

Lemur dispersal distances may not be as long as those of other primates of comparable size (Razafindratsima et al., 2014). However, lemur digestion was found to improve germination speed and success of certain plant species in their diet (Dew & Wright, 1998; Simmen et al., 2006; Razafindratsima & Razafimahatrarta, 2010), by as much as 60-80 % (Dew & Wright, 1998; Overdorff & Strait, 1998; Simmen et al., 2006). Some plant species seem to require lemur digestion for the removal of their seeds' aril, which impedes germination capacity (Howe, 1986). Other benefits of lemur gut passage include a decreased appeal of the digested seeds to the seed predators (i.e., rodents), as well as lower insect damage and mould susceptibility due to the removal of fruit pulp during digestion (Spehn & Ganzhorn, 2000).

Littoral forests of Sainte Luce and Mandena in southeastern Madagascar are well-known for their plant species diversity (Ganzhorn et al., 2007) and endemism (Lowry et al., 2008). In addition to being heavily fragmented, they are also among the most threatened ecosystems in the country (Bollen & Donati, 2006; Vincelette et al., 2007). This has put at risk the largest lemur species still inhabiting these forests – the red-collared brown lemur (*Eulemur collaris*). This frugivorous lemur, classified as Endangered by the IUCN Red List (Donati et al., 2020) is the only seed disperser of plants whose seeds exceed 12.5 mm in diameter (Bollen et al., 2004; Bollen & Donati, 2006). This lemur species has already been extirpated from several forest fragments across Sainte Luce (Bollen & Donati, 2005; Donati et al., 2007), which has been attributed to the hunting pressures (M. Aimeé, personal communication). However, the lemur remains present in other fragments, thereby creating a natural experiment setting for examining the consequences of large-bodied seed disperser's absence on the regeneration of forest species in its diet.

In this study, I address the question of whether the presence (and absence) of the red-collared brown lemur is related to the regeneration of large-seeded tree species thought to be exclusively dispersed by it. I offer the following hypotheses and predictions:

H1: Regeneration of primate-dispersed tree species is higher in forests inhabited by their seed dispersers than in forests in which they are not present (Ganzhorn et al., 1999).

Prediction: Since the red-collared brown lemur is the exclusive disperser of large-seeded tree species in the littoral forest, there will be more seedlings and saplings of these species in the forest fragments in which this lemur occurs than in those from which it has been extirpated.

H2: Regeneration of primate-dispersed tree species is higher in forests in which their seed dispersers are more abundant (Stevenson, 2011).

Prediction: Due to the exclusive seed-disperser relationship between the red-collared brown lemur and large-seeded tree species, tree regeneration will be dependent on this lemur' population density. The fragment with the highest population density (i.e., S9) will have the highest number of seedlings and saplings of large-seeded tree species, while the fragment from which the red-collared brown lemur has been extirpated (i.e., S7) will have the lowest number of these tree species' seedlings and saplings. The number of seedlings and saplings in the fragment with a lower population density of red-collared brown lemurs (i.e., MCZ) will be an intermediate between the other two.

H3: Seedling recruitment of primate-dispersed tree species is higher in seed dispersers' defecation locations than in non-defecation locations within the same forest (Pouvelle et al., 2009).

Prediction: Large-seeded tree species' regeneration will be higher in red-collared brown lemurs' defecation locations than in random locations.

Methods

Data collection

Data collection took place in two fragments in Sainte Luce – S9 (protected fragment, 275 ha) and S7 (unprotected fragment, 198 ha), and in Mandena Conservation Zone – MCZ (M15+M16 joined forest fragments, 230 ha) between August 2017 and October 2018. In each of the forest fragments, I collected data from 60 plots, adding up to the total of 180 plots. In two of the forests (i.e., S9 in Sainte Luce, and MCZ in Mandena), I followed four groups of red-collared brown lemurs (*Eulemur collaris*) between August 2017 and August 2018, recording their defecation locations. In each of the two forests, half of the plots (n=30) were created in the lemurs' (previously identified and marked) defecation locations, which were randomly selected from the dataset. The other half of the plots were selected using grids set up in random locations within each lemur group's territory, to include two distinct forest types – forest and swamp edge. The two fragments populated by red-collared brown lemurs differed in their population densities, which was 37 individuals per km^2 in Sainte Luce (Bollen & Donati 2006), and 12 individuals per km^2 in Mandena (Donati et al., 2007). This made them a good setting for a comparative study of the potential effects of this species' presence on the regeneration of the tree species they disperse. The study design was implemented to allow an additional level of comparison of forest regeneration, i.e., known defecation locations *versus* random locations. In the remaining forest (i.e., S7), red-collared brown lemurs have been extirpated since the 1990s (G. Donati, personal communication). For this reason, all 60 plots were selected using grids, positioned in six different areas in the fragment, following the same rule (i.e., the inclusion of both upland forest and swamp forest edge). The random plots within the same grid were separated by ~ 15 m.

In the centre of each plot, I created a 2 m^2 micro-plot, in which I counted, measured, and identified the species of all seedlings and saplings (Ganzhorn et al., 1999). In accordance with previous research, saplings were defined as tree plants with a DBH < 5cm and with height < 400 cm, which are assumed to be less than 15 years old (Vincelette et al., 2007b), as the average annual growth of littoral forest tree species is estimated at < 22 cm (Vincelette et al., 2007b). These saplings therefore represent the plants established after the red-collared brown lemur was extirpated from the forest in which it remains absent today (i.e., S7). Seedlings were defined as plants of < 22 cm in height, which are less than a year old, based on Vincelette et al. (2007b). All tree species were identified *in situ,* with help from local experts, based on their physical appearance and using their vernacular names, while their scientific names were obtained from the previously published literature (Bollen, 2003; Ingram & Dawson, 2006; Ganzhorn et al., 2007b; Donati et al., 2007; 2011; 2020). Additionally, a herbarium of unidentified species was collected and identified by *a Kew Madagascar Conservation Centre – Royal Botanic Gardens'* botanist David Rabevohitra.

<u>Microhabitat characteristics</u>

For each plot, I collected data on tree density, species diversity, and canopy closure, to enable comparison of microhabitat characteristics between the three forest fragments and between the two types of locations (i.e., defecation locations, and random locations). In addition, I calculated adult tree species frequency (defined as the number of sample locations at which a particular species occurs), to better understand the relationship between seedlings, saplings and adult trees.

To provide a measure of tree density, I used the point-quartile method (PCQ; Brower et al., 1998) to record the distance between the centre of each micro-plot and the nearest adult tree, defined as trees with a DBH ≥ 5 cm. This was based on the observation that in the littoral forest of southeastern Madagascar trees start to produce fruits when they attain a size larger than 4-5 cm DBH (Rabenantoandro, personal communication). In lemur defecation locations, the plots were positioned around the exact defecation points, and in the random locations, the centre was placed at ~ 15 m from the centre of the previous plot in the grid. The grids comprised 15 plots, positioned in a 3 x 5 layout.

I measured canopy closure using a convex spherical densitometer, with a cross-shaped grid of 24 quarter-inch squares delineating the plot overhead, and a built-in levelling bubble (*Forestry Suppliers Spherical Crown Densiometer, Convex Model A*). In each plot, I took the measurements by holding the densitometer about 15 inches in front of my body, at an elbow height. Four equispaced dots were assumed in each square of the grid, and those equivalent to quarter-square canopy openings were systematically counted. To obtain the area not occupied by canopy, the total was multiplied by 1.04. Assuming each dot represents one percent of the overstory is often accurate enough, so the difference between this number and 100 was used as an estimate of the canopy closure (in %). In each plot, I made four readings - facing North, East, South, and West, and recorded their average (Strickler, 1959).

Statistical analysis

Average adult tree height and DBH were presented as Medians. Tree density was calculated using the following formula:

$$Density\ (all\ species) = \frac{1}{Mean\ point - to - plant\ distance^2}$$

As neither tree density nor canopy closure were normally distributed, based on the Kolmogorov-Smirnov test results (canopy closure: Z=0.265, p<0.001; tree density: Z=0.161, p<0.001), comparisons between the three forests were made using Kruskal-Wallis test, with Mann-Whitney U test for *post hoc* analyses. To compare the community similarity between the forests included in the study, I used Sorenson's coefficient, calculated as $2C/S_1 + S_2$, in which *C* represents the total number of species that two areas have in common, while S_1 and S_2 represent the total number of species in each forest, respectively. Species diversity was calculated using the Shannon-Wiener index of diversity (Pielou, 1966), separately for seedlings, saplings, and mature trees. Shannon-Wiener index (H) was calculated using the following formula:

$$\mathrm{H} = \sum_{i=1}^{R} p_i \ln p_i$$

where p_i is the fraction of the entire population of a species (*i*), R is the number of species found in the area, and Σ is the sum of all the individuals of species encountered in the area. The relationships between seedling, sapling, and adult trees species were tested using a Spearman correlation coefficient.

To compare the forest regeneration of two forest fragments, and test whether the population density of red-collared brown lemur affected the regeneration, I ran a Generalized Linear Model with a negative binomial distribution, using the total count of seedling/sapling per species as a response variable. The model was selected based on the Akaike information criterion (AIC) for generalized models; I selected the model with the smallest AIC. Fragments were treated as fixed effect factors, while the number of adult trees per species was entered into the model as a covariate, due to their potential predictive value in the numbers of seedlings and saplings of the same species (as some degree of seed dispersal is likely to come directly from the parent tree). I also ran additional models using the total count of seedlings/saplings in defecation/random locations as response variables.

The same model was applied for the total regeneration (i.e., accounting for all the species found regenerating in the forest), and for the species dispersed only by the red-collared brown lemur (i.e., species with seeds larger than 12.5 mm in length; Bollen et al., 2004; Bollen & Donati, 2006) (also selected based on the AIC). Additionally, separate models were run using only the species overlapping between all three forest fragments, but as these analyses showed similar results, I opted for the models on full species lists, for increased statistical power associated with larger sample sizes.

Before the analyses, I excluded the exotic species (i.e., *Eucalyptus robusta, Psidium guayave*) from the sample, as well as species that I was not able to identify correctly (i.e., for which their scientific name was not available). I have done this because it is possible that some of the species are given different vernacular names in the two field sites (i.e., Sainte Luce and Mandena) but are actually the same species. This method therefore allowed me to be more conservative in my conclusions. All data were analysed in SPSS 26.0 (IBM, 2019).

Results

Microhabitat characteristics

I found between-site differences in canopy closure ($H=56.903$, $df=2$, $p<0.001$), which was significantly lower in the fragment from which the red-collared brown lemur was extirpated (i.e., S7) than in the two fragments in which this lemur is present (i.e., S9 and MCZ) (S7 and S9: $U=569.00$, $p<0.001$; S7 and MCZ: $U=548.00$, $p<0.001$). The fragments in which red-collared brown lemurs are present did not differ in canopy closure ($U=1769.00$, $p=0.870$). The three forest fragments differed in tree density ($H = 23.946$, $df=2$, $p<0.001$), which was significantly lower in the fragment without the red-collared brown lemurs (i.e.,S7) than in the other two fragments (S9 ($U=1195.50$, $p<0.001$), and MCZ ($U=921.50$, $p<0.001$). Additionally, tree density was higher in MCZ than in S9 ($U=1388.50$, $p=0.031$) (Table 1, Figures 1 and 2).

Table 1. Average canopy closure and tree density of the three study sites. Red-collared brown lemur (*Eulemur collaris*) is present in two fragments (S9, MCZ), and absent from one (S7).

		Minimum	Maximum	Median	IQR
Canopy closure	**S9**	81.80	100.0	98.570	2.08
	S7	46.18	99.74	92.590	12.09
	MCZ	48.00	100.00	98.570	2.02
		Minimum	**Maximum**	**Median**	**IQR**
Tree density	**S9**	0.001	1.214	0.169	0.176
	S7	0.030	0.724	0.117	0.098
	MCZ	0.034	0.834	0.249	0.259

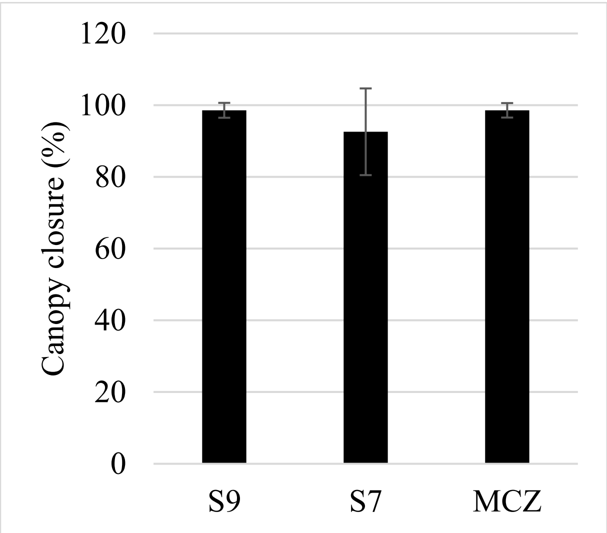


Figure 1. Average canopy closure in the three forest fragments, expressed as Medians with IQR.

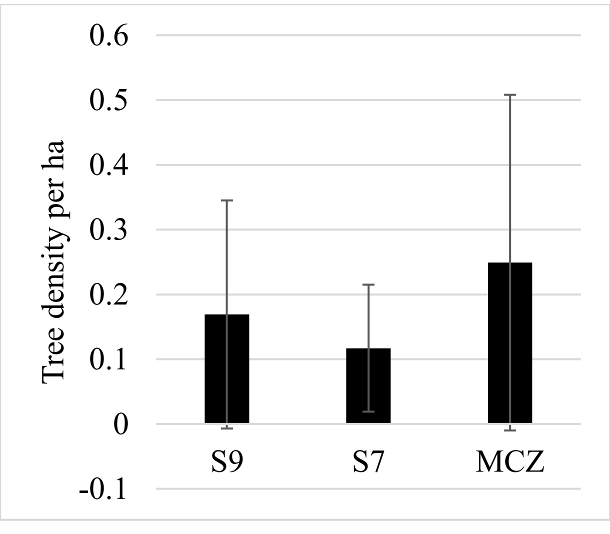


Figure 2. Average tree density per hectare the three forest fragments, expressed as Medians with IQR.

Forest composition and community similarity

The three forest fragments differed in their adult tree species composition. In S9, I found 57 species belonging to 47 families. Their average height was 9.7 ± 2.8 m, and average DBH 13.1 ± 9.7 m. In S7, there were 52 species belonging to 33 families. The average height was 8.6 ± 2.7 m, and average DBH was 12.5 ± 8.8 m. Finally, in MCZ, there were 65 species belonging to 42 families (Table A1, Appendix II). Their average height was 8.4 ± 2.2 m, and average DBH was 12.7 ± 8.8 m.

Within 180 plots I analysed in this study, I found a total of 110 regenerating plant species, belonging to 55 families. In S9, I found 78 species (73 species of seedlings and 71 species of saplings) belonging to 51 families. In S7, there were 77 species (67 species of seedlings and 72 species of saplings) belonging to 47 families, and in MCZ, there were also 77 species (58 species of seedlings and 68 species of saplings), which belonged to 45 families (Table A2, Appendix II). A total of 16 species are believed to be dispersed solely by the red-collared brown lemur, 13 of which are present in S9 and S7, and 10 in MCZ (Table A2, Appendix II). The two Sainte Luce fragments shared a large number of species, and their Sorenson's community similarity index was 0.941. The species overlap between each of the two Sainte Luce fragments and MCZ was lower, and Sorenson's indices were 0.614 in both cases. The two fragments in which the red-collared brown lemur is present (i.e., S9, and MCZ) were subjected to further analysis – a comparison of regeneration in lemur defecation locations and random locations. While the species similarity within defecation locations was high within each of the two examined categories (i.e., seedlings and saplings) in both fragments (Table A3, Appendix II), as well as within random locations, the Sorenson's index was much lower when defecation and random locations were compared. Finally, the species similarity of seedlings and saplings within each fragment was relatively high (Table A3, Appendix II).

Between-fragment differences in forest regeneration

1. *Total regeneration (all the found species)*

According to Wald Chi squares, the regeneration of seedlings is in a significant relationship with the interaction of the two main effects, and the main effects on their own (Table 2). GLM estimates show that regeneration is higher in the protected S9 fragment than in the unprotected S7 fragment (Median=2, IQR=16), and higher in MCZ than in S7, while there is no difference between S9 and MCZ (Tables 1 and 2). At the sapling level, Wald Chi squares show that the interaction of the main effects is not significant. Regeneration is not significantly related to the main effect of the forest fragment, but the number of adult trees has a significant effect on their regeneration (Table 2). According to the GLM estimates, there is no difference between S9 and S7, or S9 and MCZ in seedling regeneration, but there are more saplings in S7 than in MCZ (Tables 2 and 3, Figures 3a and 3b).

Table 2. A comparison of forest regeneration of seedlings and saplings in the three studied forest fragments (i.e., S9, S7 and MCZ) based on the Wald Chi squares. Significant relationships are presented in **bold**.

			Median	**IQR**	**Main effects**	**χ^2**	**df**	**p**
Total regeneration (i.e. all tree species)	Seedlings (< 22 cm)	S9	6	32	Forest fragment	28.098	2	**<0.001**
		S7	2	16	No. of adult trees	28.098	2	**<0.001**
		MCZ	1	18	Interaction	8.740	2	**0.013**
	Saplings (> 22 cm)	S9	2	12	Forest fragment	2.289	2	0.318
		S7	4	13	No. of adult trees	43.071	2	**<0.001**
		MCZ	1	6	Interaction	5.302	2	0.071
Regeneration of species dispersed by *E. collaris*	Seedlings (< 22 cm)	S9	23.5	40	Forest fragment	4.249	2	0.120
		S7	2	16	No. of adult trees	15.644	2	**<0.001**
		MCZ	1	7	Interaction	0.504	2	0.777
	Saplings (> 22 cm)	S9	8.50	17	Forest fragment	1.362	2	0.506
		S7	8	18	No. of adult trees	4.449	2	0.035
		MCZ	1	7	Interaction	3.267	2	0.195

Table 3. A comparison of forest regeneration between the three studied forest fragments (i.e., S9, S7, and MCZ), considering the seedlings and saplings belonging to all species. Significant relationships are presented in **bold**.

		Estimate	**SE**	**df**	**p**
Seedlings (< 22 cm)	S9 vs. S7	9.67	2.171	1	**<0.001**
	S9 vs. MCZ	2.86	2.533	1	0.259
	MCZ vs. S7	6.81	1.927	1	**<0.001**
Saplings (> 22 cm)	S9 vs. S7	-1.01	1.089	1	0.355
	S9 vs. MCZ	1.64	0.912	1	0.072
	MCZ vs. S7	-2.65	0.990	1	**0.007**

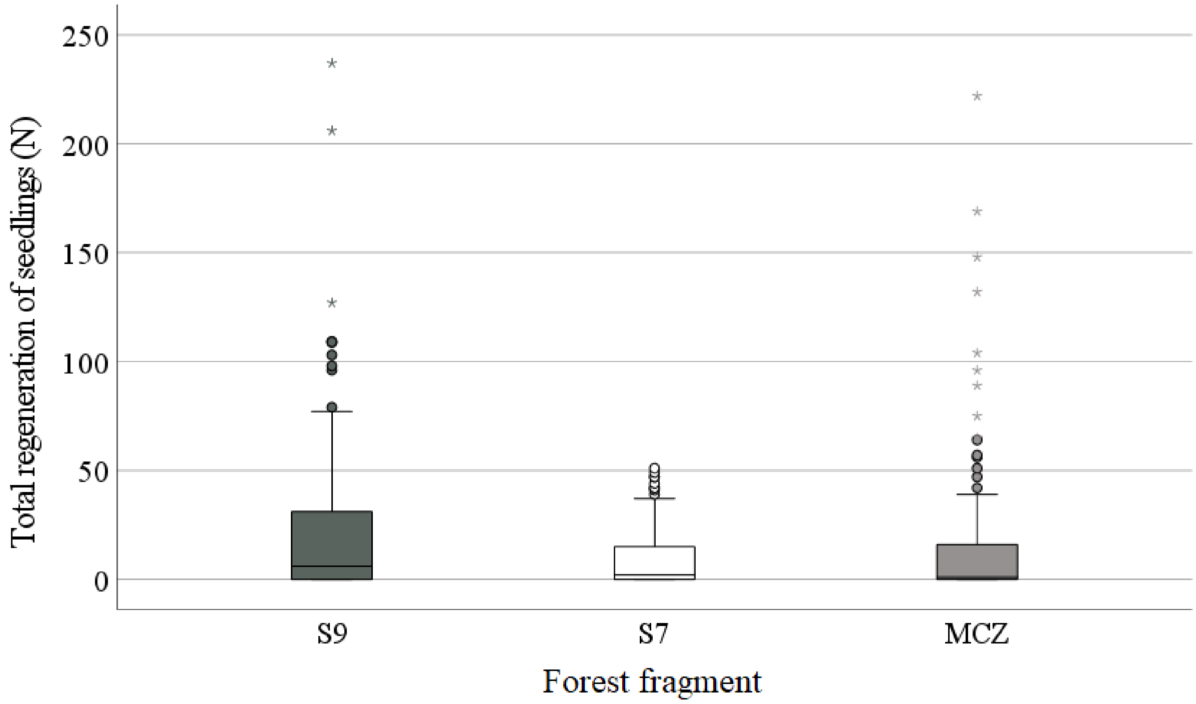


Figure 3a. A comparison of the numbers of seedlings found in each of the three forest fragments.

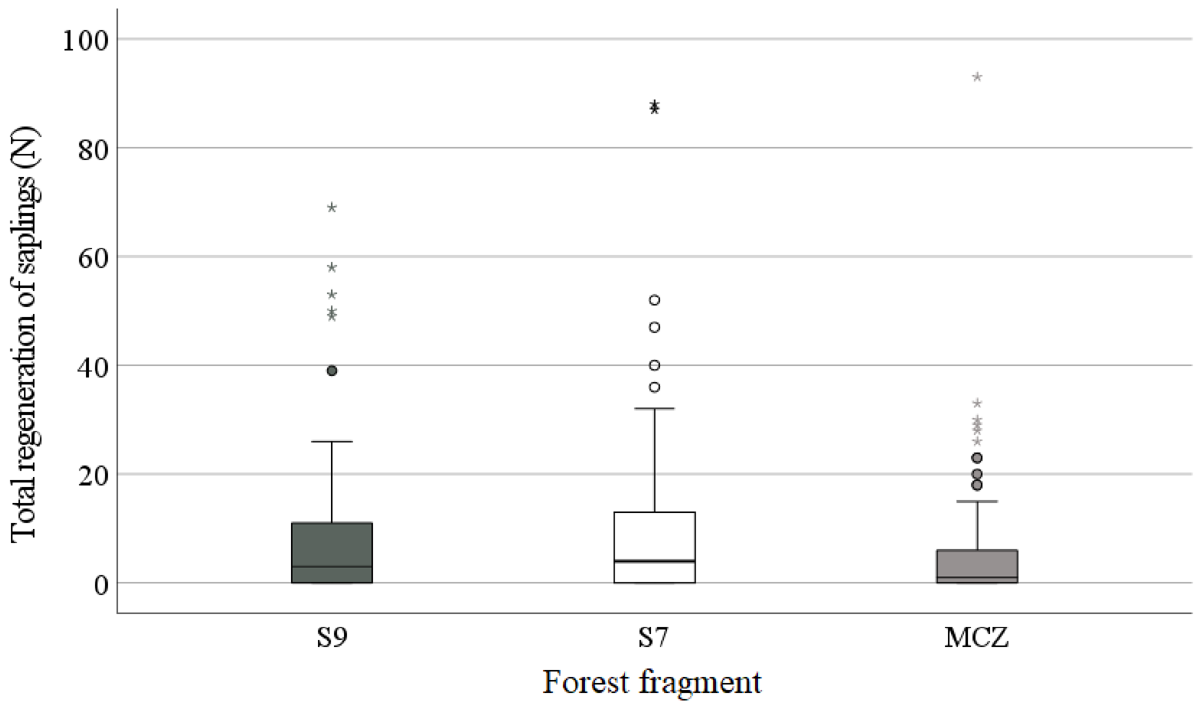


Figure 3b. A comparison of the numbers of saplings found in each of the three forest fragments.

2. *Species dispersed by the red-collared brown lemur (Eulemur collaris)*

When only the seedlings of species dispersed by the red-collared brown lemur are considered, Wald Chi squares show that that the interaction of the two main effects is not significant. The main effect of forest fragment is not significant, but the effect of the number of adult trees of the same species is (Table 2). According to the GLM estimates, the regeneration of seedlings is higher in S9 than in S7, but there is no difference between S9 and MCZ, or MCZ and S7 (Tables 2 and 4, Figure 4a). Similarly, at the sapling level, Wald Chi squares show that the interaction of the two main effects is non-significant. The effect of forest fragment is not significant, while the effect of the number of adult trees is. GLM estimates show there is no difference between S9 and S7 or MCZ, or between MCZ and S7 (Tables 2 and 4, Figure 4b). The list of regenerating species dispersed by the red-collared brown lemur is in Table A4 (Appendix II).

Table 4. A comparison of forest regeneration between the three studied forest fragments (i.e., S9, S7, and MCZ), considering the seedlings and saplings of species dispersed by the red-collared brown lemur (*Eulemur collaris*). Significant relationships are presented in **bold**.

		Estimate	**SE**	**df**	**p**
Seedlings	S9 vs. S7	19.68	8.872	1	**0.027**
(< 22 cm)	S9 vs.	13.57	9.554	1	0.155
	MCZ vs.	6.11	5.832	1	0.295
Saplings	S9 vs. S7	4.36	4.258	1	0.306
(> 22 cm)	S9 vs.	3.29	4.408	1	0.456
	MCZ vs.	1.07	3.588	1	0.766

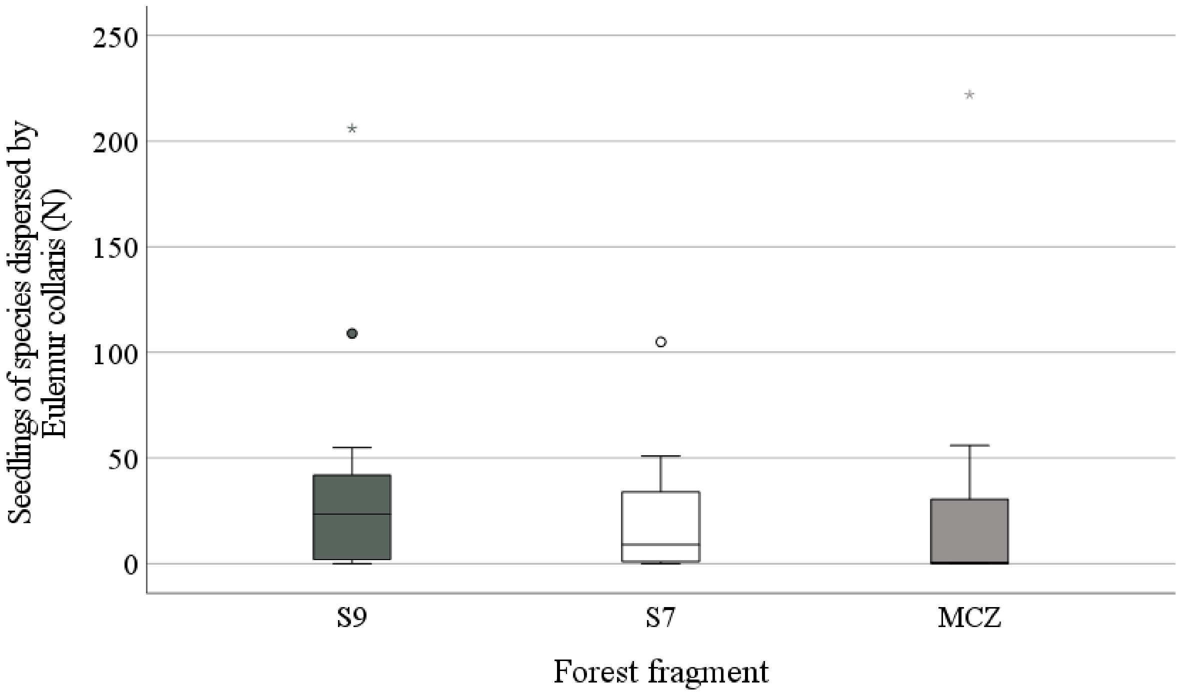


Figure 4a. A comparison of the numbers of seedlings of species dispersed by the red-collared brown lemur (*Eulemur collaris*) found in each of the three studied forest fragments.

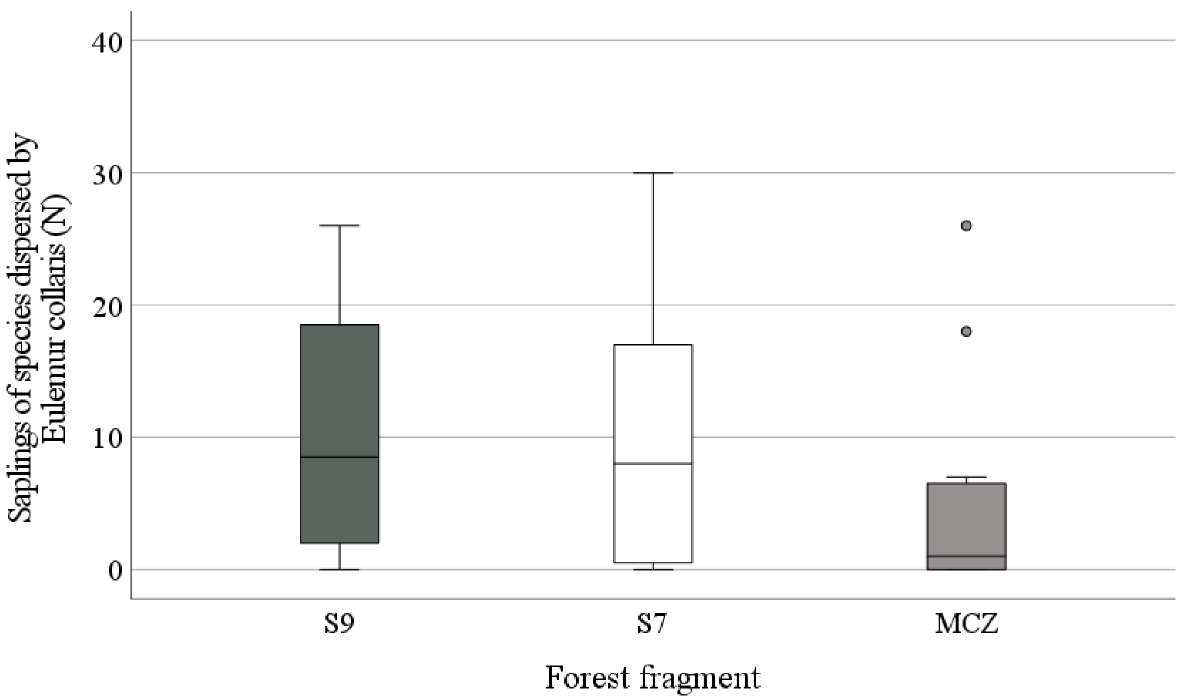


Figure 4b. A comparison of the numbers of saplings of species dispersed by the red-collared brown lemur (*Eulemur collaris*) found in each of the three studied forest fragments.

Additional comparisons: forest regeneration in lemur-defecation locations vs. random locations

1. Total regeneration

When total regeneration of seedlings in lemur defecation locations is considered, Wald Chi squares indicate that the interaction of the two main effects is non-significant. The main effect of forest fragment is not significant, while the main effect of the number of the adult trees is. GLM estimates show that regeneration does not differ between the fragments, as the interaction of the two main effects is not significant. The main effect of forest fragment is not significant, but the main effect of the number of adult trees of the same species has a significant effect (Tables 4 and 5). If only the seedlings regenerating in random locations are considered, Wald Chi squares show that the interaction of the two main effects is not significant. While the main effect of forest fragment is also not significant, the main effect of the number of adult trees of the same species has a significant positive effect on seedling regeneration. GLM estimates also indicate that the interaction of the two main effects is not significant. The main effect of forest fragment is also not significant, but the main effect of the number of adult trees of the same species is significant (Tables 4 and 5).

In terms of total regeneration of saplings in lemur defecation locations, Wald Chi squares show that the interaction of the two main effects is not significant. The main effect of forest fragment is also not significant, while the main effect of the number of adult trees of the same species has a significant positive effect. According to the GLM estimates, the interaction of the two main effects is not significant. The main effect of forest fragment is not significant either, but the main effect of the number of adult trees of the same species is (Tables 4 and 5). Finally, when the total regeneration of saplings in randomly selected locations is considered, Wald Chi squares indicate that the interaction of the two main effects is significant. The main effect of forest fragment is not significant, while the main effect of the number of adult trees of the same species is significant. GLM estimates show that the interaction of the two main effects is significant, and the presence of adult trees has a stronger effect in Mandena (MCZ). Neither of the main effects are significant (Tables 5 and 6).

Table 5. A comparison of forest regeneration of all seedlings and saplings in defecation locations and randomly selected locations within two forest fragments inhabited by *Eulemur collaris* (S9, MCZ) based on the Wald Chi squares. Significant relationships are presented in **bold**.

			Median	**IQR**	**Main effect**	**χ^2**	**df**	**p**
Seedlings (< 22 cm)	DL	S9	2	14	Forest fragment	0.021	1	0.885
					No. of adult trees	35.869	1	**<0.001**
		MCZ	0	7	Interaction	3.826	1	0.05
	RL	S9	3	15	Forest fragment	0.184	1	0.668
					No. of adult trees	30.195	1	**<0.001**
		MCZ	0	5	Interaction	1.762	1	0.184
Saplings (> 22 cm)	DL	S9	1	6	Forest fragment	0.122	1	0.727
					No. of adult trees	29.100	1	**<0.001**
		MCZ	0	3	Interaction	3.690	1	0.055
	RL	S9	1	6	Forest fragment	0.002	1	0.965
					No. of adult trees	14.028	1	**<0.001**
		MCZ	0	4	Interaction	6.140	1	**0.013**

* DL = defecation locations; RL = random locations.

Table 6. A comparison of total forest regeneration between two types of locations (defecation, random) in two forest fragments (S9, MCZ) based on the GLM. Significant relationships are presented in **bold**.

			Fragment			**Adult tree species**			**Fragment * Adult**		
			B	**SE**	**p**	**B**	**SE**	**p**	**B**	**SE**	**p**
Seedlings (< 22 cm)	**DL**	Intercept	1.878	0.133	**<0.00**	0.123	0.45	**0.00**			
		MCZ, S9	0.026	0.182	0.885				0.119	0.60	0.050
	RL	Intercept	1.916	0.129	**<0.00**	0.122	0.04	**0.00**			
		MCZ, S9	-0.077	0.180	0.668				0.077	0.05	0.184
Saplings (> 22 cm)	**DL**	Intercept	0.813	0.141	**<0.00**	0.104	0.04	**0.01**			
		MCZ, S9	0.068	0.196	0.727				0.115	0.06	0.055
	RL	Intercept	0.887	0.140	**<0.00**	0.038	0.04	0.39			
		MCZ, S9	-0.009	0.195	0.965				0.149	0.06	**0.013**

* DL = defecation locations; RL = random locations.

2. Regeneration of species dispersed by the red-collared brown lemur

According to Wald Chi squares, the interaction of the two main effects is not significant. The forest fragment does not have a significant effect on the regeneration of species dispersed by the red-collared brown lemur found in defecation locations at the seedling level, but the main effect of the number of adult trees of the same species does. GLM estimates show that neither the interaction of the two main effects nor the main effects on their own are significant (Tables 6 and 7). If the seedlings regenerating in the random locations are considered, Wald Chi squares show that the interaction of the two main effects is not significant. The same is true of the main effect of forest fragment, but the main effect of the number of adult trees of the same species is significant. GLM estimates show that the interaction of the two main effects is not significant. The main effect of forest fragment is not significant, and the two forest fragments do not differ in this aspect of their regeneration. On the other hand, GLM estimates show that the number of adult trees of the same species has a significant positive effect (Tables 7 and 8).

If saplings of species dispersed by the red-collared brown lemur in its defecation locations are taken into consideration, Wald Chi squares show that the interaction of the two main effects is significant. However, the main effects are not significant. GLM estimates show that the interaction of the two main effects is significant, while the main effects are not. This suggests that the number of adult trees of the same species only has an effect on the regeneration of saplings in lemur defecation locations in Mandena (MCZ) (Tables 6 and 7). Finally, when sapling regeneration in the random locations is considered, Wald Chi squares indicate that the interaction of the main effects is not significant, and neither are the main effects. The same is indicated by the GLM estimates, showing that the two forest fragments do not differ (Tables 7 and 8).

Table 7. A comparison of forest regeneration of seedlings and saplings of species dispersed by the red-collared brown lemur (*Eulemur collaris)* in defecation locations and randomly selected locations within two forest fragments inhabited by this lemur (S9, MCZ) based on the Wald Chi squares. Significant relationships are presented in **bold**.

			Median	**IQR**	**Main effect**	**χ^2**	**df**	**p**
Seedlings (< 22 cm)	DL	S9	8	16	Forest fragment	1.118	1	0.290
					No. of adult trees	11.248	1	**0.001**
		MCZ	0	17	Interaction	0.398	1	0.528
	RL	S9	13	32	Forest fragment	3.207	1	0.073
					No. of adult trees	8.784	1	**0.003**
		MCZ	0	17	Interaction	2.518	1	0.113
Saplings (> 22 cm)	DL	S9	3	9	Forest fragment	1.927	1	0.165
					No. of adult trees	0.931	1	0.335
		MCZ	0	4	Interaction	5.771	1	**0.016**
	RL	S9	7.50	11	Forest fragment	0.110	1	0.740
					No. of adult trees	1.176	1	0.184
		MCZ	1	5	Interaction	0.652	1	0.419

* DL = defecation locations; RL = random locations.

Table 8. A comparison of forest regeneration of species dispersed by the red-collared brown lemur (*Eulemur collaris*), between defecation and random locations, in two protected forest fragments (S9, MCZ) based on the GLM. Significant relationships are presented in **bold**.

			Fragment			Adult tree species			Fragment * Adult		
			B	**SE**	**p**	**B**	**SE**	**p**	**B**	**SE**	**p**
Seedlings (< 22 cm)	**DL**	Intercept	1.364	0.414	**0.001**	0.251	0.13	0.06			
		MCZ, S9	0.573	0.542	0.290				0.116	0.18	0.528
	RL	Intercept	1.268	0.657	**0.025**	0.579	0.22	**0.00**			
		MCZ, S9	1.189	0.664	0.073				-0.404	0.25	0.113
Saplings (> 22 cm)	**DL**	Intercept	1.989	0.388	**<0.00**	-	0.13	0.35			
		MCZ, S9	-0.725	0.523	0.165				0.413	0.17	**0.016**
	RL	Intercept	1.370	0.398	**0.001**	0.046	0.12	0.72			
		MCZ, S9	0.177	0.533	0.740				0.143	0.17	0.419

* DL = defecation locations; RL = random locations.

Discussion

The findings of this study show that forest density and canopy closure differ between the forest fragments inhabited by the red-collared brown lemurs and that from which this lemur species has been extirpated. The canopy is more closed, and the tree density lower in the latter. The presence of red-collared brown lemurs was related to higher regeneration of seedlings, but this relationship did not persist to the sapling level. Results indicate the importance of adult conspecifics at both levels of regeneration. In the two forest fragments in which the red-collared brown lemur is present, the regeneration in their defecation locations did not significantly differ from that in the randomly selected locations.

Microhabitat characteristics

All three fragments included in the study have similar composition of botanical species. This is especially true of the two fragments located in the same area (i.e., S9 and S7 in Sainte Luce), which is in accordance with previous findings (Rabentoandro et al., 2007). Before considering the implications of the red-collared brown lemur's presence on the regeneration of tree species of which this lemur is believed to be the sole disperser, it is necessary to recognise the differences in microhabitat parameters between the three fragments, which are likely to affect forest regeneration. Based on the results of this study, canopy closure is significantly more open in the forest fragment from which this lemur has been extirpated (i.e., S7) than in the two fragments in which it still occurs. However, it is not easy to relate this finding to the red-collared brown lemur's historic presence in this fragment. Some local people's reports state that this species has been extirpated in the 1960s. These differences might also be a result of the differing anthropogenic pressures on these forests. The two protected fragments (S9 and MCZ) have historically been used intensely by the local human communities for extraction of construction material, fuelwood, medicinal plants, and other purposes. Since becoming protected (in 2005, and 2002, respectively), the human pressures on these forests have declined, while the opposite has been the case for the S7 fragment (Chapter 8). An (ongoing) increase in adult tree extraction has opened up the canopy in S7 and concomitantly reduced forest density.

Tree density is not only a useful proxy of human forest use, but is also a factor expected to impact forest regeneration. Tree density often increases because of canopy gaps, created by the harvested trees. This is likely to facilitate seedling germination, establishment, and growth (Hartshorn, 1978; Denslow, 1995), increase tree density (Denslow, 1995), and reduce the dominance of more competitive species (Connell, 1978; Huston, 1979), thus promoting species diversity. As a result, over time, timber extractions (and other events that result in canopy opening, such as tree fall) are likely to lead to higher tree density. As S9 and MCZ have been heavily logged in the past, their current tree density is now higher than that of S7, as would be expected. Moreover, MCZ was more degraded than S9 prior to becoming protected, so it is not surprising that it is now significantly denser than S9, which has been regarded as the more intact of the two even before forest protection measures were in place (Rabevohitra et al., 1996; Dumetz, 1999; Bollen & Donati, 2006). There are other factors that determine forest regeneration patterns, such as the intensity and frequency of forest disturbance, and the biology of species present in a particular area. More specifically, of importance are the species' life history traits, physiology, modes of regeneration (Kennard et al., 2002), position within the canopy gap, substrate type and conditions such as moisture (Wright et al., 1998), and seed dispersal types. Species which rely on more seed dispersers are likely to be more resilient to changes in the structure of seed dispersers' community (i.e., presence, or abundance of particular frugivore species). Contrarily, those dispersed exclusively by one could decrease in abundance over time if their disperser is extirpated.

Forest regeneration

When the total regeneration is considered at the seedling level, the regeneration is higher in the S9 protected fragment (in which the red-collared brown lemur occurs) than in the S7 fragment (from which the species has been extirpated). It is expected that the presence of red-collared brown lemurs contributes to regeneration of other species, for which they are not the only disperser. This difference could also be related to the forest composition (i.e., the numbers of adult trees belonging to specific species), and tree density, which is higher in S9 and MCZ than in S7. More adult trees should, regardless of their species' dispersal system, result in higher numbers of seedlings of the same species. This is because some of the seeds are expected to germinate beneath their maternal plants after the fruit falls from them. However, the likelihood of their successful establishment is lower, according to the Janzen-Connell hypothesis (Janzen, 1970; Connell, 1971), so as expected, when the saplings (i.e., the established regeneration) are considered, the difference between S9 and S7 is no longer significant. This suggests similar seedling survival rates in the two fragments, while the difference between MCZ and S7 is reversed, suggesting higher seedling survival in S7. A possible explanation could be in the previously described difference of the microhabitats between the fragments, namely the canopy openness and tree density. Open canopy and low tree density are the conditions which are typically more favourable for regenerating seedlings.

When the regeneration of species dispersed only by the red-collared brown lemur is regarded, there are on average significantly more seedlings in S9 than in S7 (i.e., the fragment from which this lemur has been extirpated), while S9 and MCZ do not differ in this aspect. The difference between S9 and S7 does not persist into the sapling stage of regeneration, suggesting similar establishment rates in all three fragments. This lack of difference could be related to the presence of adult trees, as some regeneration is a result of seedlings germinating from the fruits that have fallen close to their maternal plants. It is important to note that many of the tree species in the littoral forest do not need red-collared brown lemurs to disperse their seeds, and several do not rely on frugivore dispersal at all, but are instead autochorous, or self-dispersing. Moreover, a number of other factors are likely to affect which seeds are dispersed, to which distance and in which direction, as well as whether or not they arrive in suitable microhabitats (Howe & Miriti, 2004; Côrtes & Uriarte, 2013; Morales et al., 2013). Even the large-seeded plants can disperse to some extent with help of abiotic factors, such as wind (Forget et al., 2007). Finally, the environmental context and seeds' interaction with it will influence which seeds are successful in germination and establishment.

Parent tree species proximity and abundance are well-known correlates of seedling emergence and survival (Ribbens et al., 1994), with some studies even showing that the intensity of seedling recruitment is higher closer to the parent tree, and diminishes as the distance from the parent tree increases (Hubbell, 1980; Augspurger & Kitajima, 1992). This type of development can be a result of pathogen activity, whose increased density in aggregated seed clumps away from the parent tree can decrease seedling survival (Beckman et al., 2012). In other cases, the proximity of parent plants may even have a negative effect on the number of saplings (Ganzhorn et al., 1999). However, that is not the case in this study, where the presence of adult trees is a strong predictor of the presence of more seedlings, and saplings of the same species. The reason for this increased survival of the regenerating plants so close to their parent (i.e., maternal) trees could be explained especially well in the case of the species dispersed by the red-collared brown lemurs, which are all large-seeded plants (i.e., plants with seeds of ≥ 12.5 mm length; Bollen et al., 2004; Bollen & Donati, 2006). The seedlings of large-seeded plants are more likely to survive in areas of high post-dispersal seed density, with high levels of insect and pathogen predation (attracted to or supported by their parent plants).At the same time, smaller seeds are more likely to be dispersed by frugivores (Howe & Richter, 1982; Stamp & Lucas, 1983; Howe, 1989; Terborgh et al., 1993). This suggests a trade-off between seed size and dispersal type. An experimental set up of long-term germination trials of these large-seeded plant species growing in the littoral forests would provide the most ecologically valid conclusion on the extent to which this evolutionary trade off could explain the strong relationship between adult trees' presence and the high (established) regeneration of the same species in their proximity. However, this competitive advantage of large-seeded plants can be diminished as a result of a decrease in the large-bodied seed dispersers' abundance (Ruxton & Schaefer, 2012).

A comparison of total regeneration (i.e., regeneration of all tree species) between defecation locations and randomly chosen locations within the same fragments showed a significant effect of forest fragment at both seedling and sapling levels, but S9 and MCZ did not significantly differ in either. The same was true when only the regeneration of species dispersed by the red-collared brown lemur was considered. The effect of presence of adult trees of the same species was significant when at the seedling level, but there was no difference between the two fragments. At the sapling level, number of adult trees was only significant in Mandena. Similar numbers of seedlings in the two fragments do not reflect the higher number of red-collared brown lemurs in S9 than in MCZ (Bollen & Donati, 2006; Donati et al., 2007), which I predicted would lead to higher seedling regeneration in S9, where this lemur is more abundant. However, the lower abundance of red-collared brown lemurs in Mandena seems to be compensated at the sapling level by the significant effect of the presence of adult trees. While the effect of forest fragment was again significant at both the seedling and the sapling level when total regeneration in the randomly selected locations was considered, S9 and MCZ showed no significant difference. However, it is important to state that my predictions were based on population densities estimated more than a decade ago (Bollen et al., 2006; Donati et al., 2007). While population censuses have been conducted yearly in MCZ since 2001 (by TBSE), and in Sainte Luce in 2012, they have not been published. It is possible that current population densities are higher in both areas than the last available reports suggest. However, due to the difference in size of the forest fragment, it is likely that there are still more brown lemurs in Sainte Luce (specifically, S9 fragment in which this study was conducted) than in MCZ. More recent population size estimates are necessary to validate the explanation of these findings. The effect of presence of adult trees was significant at the seedling level, but the difference did not persist to the level of saplings. This suggests that outside the two fragments might be regenerating similarly.

Due to the challenges brought about by introduced and invasive tree species, a change in the human land use, and the climate change, seed dispersal is becoming an increasingly important aspect of conservation of plant species (Ruxton & Schaefer, 2012). This stage of plants' life-history is the only one in which plants are mobile, and therefore of crucial importance for the future distribution of plant species. The large majority of tropical plants rely on frugivorous vertebrates for their seed dispersal (McKey, 1975; Howe & Smallwood, 1982; Janson, 1983; Jordano, 1992; 2000).They are likely to be affected by the anthropogenic pressures, due to the effects these pressures have on the animal populations. Hunting, loss of food sources and breeding sites for vertebrate dispersers can leave the large-seeded plants particularly vulnerable as their fruits are typically dispersed by fewer animals, which are often also larger in size (Wright et al., 2007). Larger-bodied animals are more likely to become the targets of hunters (Corlett, 2007; Benítez-López et al., 2017), while also being more vulnerable to forest fragmentation (Terborgh, 2013). Sainte Luce and Mandena can both be described as heavily fragmented littoral forests, thus representing a challenging environment for the comparably large lemur species (i.e., red-collared brown lemur) to inhabit, survive, and in which to disperse the seeds of the fruiting plants in their diet. Larger-bodied animals tend to have lower population densities, which further increases their extinction risk. Decline in their population sizes can decrease their dispersal effectiveness even before they are extirpated or extinct (McConkey & O'Farrill, 2016), jeopardising the conservation of plant species they disperse. Species loss can lead to defaunation or empty forest syndromes (Redford, 1992), in which the species diversity declines over time, due to the restricted regeneration brought about by dispersal limitations.

Besides impacting plant populations and community composition, the loss of large-bodied seed dispersers can diminish ecosystems' resilience to climate variability and jeopardise one of the most valuable ecosystem services – its carbon storage properties (Poulsen et al., 2013; Dirzo et al., 2014; Bello et al., 2015; Peres et al., 2016; Osuri et al., 2016; Culot et al., 2017). Carbon storage loss can vary between 2 % to 12 %, depending on the habitat and the defaunation scenario (Osuri et al., 2016; Granados et al., 2017; Chanthorn et al., 2019). This can happen through an increased plant species competition, resulting in clustered conspecific distributions, which enhances the risk of predation and pathogens (Janzen, 1970; Connell, 1971). There is also an associated expectation of a decrease in these plants' ability to disperse and germinate in optimal environmental conditions, and travel across the landscape and colonise new areas, away from the parent trees. Differences in the ecological strategies between plants dispersed by animals and other dispersal vectors are likely to create disparities, as the plants dispersed by the lost frugivores will not be able to compensate fully for this loss.

When it comes to the regeneration of the littoral forests of southeastern Madagascar, the loss of red-collared brown lemur and its ecological functions might not be possible to compensate by other species of frugivorous seed dispersers (i.e., other lemur species, birds, and bats). This is primarily due to their body sizes, which are too small to process large-seeded plants' fruit without destroying it. Conservation measures should therefore be taken to ensure that the species remains present, and its populations viable, in the protected habitats which it currently inhabits, to keep this habitat ecologically functional (McConkey et al., 2012). Species reintroductions could help restore the functionality and species diversity of the S7 fragment (which this lemur no longer inhabits). However, this is not a valid option in this case: this forest remains under heavy anthropogenic pressure (Chapters 7 and 8), which became even stronger since forest protection measures restricted resource extraction from the forest fragments closer to human settlements (i.e., S9 and S8). This is a situation which is not expected to change under the current forest management plan.

Conclusion

The findings of this study show that canopy is more closed, and forest less dense in the fragments from which the red-collared brown lemurs have been extirpated. While the adult tree species diversity was the highest in MCZ, the numbers of regenerating tree species found in each of the three fragments were similar. The presence of red-collared brown lemurs is related to the regeneration at the seedling level, but the relationship does not persist to the sapling level. The presence of adult trees of the same species and forest density likely play important roles. When only the regeneration of the two fragments in which red-collared brown lemurs are present is considered, there are no differences between defecation- and randomly selected locations. While this may suggest that even lower population sizes of this lemur might be enough to maintain their seed dispersal effectiveness, the differences in the population sizes between the two areas should be confirmed by more recent population census data. When examining the effects of frugivore species extirpation, it is necessary to study the full picture, instead of focusing only on the fruit-frugivore interactions. Anthropogenic pressures and forest management are likely to play significant roles in forest regeneration, potentially moderating these relationships through hunting, logging, cattle grazing, and other forms of forest use.

CHAPTER 6

Local ecological knowledge about red-collared brown lemur (*Eulemur collaris*) among the people of Sainte Luce and Mandena, southeastern Madagascar

Introduction

When the relationship between humans and biodiversity is mentioned, it is most often done in the context of the biodiversity loss caused by human modifications of ecosystems. Biodiversity has, however, always been an essential part of human societies and culture, many aspects of which are built on - and because of - the natural resources used for everything from subsistence to construction materials, fuel or medicine (Díaz et al., 2006). Similarly, the interactions of humans and nonhuman animals (from here on "animals") are among the most fundamental aspects of human societies, with animals being one of the central characters of the human world (Manning & Serpell, 2002).

Ethnozoology is a discipline within ethnobiology that investigates knowledge about animals that human societies have accumulated, as well as animals' significance and use (Alves, 2012). Animals are an integral part of almost all cultures' folklore, which often influence attitudes towards them (Alves, 2012). In some cases, beliefs about wildlife can protect them (Colding & Folke, 1997). Taboos concerning primates which prevent people harming them can be found around Africa and Asia (e.g., Saj et al., 2006; Riley, 2010; Zinner et al., 2013; Nijman & Nekaris, 2014). Similar taboos surround other wildlife, from civets to big cats, snakes and elephants (Jimoh et al., 2012). A way to understand these very often locally specific ways of perceiving and interacting with wildlife species is through studying local ecological knowledge (LEK) of the indigenous communities. It comprises "knowledge, practices, and beliefs regarding ecological relationships that are gained through extensive personal observation of and interaction with local ecosystems, and shared among local resource users " (Charnley et al., 2007, p 15). These are sometimes also referred to as traditional ecological knowledge (TEK), indigenous knowledge (IEK) or traditional forest-related knowledge (TFRK), suggesting a terminological ambiguity (see Joa et al., 2018 for a review of terms and definitions). However, LEK is often understood to signify local-specific knowledge, which may eventually become TEK, or "a cumulative body of knowledge, practice, and belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment" (Berkes et al., 2000, p 1252). Due to it being specific to the residents of a particular area, LEK can only be understood within that particular region (Turvey et al., 2014).

LEK is considered a valuable source of information (Charnley et al., 2007; Junqueira et al., 2011) that can be especially useful for studying rare and elusive wildlife. It is also up to 100 times cheaper than traditional methods of presence sampling, as well as timesaving (Anadón et al., 2009). It can help determine species' conservation status through access to information regarding their distribution, abundance, and ecology (Newton et al., 2008; Nash et al., 2016), as well as the threats that the wildlife species face. The local human population will often differ in the extent of their experience with the wildlife, with the people who spend more time in the forest or hunt a particular species often demonstrating better ecological knowledge (Boud et al., 2013; Kolb, 2014; Miard et al., 2017). Nevertheless, there is still value in including a broader and more diverse sample than limiting it to hunters alone. This is especially true when it comes to species inhabiting the anthropogenically altered areas, where the majority of people are most likely to have encountered them, regardless of a person's occupation. LEK is generally tied to a specific resource and will be relevant to sustainable use of said resource (Gadgil et al., 1993). It is important to note, however, that not all indigenous practices are sustainable, and some that have been in the past, could have become unsustainable or maladaptive over time. Similarly, when traditional ways of using a resource are seemingly restrained, it does not necessarily reflect a long-term goal of resource conservation (Gadgil & Berkes, 1991). LEK studies can, however, engage the local population and encourage its members to protect their natural resources (Silvertown, 2009; Luzar et al*.,* 2011).

The value of LEK to conservation has been gaining recognition since the 1980s (e.g., Norgaard, 1984; Ruddle & Johannes, 1985; McNeely & Pitt, 1985; Freeman & Carbyn, 1988), which has substantially increased since the late 2000s (Huntington, 2000; Gilchrist et al., 2005; Charnley et al., 2007; Anadón et al., 2009; Joa et al., 2018). Regardless, many western scientists remain unwilling to use indigenous knowledge as data (Mackinson & Nottesad, 1998; Schmuck-Widmann, 2001). There still remains a geographical bias, with the majority of studies having been conducted in Asia, especially India and China (Joa et al., 2018). Furthermore, although LEK is site-specific, very few studies have included a comparison between sites.

Stronger reliance on western knowledge and modernisation can lead to an abandonment of indigenous knowledge and strategies by the indigenous communities themselves (Mercer et al., 2007). LEK is dynamic and likely to (with time) reflect change in the ecosystems (Joa et al., 2018), which is why it is currently at risk of a rapid loss due to a loss of biodiversity, species extirpation, and a change in indigenous peoples' livelihoods (Kai et al., 2014). Changes in social, economic and political systems also affect LEK (Barbosa, 1996; Gilmour, 1990; Shepherd, 1992; Wiersum, 1997). As a species becomes rare, so the knowledge and culture associated with it declines (Grenier, 1998), resulting in a decreased "biocultural diversity" (Loh & Harmon, 2005). This change is likely to manifest in a decreased environmental awareness, and reduced sustainability of resource use at the local level (Cullen et al., 2007), which could make conservation efforts progressively more difficult (Papworth et al., 2009). Consequently, a sense of urgency to study and document LEK has strengthened with time.

Madagascar is brimming with taboos (*fady*) preventing people from harming wildlife (e.g., Wilson et al., 1989b; Vargas et al., 2002; Jones et al. 2008). However, some taboos lead to wildlife avoidance due to their perception as harmful. An encounter with an aye-aye (*Daubentonia madagascariensis*) can lead to entire villages being burned down or abandoned (Glaw et al., 2008). Radiated tortoises are in some areas perceived as dirty, which prohibits their use (Lingard et al., 2003). In this chapter, I focus on local people's attitudes towards and ecological knowledge about red-collared brown lemur (*Eulemur collaris*). This species of predominantly frugivorous lemur (Donati et al., 2007), classified as Endangered by the IUCN Red List (Donati et al., 2020), inhabits the inland lowland semi-montane humid and littoral forests of southeastern Madagascar, where it is considered to be of high importance as a seed disperser of large-seeded plants (Bollen et al., 2004; Sato, 2012) - a role of increasing importance with the progressively more fragmented habitat. It has been recorded feeding on over 100 species of native trees and vines (Donati, 2002). Typically living in multi-male multi-female groups (Donati et al., 2007), this medium-sized lemur has another unusual characteristic - its activity pattern. While most primates tend to be either diurnal or nocturnal, the red-collared brown lemur is, much like other members of *Eulemur* genus, cathemeral. This means that its activity is distributed across the 24-hour cycle (Tattersal, 1987). This lemur is more abundant in Sainte Luce than in Mandena (Bollen & Donati, 2006; Donati et al., 2007), but little is known about local people's ecological knowledge about this species.

Anosy region is the most isolated and economically poorest region of Madagascar, with difficult living conditions and low agricultural productivity (Vincelette et al., 2007). As a result, many members of the local population rely on the forest resources for their sustenance and income (Ingram et al., 2005; Razafindraibe et al., 2013). The littoral forest fragments of Mandena and Sainte Luce are among the most threatened ecosystems in Madagascar (Bollen & Donati, 2005). This is largely due to unsustainable human use over the past decades (Dumetz, 1999; QMM, 2001). Prior to forest protection, Sainte Luce has been considered the most intact littoral forest in Madagascar (Bollen & Donati, 2006; Rabevohitra et al., 1996; Dumetz, 1999) while Mandena has been viewed as more degraded than Sainte Luce (Rabenantoandro et al., 2007). Additionally, traditional livelihoods of the two areas are different. While Sainte Luce is a marine fishing community (SEED Madagascar, unpublished survey; Holloway & Short, 2014), Mandena community largely depends on crop cultivation and wood extraction (Ingram et al., 2005b; Evers & Seagle, 2012; Kraemer, 2012).

Since the protected areas were established in Mandena and Sainte Luce, in 2002 and 2005 respectively, local people have experienced considerable restrictions on their use of forest resources. How this change has reflected in the way they perceive and interact with the local wildlife has not yet been investigated. In this study, I address the following questions:

1. Is there a difference between people's capacity to recognise the red-collared brown lemur in Sainte Luce and Mandena?
2. Is there a difference between the two communities in what they know about this lemur's ecology (i.e., diet, activity pattern)?
3. Do the two communities differ in their attitudes towards this lemur? What arguments are at the basis of their positive or negative attitudes towards this species?
4. What are the practices involving this lemur (i.e., hunting)? Do the two communities differ in this respect?

Methods

Data collection

The data were collected between April and October 2018. Participants were selected using quota sampling (Newing, 2010) to ensure equal representations of women and men. My sample comprised 60 adults, ten from each village (Nash et al., 2016): three in the Sainte Luce area (i.e., Ambandrika (24°46'57.75" S, 47°10'23.99" E), Ampanasatomboky (24°46'48.4" S, 47°11'35.9" E), and Manafiafy (24°46'34.4" S, 47°11'53.5" E)), and three in the Mandena area (i.e., Ampasy Nahampoana (24°58'51.24" S, 46°58'53.73" E), Betaligny (24°59′28.2" S, 46°58′43.1" E), and Mangaiky (24°56′09.0" S, 46°59'20.1" E)). I used semi-structured interviews (Bernard, 2017), based on an interview guide prepared ahead of time (General Appendix). I collected qualitative data to gain a more refined examination of what constitutes ecological knowledge about red-collared brown lemurs locally, and how the practices surrounding this endangered species may have changed with the new forest management, and why. As hunting may be perceived as a sensitive subject, using this approach has allowed me to establish a rapport with the participants and make sure they feel comfortable and safe discussing this topic. All interviews were conducted in Malagasy with help of a local Antanosy translator (N=3).

To make sure that all questions were suited to the local people, I employed the help of my local translators. Before starting the data collection, we discussed the themes and questions, and I explained the kind of information I wanted to obtain. The contribution of my translators extended simply translating the questions, and included advice on how to ask them, in a culturally appropriate way. During data collection, the translators provided additional explanations to both me and the participants, as needed. This way, I hoped to transcend the role of a foreigner asking questions that may or may not be relevant or clear. Despite being respectful, I was aware of being an outsider in their community. My positionality might have led the participants to subconsciously equate me to other foreigners of similar gender, age, race or cultural background, which they might have previously encountered. Even in this research set up, it would have been impossible to completely remove their (or my) bias and expectations. I tried not to convey any specific expectations and ensure that participants knew that no matter what they said, it would remain confidential. The same was true of my translators, who signed an agreement not to reveal anything they learned during the interviews to any third parties. All answers were received with empathy and interest. While biases are normal and expected, this was my effort to minimise them. Ethical approval for the study was granted by the University Research Ethics Committee of Oxford Brookes University.

At the beginning of the interview, each participant was presented with a photograph of the male of the species and asked whether they recognise it (Nash et al., 2016; Silvano et al., 2006; Miard et al., 2017; Turvey et al., 2014; 2018) If they did not recognise it from the photograph, participants were asked whether they have ever heard of it, at which time the species' vernacular name was mentioned (i.e., *varika*) (Turvey et al., 2018). These two questions were joined in a compound variable of "species recognition", calculated as an average. If the participants recognised the species from the photograph, or had heard of it, I proceeded with the following questions:

1. What does this species eat?
2. When is this species active?
3. Have you hunted this species? If yes, when?
4. Have you ever consumed this species? If yes, when?
5. What do you think about this species?

As a measure of participants' knowledge of species' diet, participants were given a point if they were correct about the species' predominant diet type (i.e., frugivory). Additionally, I quantified all the forest species the participant listed. The two variables together were compounded into "diet knowledge", calculated as an average (I added the set of numbers and divided the sum by the total number of values in the set). Only the species I was able to identify, and which I was able to confirm are present in this lemur's diet were included in the analysis. Human crops were excluded because there are no published studies on which human crops these lemurs consume. For knowledge of species activity pattern, participants received 2 points if they answered that they are active during both the day and the night, 1 point if they only answered they were active in the day, and 0 points if they did not know the answer. The forest species listed by the participants were checked for accuracy against the lists in the previously published studies (Bollen, 2003; Ingram & Dawson, 2006; Ganzhorn et al., 2007b; Donati et al., 2007; 2011; 2020). Sainte Luce is slightly more represented in the literature than Mandena. However, as the number of species mentioned by my participants for which the scientific name was not available is very low in Mandena (i.e., one), I do not think this difference has affected my results. The "diet knowledge" and knowledge of activity pattern were later joined into a compound variable called "ecological knowledge", calculated as an average.

Lemur hunting is illegal throughout Madagascar (Jones et al., 2008; Rakotoarivelo et al., 2011). Killing a lemur is fined between US $5 and US $200, and/or between one month and two years in prison, but these are rarely implemented (Jenkins et al., 2011). Due to hunting being a sensitive topic, I wanted to approach this topic with care. After consulting with local collaborators and holding numerous informal conversations with members of the community, which took place outside of the research protocol, I realised that people were in general very open and willing to talk about their lemur hunting practices. To make sure participants remained comfortable throughout, I used neutral language and did not mention the legal aspects of practices relating to any kind of forest use. I also broadened our interview to include wider questions concerning the hunting of all wildlife, as well as keeping (production) animals in general, to divert the focus away from the lemurs. Participants who reported hunting or having hunted lemurs openly talked about it, and were happy to discuss the details of it, such as the hunting tools they used. Those who answered questions regarding hunting and eating this lemur were scored as 1 and 0, depending on whether or not the participant had engaged in either behaviour. For those who answered positively, a follow up answer of when was scored as 0 if it had happened a long time ago, before the area became protected; no participants reported still hunting or consuming lemurs at the time of the study. The attitudes towards red-collared brown lemur was scored as 1 if positive, and 0 if negative. Explanations of the reasons for positive or negative attitude were, based on participants' answers, subsequently divided into the following categories: tourist attraction, ecological importance, perceived character features, physical appearance, desire to keep as pets, good food, crop damage, and other.

Statistical analysis

I used nonparametric statistics (e.g., Turvey et al., 2014; Nash et al., 2016; Şen & Güngör, 2019; Sharma et al., 2020). Differences between the two communities in the recognition of this lemur were tested using a Chi square test (Nash et al., 2016; Sharma et al., 2020). A Mann-Whitney U test was used to test the difference between the two communities in knowledge of the red-collared brown lemur's diet type and activity pattern. The relationship between income source and other variables (e.g., knowledge, hunting, eating) was tested using a Kruskal-Wallis test (Sharma et al., 2020). Mann-Whitney U tests were used for *post hoc* comparisons where needed. A Chi-square test was used to test the gender differences in the main income source within each area, as well as in species recognition (Sharma et al., 2020). The relationship between main income source and age, and between species recognition and age was tested using Pearson's correlation coefficient. For between-community comparisons of the number of forest species or crops listed for the red-collared brown lemur's diet, I used Mann-Whitney U tests. I used a Mann-Whitney U test to test for gender differences in hunting, while a comparison of hunting between Sainte Luce and Mandena was done using a Chi square test (Turvey et al., 2014; Sharma et al., 2020). The significance of the relationship between age and LEK in each subsample was tested using a Spearman's Rho correlation coefficient. The relationship between LEK and attitudes in each sub-sample was also tested using Spearman's Rho correlation coefficients. Data were analysed in SPSS 26.0 (IBM, 2018). Additionally, I used Structural Equation Modelling (SEM) to analyse the relationship between local ecological knowledge about this lemur species and attitudes towards this species (criteria), and participants' gender, age, area of inhabitancy, whether they hunted this lemur, and whether they recognised it (predictors). This analysis was conducted in JASP Version 0.14.1 (JASP Team, 2020).

Results

<u>Study sample</u>

The sample comprised equal numbers of women and men (N=30 respectively) and was heterogeneous in terms of participants' age. There was a between-area difference in participants' occupation (i.e., main source of income): in Sainte Luce, the majority of women earned their income from selling woven mats and baskets made from sedge locally known as *mahampy* (*Lepironia mucronata*), and the majority of men were fishermen, while in Mandena, the majority of participants earned their income from selling crops (Table 1). The difference was statistically significant (χ^2=28.040, df=4, p<0.001). Gender differences were significant in both Sainte Luce (χ^2=19.506, df=4, p=0.001) and Mandena (χ^2=9.529, df=3, p=0.023), but age and occupation were not related among participants from either area (Sainte Luce: r=0.187, p=0.321, N=30; Mandena: r=-0.022, p=0.910, N=30).

Table 1. The main source of income of participants from Sainte Luce (N=30) and Mandena (N=30).

	Sainte Luce			**Mandena**		
	men	**women**	**total**	**men**	**women**	**total**
Weaving	0 %	100 %	**33.3 %**	0 %	100 %	**20.0 %**
Fishing	90.9 %	9.1 %	**36.7 %**	0 %	0 %	**0 %**
Agriculture	100 %	0 %	**3.3 %**	58.8 %	41.2 %	**56.7 %**
Timber collection	100 %	0 %	**3.3 %**	100 %	0 %	**10.0 %**
Other/no income	57.1 %	42.9 %	**23.3 %**	50 %	50 %	**13.3 %**

1. Species recognition

All participants from both areas had heard of the red-collared brown lemur and were able to recognise the species from its vernacular name (i.e., *varika*). 96.7 % of Sainte Luce participants and 90 % of Mandena participants were able to recognise the species from its photograph, but the difference between the two communities was not significant (χ^2=1.071. df=1, p=0.301, N=60). There were no gender differences in species recognition in Sainte Luce (χ^2=1.034, df=1, p=0.309, N=30) or Mandena (χ^2=0.370, df=1, p=0.543). There were also no age differences in either Sainte Luce (r=0.063, p=0.742, N=30) or Mandena (r=0.039, p=0.836, N=30).

2. Local ecological knowledge (LEK)

2. 1. Red-collared brown lemur diet

The majority of participants from both areas knew the red-collared brown lemur was a predominantly frugivorous species (Sainte Luce: 86.7 %, Mandena: 90 %), and the between-area difference was not significant (χ^2=0.162. df=1, p=0.688). There were no differences in the knowledge of this lemur's diet type between participants according to their main income sources (Sainte Luce: H=5.51, df=4, p=0.239; Mandena: H=7.72, df=3, p=0.052). However, participants who earn their income from wood extraction knew more than participants earning their income from sedge weaving (U=1.50, p=0.048, N=9), and those earning their income from agriculture (U=2.50, p=0.007, N=20). Participants from Sainte Luce listed significantly more forest species on which this lemur feeds than Mandena participants, mentioning a total of 31 forest species, compared to only six mentioned by the participants in Mandena. Of those species, only 21 (77.42 %) in Sainte Luce, and four (66.66 %) in Mandena have independently been confirmed in the diet of this lemur, and were therefore the only ones entered in the analysis (Table A1, Appendix III). The two subsamples also differed in average number of forest plants listed by participants (Table A1, Appendix III and Table 2) (U=229.50, p=0.001, N=60), as well as human crops (U=208.00, p<0.001, N=60).While Sainte Luce participants listed more forest species than Mandena participants, Mandena participants listed more human crops than Sainte Luce participants (Table 2 and Table A2, Appendix III).

Table 2. Average number of forest plants in the diet of the red-collared brown lemur (*Eulemur collaris*) listed by the participants in Sainte Luce (N=29) and in Mandena (N=29).

		Minimum	Maximum	Median	IQR
Forest species	Sainte Luce	0	8	3.5	2
	Mandena	0	7	2	2
Human crops	Sainte Luce	0	2	1	1
	Mandena	0	4	2	2

In Sainte Luce, participants with different main income sources did not differ in the number of forest species they listed (H=5.24, df=4, p=0.264), but there was a trend in Mandena (H=7.19, df=3, p=0.066). Participants who earned income from wood extraction showed a tendency to list more species than those earning income from agriculture (U=2.00, p=0.070, N=20). The relationship between income source and human crops mentioned by Sainte Luce participants was significant (H=9.93, p=0.042). Participants who earned their income from weaving sedge listing more crops than participants who earned their income from fishing (U=20.50, p=0.013, N=21). Main income source was also related to the number of human crops listed in the red-collared brown lemur's diet in Mandena (H=8.20, df=3, p=0.042). Participants who earned their livelihoods from collecting wood and selling timber listed more forest species than did participants whose main income source was agricultural products (U=2.00, p=0.007, N=20).

2. 2. Red-collared brown lemur activity pattern

Most participants in both Sainte Luce and Mandena stated that this species is active in the daytime (80.0 %). One participant explained “They are active in the day, but sometimes they also travel at night.” (man, 67, Ambandrika). While only a fifth of the Sainte Luce sample responded that this species was cathemeral, no one from Mandena gave this answer, but a fifth of the sample believed this lemur to be active at night. The between-area difference in this type of knowledge was statistically significant (U=288.00, p=0.001, N=60). Participants of different main income source did not differ in their knowledge of this species' activity pattern in Sainte Luce (H=0.82, df=4, p=0.936) nor in Mandena (H=3.65, df=3, p=0.302).

2. 3. Local ecological knowledge

Participants from Sainte Luce showed higher ecological knowledge of red-collared brown lemurs than participants from Mandena (U=220.50, p=0.001, N=60). In Sainte Luce, there were no gender differences in ecological knowledge about this lemur (U=73.00, p=0.097, N=30), but in Mandena, men scored higher (U=67.00, p=0.029, N=30). Age was not correlated to LEK in Sainte Luce (r=-0.17, p=0.377) nor Mandena (r=0.13, p=0.487). Main income source was not related to differences in overall LEK in Sainte Luce (H=5.08, df=4, p=0.279), but it was in Mandena (H=8.09, df=3, p=0.044).Participants who earned their income from wood extraction demonstrating better LEK than those who earned their income from selling products woven from sedge (U=1.50, p=0.048, N=9), and those who earned their income from agriculture (U=2.50, p=0.007, N=20).

3. Local practices involving red-collared brown lemur

3.1 Hunting

Most people reported never having hunted the species (Sainte Luce: 83.3 %, Mandena: 80.0 %), and no one reported still hunting the species. Participants from Sainte Luce said they used to hunt red-collared brown lemur using traps (N=1) and slingshots (N=3), but the species was difficult to catch, with one participant saying he would only catch one every two months. They used to hunt in many forest fragments, including those that are now under protection (i.e., fragments S8 and S9), with one participant stating they stopped hunting when the "white people" (*vazaha*) came and started conservation work. Interestingly, one participant stated he found hunting the lemurs (as well as other wildlife) "embarrassing" for the community. He explained that only a weak man would hunt, while a couple of other participants stated they did not hunt simply because they did not know how to (please see Chapter 8, p 174 for a more thorough discussion of this finding).

Similarly, participants from Mandena also used traps (N=2) and slingshots (N=3) to catch this lemur. Guns were only mentioned once, and their use in hunting seems to be rare. Participants used to hunt in the mountains around Mandena, as well as in the area that is now protected, but they are now afraid to hunt there. One participant mentioned he would never hunt lemurs with radio collars, as in that case, it would become known because the lemur would be missing, and people would know he had caught it. Another participant reported that, before the area was protected, he would catch about two brown lemurs a month using traps, while another participant reported he was able to catch a lemur every few days, or once a week, using a slingshot. A participant reported previously having used traps and catching about one lemur every two weeks, while another recollected having hunted approximately 20 brown lemurs per year. A participant who previously hunted lemurs with guns and slingshots explained how this species' protected status affected his behaviour towards them: "They are one of the protected animals." (man, 65, Mangaiky). In most cases, however, it was an older relative (i.e., the participant's father or grandfather), or an older friend who was reported to have done the hunting when the participant was a young child or a teenager. As one participant from Sainte Luce remembered, "A teacher who was a friend of my father would catch them with a gun on the weekend in S9. One day he brought home four or five animals and gave them to my father. I was 15." (woman, 56, Manafiafy). Some hunting also used to occur opportunistically, during firewood collection.

Between-area difference in reported hunting of red-collared brown lemur was not statistically significant (χ^2=0.11 df=1, p=0.739, N=60). Moreover, participants from Sainte Luce who reported having hunted red-collared brown lemurs demonstrated greater ecological knowledge of the species (U=20.00, p=0.016, N=30), but the same relationship was not found in Mandena (U=65.00, p=0.674, N=30). Respondents' main income source was not related to hunting in Sainte Luce (H=5.32, df=4, p=0.256) or Mandena (H=4.00, df=3, p=0.261).

3.2 Eating

The majority of the surveyed population reported never having consumed this lemur (Sainte Luce: 76.7 %, Mandena: 60.0 %). In Sainte Luce, for those that have, it was mostly in their childhood (i.e., 30-50 years ago), with one participant saying the last time was around 2005. The situation in Mandena was very similar, with many participants saying they had not eaten a brown lemur since they were a teenager (i.e., when they were 12-18). The more recent case I recorded was from a participant whose uncle brought one home around 13 years ago (time deduced from her current age and the age she mentioned being when it happened), which he caught while collecting firewood. A participant from Mandena recalled eating a lemur caught in the area that is now protected: "I ate one as a child, I was still in school. My parents brought it from the Mandena Conservation Zone before the QMM came." (woman, 36, Mangaiky). There was no significant difference between the two areas (U=375.00, p=0.169, N=60). Main income source was not related to differences in reports of having eaten this lemur in Sainte Luce (H=4.77, df=4, p=0.312) or Mandena (H=3.35, df=3, p=0.340).

4. Attitudes towards the species

Most respondents reported holding a positive attitude toward the species (Sainte Luce: 96.7 % or N=29; Mandena: 85.7 % or N=18). There was no significant difference between the two areas (U=280.50, p=0.156, N=51). Main income source was not related to differences in attitudes towards this lemur in Sainte Luce (H=3.29, df=4, p=0.511) or Mandena (H=3.54, df=3, p=0.316).

The most frequent reason for having a positive attitude was the species' ecological importance, and presence in the forest (N_{SL}=8, N_{MND}=6). As one participant explained, "They help with seed dispersal." (man, 66, Ambandrika). Another participant said, "It makes me happy to see them jump around." (woman, 45, Ampanasatomboky). One participant explained that they are also good for tourism: "They attract the *vazahas* (foreigners)." (woman, 32, Ambandrika). For the participants from the Sainte Luce area, the second most frequently given reason was either a desire to keep this lemur as a pet (N=4), or the features of its (perceived) character (N=4) - namely, it being "good" (i.e., not damaging their crops, and not causing any harm to the people) or intelligent. As one participant detailed, "I can show them to my children and talk about their behaviour. They are smart, when someone tries to shoot them with a slingshot, they cover their heads." (man, 32, Ampanasatomboky). Another one stated that they liked them because "they are not an aggressive animal and they do not disturb people." (man, 32, Manafiafy). One participant disclosed they used to have it as a pet when they were a teenager, while another mentioned his father kept one as a pet when he (the participant) was a child: "It (the animal) is wise. When it is your pet, it can come close or jump on your shoulder. It is friendly." (man, 67, Ambandrika). Mandena participants also mentioned this lemur being a good food source (N=5), as well as a desired pet (N=3) (Table 3). As one participant explained, "If you catch one, you can feed a lot of people. It is good meat." (woman, 52, Betaligny). Another participant illustrated that their good taste comes from their diet: "They do not eat rotten animals or dirty things, only fruits." (man, 48, Betaligny). One participant stated they liked lemurs because of their similarity to humans: "We were created by the same creator." (man, 35, Mangaiky). According to a different participant who used to know someone who kept a brown lemur as a pet before, "Brown lemurs are good, intelligent and kind animals. They are adapted to stay with people as pets. Now people are afraid to keep them because they are protected." (man, 65, Mangaiky).

Negative attitudes towards red-collared brown lemurs were a lot less prevalent among the surveyed population - only 7.8 % of the total sample reported not liking this lemur (Sainte Luce: 3.3 % or N=1; Mandena: 14.3 % or N=3). In Sainte Luce, the only reason given for not liking the animal was its physical appearance (i.e., the lemur was considered "ugly" by one participant who stated they did not like it, which led the participant to be scared of lemurs). "I am scared of their face." (woman, 76, Manafiafy). Similarly, in Mandena the reasons behind people's negative views of the species were its perceived scary character or it being considered "smelly" (Table 4). One participant compared its looks to those of a cat: "I do not like their face, they look like a cat." (woman, 52, Betaligny). Another participant said they did not like them because there were no associated economic benefits: "I get no money from them." (woman, 27, Betaligny). LEK was not correlated to attitudes among the Sainte Luce sample, but there was a trend that those with better knowledge expressed more positive attitudes ($r=0.317$, $p=0.088$, $N=30$). In Mandena, LEK was not correlated with more positive attitudes ($r=-0.240$, $p=0.295$, $N=21$).

Table 3. The reasons behind positive attitudes towards red-collared brown lemur (*Eulemur collaris*) among participants from both surveyed areas (N=47).

	Sainte Luce	**Mandena**	**Total**
Positive attitude	29	18	47
Reasons behind the attitude			
Tourist attraction	3	0	3
Species ecology	8	6	14
Perceived character	4	2	6
Physical appearance	4	0	4
Desirable as pets	4	3	7
Desirable as food	2	5	7
Crop damage (the lack of it)	0	2	2
Other	2	2	4

Table 4. The reasons behind negative attitudes towards red-collared brown lemur (*Eulemur collaris*) among participants from both surveyed areas (N=4).

	Sainte Luce	**Mandena**	**Total**
Negative attitude	1	3	4
Reasons behind the attitude			
Attracts tourists	0	0	0
Species ecology	0	0	0
Perceived character	0	1	1
Physical appearance	1	0	1
Desirable as pets	0	0	0
Desirable as food	0	0	0
Crop damage	0	1	0
Other	0	1	2

Finally, the results of a structural equation model (RMSEA=0, CFI=1) indicate that LEK was significantly associated with the participants' area of inhabitancy. Sainte Luce participants demonstrated better LEK of red-collared brown lemurs than their Mandena counterparts. The model also revealed a trend for men to have higher LEK than women, and more positive attitudes towards red-collared brown lemurs (Table 5, Figure 1). This model explained 50.3 % of LEK variance and 12.8 % of variance of attitude towards this lemur species.

Table 5. Model parameters of a structural equation model of LEK and attitude towards red-collared brown lemurs (*Eulemur collaris*) using participants' area of inhabitancy, gender, age, whether they recognised the species and whether they hunted it as predictors.

	Estimate	**SE**	**p**
LEK ~ Area	-0.857	0.133	**<0.001**
LEK ~ Gender	0.264	0.141	0.062
LEK ~ Age	-0.004	0.004	0.270
LEK ~ Hunting	0.311	0.192	0.105
LEK ~ Recognition	-0.144	0.556	0.796
Attitude ~ LEK	-0.001	0.076	0.991
Attitude ~ Area	-0.113	0.098	0.249
Attitude ~ Gender	0.145	0.080	0.068
Attitude ~ Age	-0.001	0.002	0.612
Attitude ~ Hunting	0.040	0.107	0.710
Attitude ~ Recognition	-0.267	0.304	0.379
LEK ~~ LEK	0.212	0.042	**<0.001**
Attitude ~~ Attitude	0.063	0.012	**<0.001**
Area ~~ Area	0.242	0.000	
Area ~~ Gender	-0.017	0.000	
Area ~~ Age	-1.245	0.000	
Area ~~ Hunting	-0.006	0.000	
Area ~~ Recognition	-0.007	0.000	
Gender ~~ Gender	0.249	0.000	
Gender ~~ Age	2.337	0.000	
Gender ~~ Hunting	0.063	0.000	
Gender ~~ Recognition	0.004	0.000	
Age ~~ Age	294.914	0.000	
Age ~~ Hunting	1.400	0.000	
Age ~~ Recognition	0.200	0.000	
Hunting ~~ Hunting	0.132	0.000	
Hunting ~~ Recognition	0.005	0.000	
Recognition ~~ Recognition	0.014	0.000	

~ regression parameters; ~ ~ (co)variance estimates

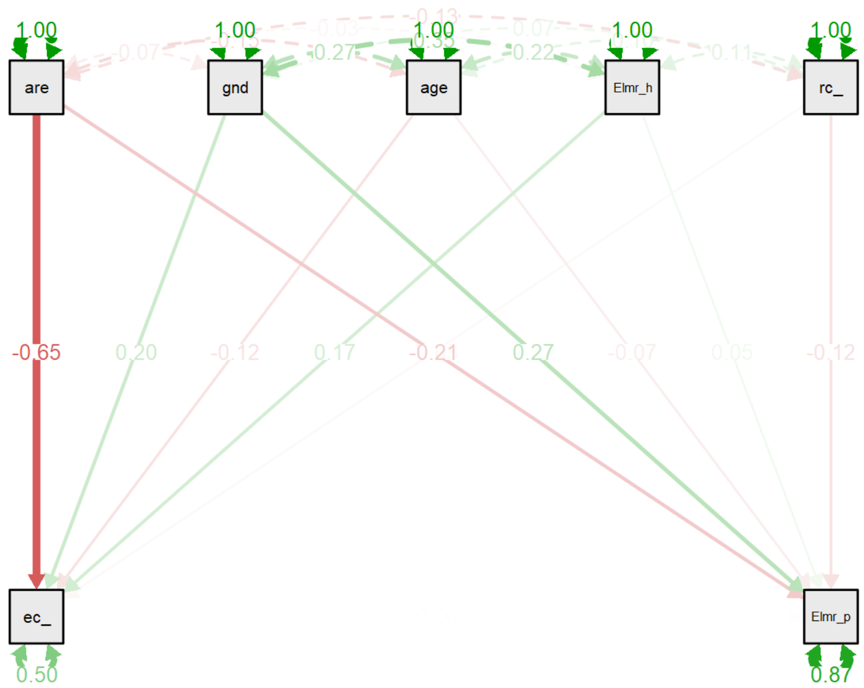


Figure 1. Path diagram of a structural equation model of LEK and attitude towards red-collared brown lemur (*Eulemur collaris*) using participants' area of inhabitancy, gender, age, whether they recognised the species and whether they hunted it as predictors.

Discussion

The findings of this study show that red-collared brown lemur is highly recognisable locally, both from the photograph and by its local name, which indicates the species' local importance (Rachmatika & Samsoedin, 2006). Sainte Luce participants demonstrated better knowledge of this lemur's diet and activity pattern than their Mandena counterparts. This is possibly a result of this species' higher population size in Sainte Luce (Bollen et al., 2006; Donati et al., 2007), as LEK has been found to relate to species population sizes (Nash et al. 2016; Afriyie & Asare, 2020). Most participants in both areas had a positive attitude towards this lemur species. According to the participants, red-collared brown lemurs are no longer hunted or eaten locally.

Species recognition

The ability to recognise a species points towards its cultural significance to the local people. This can be used as a baseline for conservation actions or conservation education initiatives. Identifying a species is also related to an interest in nature (Palmberg et al., 2015), and an important component of species literacy (Hooykaas et al., 2019). As such, it can be an indicator of people's attitude and connection to nature (Hooykaas et al., 2019). Understanding what species are important to local people can improve decision making, and help avoid predictable conflicts (Rachmatika & Samsoedin, 2006). The overwhelming majority of the surveyed participants from both communities could clearly recognise the red-collared brown lemur from the photograph, and all of them recognised the species from its local vernacular name. There were no statistically significant differences in either type of species recognition between the two areas. While men and older respondents are typically better at recognising wildlife (Nash et al., 2016; Miard et al., 2017), I found no gender- or age-related differences in species recognition in this study. This finding is not surprising, given that this lemur is well known in both Sainte Luce and Mandena. Features of its ecology, such as day-time activity and conspicuous behaviour (i.e., their movement through the trees tends to be very loud as they are quite large (the largest lemur currently inhabiting the littoral forests in the southeast of Madagascar (Donati, 2002) and live in groups of up to 17 individuals (Donati et al., 2007)), makes this species easy to spot, as well as observe. Studies of nocturnal primates found that fewer people are typically able to correctly identify them from the photograph. For example, a LEK study of the Philippine slow loris (*Nycticebus menagensis*) in Malaysian Borneo found that, depending on the village, between 46 % or 74 % of surveyed members on average correctly identified the species (Miard et al., 2017). Participants of the same study often confused the slow loris with the tarsier, another nocturnally active primate inhabiting the study area. It is not uncommon for people to misidentify smaller-bodied species (Turvey et al., 2014), which could be a limiting factor to using LEK in areas where similar-looking species occur sympatrically. However, species' diurnality, group living, and large size do not always correspond to its high recognition. A study of LEK of Hainan gibbon (*Nomascus hainanus*) among the population living around several different protected areas in Hainan, China found that only 54 % of respondents were able to correctly identify the species from its photograph, while even fewer (49 %) were familiar with its name (Turvey et al., 2018). This suggests that species' abundance in the area, and proximity to the surveyed human settlement might play an important role in its recognisability, and subsequently, LEK.

Local ecological knowledge about the species

Local ecological knowledge, local beliefs and attitudes towards a species provide important information about people-wildlife coexistence in a particular area. While beliefs and attitudes point towards species cultural importance, knowledge about species' ecology or past and present distribution can be essential for effective conservation management (Weber et al., 2015; Kelbessa, 2015; Nash et al., 2016). Joint efforts of western scientists, forest managers and people relying on forest resources ("forest practitioners") will likely result in a better understanding of how to conserve biodiversity than what any of these groups would accomplish on their own (Charnley et al., 2007). When it comes to knowledge of red-collared brown lemur's diet, participants from both Sainte Luce and Mandena knew that this species was predominantly frugivorous and did not statistically differ in this respect. Interestingly, however, participants from Sainte Luce were much better at naming forest plant species on which the red-collared brown lemur feeds, while participants from Mandena listed more human crops in its diet. Similarly, Sainte Luce participants also showed better knowledge about the species' activity pattern, which, combined with the more detailed knowledge of this lemur's diet contributed to their overall higher LEK scores. Results of structural equation modelling also point towards higher LEK scores among Sainte Luce participants. LEK declines in response to species' population size decrease (Kai et al., 2014). This relationship has, for example, been shown between the perception and knowledge of pangolins in China (Nash et al., 2016), and numerous mammal species in Ghana (Afriyie & Asare, 2020). This suggests that LEK can be used as an approximation of wild mammals' population trends. The lower LEK measured in Mandena might be related to lower population sizes of this lemur in MCZ than in Sainte Luce (Bollen et al., 2006; Donati et al., 2007). LEK erosion as a result of biodiversity loss could increase the difficulty of future conservation efforts (Papworth et al., 2009). Demographic characteristics, such as age or gender, are often correlated to LEK (e.g., Caniago & Siebert, 1998; Ross, 2002; Turvey et al., 2018). While the two sub-samples are equal in terms of gender distribution, the participants from Sainte Luce tended to be older than those from Mandena. The age difference, although not significant, could have mediated the differences in LEK, as older people typically demonstrate better ecological knowledge (Caniago & Siebert, 1998).

Red-collared brown lemurs often visit the villages in both areas. As a result, even those members of the community who do not enter the forest will have had many opportunities to encounter and observe these animals, albeit in a more limited way - for example, while the animals are feeding on their crops. While Sainte Luce is a fishing community, the population of Mandena are more reliant on agriculture and cultivating fruit crops (Evers & Seagle, 2012; Kraemer, 2012), as has also been confirmed in the present study. Consequently, one might argue that this difference in livelihood strategies could be the reason why human crop names are much more prevalent than forest species in Mandena participants' reports of red-collared brown lemur's diet. However, a closer look at the relationship between participants' income source and knowledge of this lemur's diet reveals that Mandena participants who rely on timber collection for their livelihoods are better at listing both categories of lemur food. It is also unclear whether this lemur feeds on all the crops listed by the participants of this study. As Mandena was historically more degraded than Sainte Luce, the lemurs might have been more motivated to feed on people's crops in order to meet their energy requirements. A broader study encompassing more participants from more villages in both areas could help us fully understand the reasons behind this difference in diet knowledge.

Finally, Sainte Luce has had an almost continuous presence of researchers since 1999, all of whom have hired community members as forest guides, translators, and assistants. This is likely to have increased local people's knowledge of lemurs. Furthermore, the Sainte Luce area is home to a conservation charity (i.e., SEED Madagascar, previously known as ONG Azafady), which has had a long-term presence of researchers and volunteers since 2010 (S. Hyde Roberts, SEED Madagascar, personal communication). SEED Madagascar also runs a conservation project (i.e., *SEED Conservation and Research Programme, SCRP*), with one of the projects focusing on environmental education of children in all three villages. This type of program relies heavily on children sharing the curriculum contents with their parents, thereby also increasing their parents' knowledge (e.g., Duvall & Zint, 2007; Damerell et al., 2013; Rakotomamonji et al., 2015) - a practice which could have further enhanced adults' knowledge of red-collared brown lemur ecology.

Attitudes towards the species

Investigating local people's attitudes towards wildlife, especially when combined with LEK, can provide important baseline information that can help inform and guide conservation interventions in their planning stages. For example, prioritising areas in which conservation initiatives are likely to have local support, can result in higher conservation success in the long term (Berkes, 2007; Bennet & Dearden, 2014; Archer et al., 2020). When attitudes towards the red-collared brown lemurs are considered, it seems that traditional views of this species are conflicting with the conservation-motivated ones. Overall, participants from both areas had positive attitudes towards this species. However, while there was no difference in the polarity of the attitudes, there were a few differences in the reasons for having them. Species ecology (i.e., their seed dispersal) and their presence in the forest (i.e., pride in having this species around, the happiness experienced on encountering them in the forest) were the most important in both areas. Although fewer people in Mandena overall had a positive attitude towards this lemur, a higher percentage of them listed this argument as their reason for liking it than was the case in Sainte Luce. This result suggests that people in Mandena recognise this lemur's inherent value despite not having had long-term conservation education programmes and researchers' presence. However, Mandena participants much more frequently noted that this lemur is also a good source of food. Prior to forest protection, this species was hunted in both areas. Perhaps the reason why Sainte Luce participants were less likely to offer this response was due to their more continuous contact with researchers. This might have made them more aware of researchers' general attitudes about lemurs (for example, hunting and eating them is often seen as a negative behaviour by outsiders), thus decreasing the likelihood of participants' offering this particular answer. At the same time, this contact with researchers, tourists, and NGO (SEED Madagascar) staff might have caused them to more frequently describe this lemur as beautiful. Tourists enjoy seeing the lemurs, which might have been just as powerful an influence on local perceptions of this species as conservation education. I also recognise the potential effects of my positionality: my social and racial identity are similar to those of many tourists and researchers who local people have encountered in the past. This might have affected their answers, leading them to tell me what they believed I wanted to hear. Furthermore, as my translator in Sainte Luce works for SEED Madagascar, an NGO involved in conservation, this could have also affected participants' answers in a similar manner. We worked to minimise the effects of our positionalities by creating a judgement-free atmosphere, and reminding each participant of data anonymity and confidentiality, as well as that their voluntary participation meant they could choose not to reply to any question without any consequence or having to provide an explanation.

While primate pets are fairly popular throughout the tropics (Nijman et al., 2011), with their capture and trade posing a serious threat to their conservation (Estrada et al., 2018), when it comes to Madagascar this threat often pales in comparison to habitat degradation, deforestation or hunting them for food (Mittermeier et al., 2010). It was therefore surprising to see the frequency with which red-collared brown lemur was reportedly perceived as a desirable pet. While personal pets are generally not easily distinguished from those kept in commercial establishments, Reuter and Schaefer (2017) found both types of lemur ownership present in the Anosy region. Lemurs are also often kept as tourist attractions (Reuter, 2016; Reuter & Schaefer, 2017), so it is not surprising that this reason was mentioned by some participants (N=3) in the Sainte Luce sample. This community has enjoyed the economic benefits of tourism, with a five-star tourist lodge (i.e., the *Manafiafy Beach & Rainforest Lodge*) located near one of the villages (i.e., Manafiafy). Tourists often interact with the residents of all three villages, buy local products and even give out money to children (personal observation). The situation is different in Mandena, where tourists are less common Perhaps more importantly, the tourists' interaction with the local community outside the *Nahampoana Reserve* is, according to the participants of this study, negligible and often discouraged by the tourist guides (Chapter 8). It is therefore not surprising that none of the participants mentioned tourists as a reason for their positive attitude towards this lemur, despite several reportedly wanting to keep it as a pet. A close proximity to wild lemurs, which attract tourists and researchers could be a good way to bypass the appeal of pet lemur ownership, if the local community is aware of economic benefits associated with it.

<u>Local practices involving the red-collared brown lemur</u>

There was no difference in the reported past prevalence of hunting of red-collared brown lemurs between the two areas, and this practice, reportedly, no longer occurs. According to the participants, the reason for them no longer hunting is the presence of local NGOs (SEED Madagascar in Sainte Luce) and consultancy enterprises (*TBSE* in Mandena), as well as the ongoing research activities. These results, however, are not in perfect accordance with direct observations made by me or other researchers working in Sainte Luce. In 2018, we observed a sub-adult female in Sainte Luce with a snare on her hand (personal observation, reported in Hyde Roberts et al., 2020), which the lemur subsequently freed herself from. A similar situation was observed in late 2019 (S. Hyde Roberts, SEED Madagascar, personal communication). While it is not clear whether these snares were targeting lemurs, or perhaps birds, these encounters resulted in community meetings and education sessions focused on the topics of hunting and long-term effects of snares (S. Hyde Roberts, SEED Madagascar, personal communication). Although the forest fragment nearest to the human settlements (i.e., S9) is under protection, I observed evidence of nocturnal lemur hunting activities (i.e., a wood spear stuck in a tree hole). This was confirmed as such by a member of the local forest police in 2018, while in late 2019, snares and traps were found in the same protected fragment (S. Hyde Roberts, SEED Madagascar, personal communication). While lemur hunting seems to be an abandoned practice on the surface, these instances indicate that the situation is more complex. It is apparent that at least some community members still hunt some species of lemurs, and even if hunting is only an occasional event or happens opportunistically, it highlights the need for further conservation action.

Conclusion

My findings showed that most participants were able to recognise the red-collared brown lemur from its photograph, and all could recognise it by its local name. While LEK about this lemur was higher in Sainte Luce, most participants in both areas had a positive attitude towards it. While some participants disclosed having eaten this lemur in the past, red-collared brown lemur is reportedly no longer hunted or eaten locally. With a change in biodiversity, local ecological knowledge is at risk of erosion. It is important to record local beliefs and practices, as they could serve as a baseline data for creating conservation action guidelines and help to develop more effective collaborative programmes with local people. Long-term species protection is complex, and the progress is often not linear. Monitoring changes in local ecological knowledge can provide useful information, but depending on the research aims, they may be paired with direct observations to minimise ambiguities arising from different cultural backgrounds of researchers and the studied population. Economic factors should not be left out of the equation, as they are likely to moderate the way particular species - as well as the ecosystem in its entirety - is regarded. Ultimately, it is necessary to remember that the success of any conservation action begins and ends with the local communities, and they should therefore be included in all parts of the process for it to be sustainable.

CHAPTER 7

People and plants: utilitarian species of the littoral forests of Sainte Luce and Mandena, southeastern Madagascar

Introduction

Tropical forests support an immense diversity of plant species (Janzen, 1970; Balick et al., 1996). Many human communities residing in the vicinity of these areas rely on the plants that grow there for food, medicine, construction material, or cooking fuel (Dasmann, 1976; Olindo, 1989), and are therefore typically very knowledgeable about them. The local knowledge of plants, their use, and the beliefs surrounding them are often the central focus of ethnobotanical studies (Martin, 2010). However, despite the usefulness of forest resources and ecosystem services to people, many tropical ecosystems are facing habitat fragmentation and degradation (Ritters et al., 2000; Benhin, 2006; Harper et al., 2007). When these delicately balanced ecosystems are threatened, so are the people who depend on them for aspects of their day-to-day living.

Human activities are a major driver of environmental change and biodiversity loss (Gardner et al., 2009; Morris, 2010). Among the main causes of tropical forest degradation is selective logging (Hall & Bawa, 1993; Hill & Harner, 2004; Dent & Wright, 2009; Putz et al., 2012). A particularly difficult challenge to tackle is illegal logging, which seems to be on the rise in many developing countries with unstable governments and ineffective law enforcement (Innes, 2010). Besides timber extraction, people rely on the forest for various non-timber products (NTFPs), for example medicinal plants, fuelwood, or weaving materials (Panayotou & Ashton, 1992; Shackleton & Shackleton, 2004). While timber extraction activities often target particular tree species, extraction of NTFPs typically involves many species (Dovie et al., 2002; Shackleton et al., 2002). Forests exploited for NTFPs can appear undisturbed (Peters, 1996), especially when they are only harvested for subsistence of the local communities, and consequently it was long thought that extraction of NTFPs has little ecological impact. However, this is not always the case, due to NFTPs' increasingly recognised economic importance (Shackleton & Shackleton, 2004). Furthermore, NTFPs often have great cultural significance (Posey, 1999; Cocks & Wiersum, 2003).

One of the most commonly discussed examples is medicinal plants. Traditional medicine incorporates use of natural resources to prevent, treat or heal human diseases and ailments, often as a part of a ritual, and combined with spirituality (Smith-Hall et al., 2012). It is an important part of most countries' tradition and culture (Quansah, 2005). Throughout the tropics, many people rely on medicinal plants, especially those living in rural areas. Despite this, less than 1 % of plants have been studied for their medicinal properties (Balick et al., 1996). In many developing countries, medicinal plants are the primary source of medicine (Tabuti et al., 2003; Muthu et al., 2006; Gurib-Fakim, 2006; Bhattarai et al., 2010; Maroyi, 2013). The most common reasons are the limited access to western medical resources, the effectiveness of medicinal plants, or a cultural preference (Balick et al., 1996). A decreased reliance on medicinal plants can be brought about by a change in religious beliefs, as some faiths (i.e., Protestantism) discourage this practice due it being considered a form of traditional magic (Caniago & Siebert, 1998). Similarly, the social change and an increased contact with non-community members (e.g., migrant loggers or charcoal manufacturers) affect medicinal plants' use, and the knowledge about them (Caniago & Siebert, 1998).

Madagascar is a biodiversity hotspot (Myers et al., 2000), and due to its long geographical isolation, its species evolved with a high degree of microendemism (Wilmé et al., 2006). Around 3,500 plant species were found to have medicinal properties (Rasoanaivo, 2003), many of which are endemic (Razafindrabe et al., 2013). However, not unlike other tropical and subtropical countries, Madagascar is facing biodiversity loss. Forests are cleared to make space for agriculture, which is the main source of sustenance and income in many parts of the country. Human activities, such as traditional slash and burn agriculture (locally known as *tavy*), charcoal production, or overharvesting of particular tree species can put entire forests at risk. Logging has been well documented in Madagascar, but there have been issues with reporting its export (Schuurman & Lowry, 2009). The annual deforestation has progressively increased to 1.1 % per year, mostly as a result of population growth and political instability (Vieilledent et al., 2018). These illegal activities most often bring profit to a few select individuals, and the local communities derive little benefit (Schuurman & Lowry, 2009). Simultaneously, they can often face many negative consequences, such as a reduction of medicinal plants' abundance and distribution (Primack & Lovejoy, 1995; Novy, 1997).

Littoral forests of southeastern Madagascar are among the most threatened ecosystems in the world (Bollen & Donati, 2005). Many researchers also consider them a national conservation priority (Gazhorn, 2001), but only around 10 % of the original forest remains (Consiglio et al., 2006). Forests of Sainte Luce and Mandena, located in the vicinity of the town of Fort Dauphin, are among them. Home to numerous species of flora and fauna, these forests have been community-managed until the arrival of the QIT Madagascar Minerals (QMM) mining company in the early 2000s. Some of the bigger fragments were designated for the creation of protected areas (i.e., M15+M16 in Mandena are now called Mandena Conservation Zone, established in 2005 and spanning over 230 ha; S1, S2, S8, S9 and S17 in Sainte Luce, covering 747 ha, have been protected since 2002). Sainte Luce and Mandena are similar in botanical composition (Rabenantoandro et al., 2007), yet different in their historical degree of anthropogenic use, as well as their proximity to the nearest town, Fort Dauphin. Sainte Luce is the most intact littoral forest in southeast of Madagascar (Bollen & Donati, 2006), and further away from Fort Dauphin (around 35 km). On the other hand, Mandena has been more degraded than Sainte Luce (Rabevohitra et al., 1996; Dumetz, 1999), and is much closer to Fort Dauphin (10 km). The two forests are also different in respect to mining: while the mining project started in Mandena in 2009, Sainte Luce is still in the pre-mining phase. When protected areas are created, activities such as hunting or gathering plants become prohibited even for the communities who had historically used those resources. Such activities become restricted to buffer zones or redirected to other areas. In Sainte Luce and Mandena, some of the fragments that were already heavily degraded from long-term human pressure (Dumetz, 1999) have been cleared for logging and mining. Additionally, QMM have agreed to establish a tree nursery to replace the slow-growing endemic species, as well as plant the fast-growing exotic species, such as *Acacia* sp. and *Eucalyptus* sp., to be used by the local communities for timber and fuelwood.

The Anosy region in the southeast of Madagascar, where Mandena and Sainte Luce are located, is among the most isolated and economically poor regions of the country (Vincelette et al., 2007). However, Local people are heavily reliant on the natural resources, and use 58 % of all plant species, for anything from construction materials and firewood to food and medicine (Lowry et al., 1999; Vincelette et al., 2003; Ingram et al., 2005b; Razafindraibe et al., 2013). Many of the women are engaged in weaving sedge (*Lepironia mucronata,* locally known as *mahampy*) into mats, baskets, or hats (Evers & Seagle, 2012; Holloway & Short, 2014). This is both a traditional practice, and a source of additional income. Used in many aspects of the daily life, these mats are of cultural importance to both women and men, as they are also used to shroud corpses (Holloway & Short, 2014).

For the people residing near the littoral forests of southeastern Madagascar, medicinal plants are of high importance. Western medicines are rarely used, as people reportedly doubt their effectiveness (QMM, 2001). Traditional healers (locally known as *ombiasa*) are important to women and men living near the Tsitongambarika rainforest in the southeastern Madagascar (located around 100 km from Fort Dauphin). They believe that spiritual forces govern their lives, and any violation of spirituality may result in bad spirit possession or serious illness (Lyon & Hardesty, 2005). Traditional healers' activities, however, depend on the availability of medicinal plants (Lyon & Hardesty, 2002). Although western medicines are becoming increasingly available, medicinal plants are used and learned about, and the role of traditional healers is as important as it was in the past (Lyon & Hardesty, 2005).

Firewood and charcoal are the primary sources of energy in southeastern Madagascar. While 90 % of the rural population relies on firewood, charcoal use is more prevalent in towns (i.e., Fort Dauphin) and among the migrants coming from the south of Madagascar, such as the Antandroy. They were found to use the Mandena forest for charcoal production (QMM, 2001), making this activity the primary source of deforestation in Mandena. Forest species used the most include fanola (*Asteropeia* sp.), mafotra (*Brochoneura acuminata*), nato (*Fauchera hexandra*), and rotry (*Syzigium emirnense*), while many more are used as construction materials, firewood, or medicine (Ingram et al., 2005b). The most frequently harvested species was harandrato (*Intsia bijuga*), used for timber and medicine. Other commonly cut species included forofoky (*Diospyros littoralis*) and rotry used for firewood, timber, medicine, and food (rotry only) (Ingram et al., 2005b). The establishment of protected areas has restricted forest use, but while this restriction has most likely affected the local people's way of life and resource acquirement, no studies have been published on the details of it. For example, some wetlands and swamps around Mandena have already been destroyed by mining, and *Eucalyptus* sp. plantations have been planted in their place. While sedge has also been planted elsewhere, some women do not want to use it, as it did not come from "the Creator" (locally known as *zanahary*) and they perceive it to be of lower quality (Fairhead et al., 2014).

Relating primates' use of plants to that of the local people has potential as a conservation strategy that could ultimately benefit the primates, plants, people, and traditional livelihoods. The value of primate seed dispersal, especially of utilitarian species, has been recognised as an argument for primate conservation, not only due to its importance for forest regeneration, but also for human forest use (Lambert, 1998). In this study, I cross-reference the human use of plant species to that of the red-collared brown lemur (*Eulemur collaris,* É. Geoffroy, 1817). This is species of lemur classified as Endangered by the IUCN Red List (Donati et al., 2020) and found only in the southeast of Madagascar, where it inhabits lowland semi-montane humid forests and littoral forests. Due to their body size, these predominantly frugivorous lemurs (Donati et al., 2007) are likely the exclusive dispersers of many large-seeded plant species (Bollen et al., 2004). As such, they are uniquely important for these species' regeneration, while also playing a role in overall regeneration patterns. Although tropical forests resources are used both locally and globally, the focus of this study is on their local use. Botanic similarity paired with historic differences in anthropogenic pressures and differences in the use of natural resources in traditional livelihood strategies make Sainte Luce and Mandena interesting for comparison. I explore and document the use of botanical species by people living in the two communities, and quantitatively evaluate their use while focusing on the comparison between the two areas, as well as understanding how the way people use plants might have changed since the protected areas were established. To do so, I address the following questions:

1. What species of plants are used by the communities of Sainte Luce and Mandena?
2. Which plants are used as medicine, and how are they used? Where are the plants obtained from?
3. Do people use western medicine? If so, what is the preferred way of treating illnesses (medicinal plants or western medicine), and why?
4. Which plants are used as construction materials, and where are they obtained from?

5. Which plants are used as fuelwood, and where are they obtained from? Do people prefer charcoal as firewood, and if so, why?
6. Are there any other uses of plants related to local livelihoods?
7. How many plant species within each examined category (i.e., medicine, construction, firewood) are found in the diet of *Eulemur collaris*?

Methods

Data collection

Data were collected between April and October 2018, using semi-structured interviews (Bernard, 2017). Obtaining qualitative data has allowed me to gain a more refined understanding of how the way in which people use plants has changed, and more importantly, why. To document which species were used for the three purposes, I used the free listing technique (Albequerque et al., 2014; Oliveira et al., 2019), in which I asked the participants to name all the plants they knew and used as medicine, construction material, or firewood. When participants would state that they did not know or use any other species in any of the three categories, I used nonspecific prompting (Albequerque et al., 2014), asking the participants what other plants they might be using for the surveyed purpose. This is believed to prompt the participants to remember more species used for a particular purpose, without inducing “yes” or “no” answers. My sample comprised 60 adults coming from six villages: three villages in the Sainte Luce area (i.e., Ambandrika (24°46'57.75" S, 47°10'23.99" E), Ampanasatomboky (24°46'48.4" S, 47°11'35.9" E), and Manafiafy (24°46'34.4" S, 47°11'53.5" E)), and three villages in the Mandena area (i.e., Ampasy Nahampoana (24°58'51.24" S, 46°58'53.73" E), Betaligny (24°59′28.2" S, 46°58′43.1" E), and Mangaiky (24°56′09.0" S, 46°59'20.1" E). Participants were heterogeneous in respect to their age, and each subsample comprised equal numbers of women and men. All interviews were conducted in Malagasy with help of a local Antanosy translator (N=3). The interview topics covered three uses of plants: plants used for medicinal purposes (medicinal plants), plants used as construction material, and plants used as fuelwood (firewood and charcoal). All plants were first identified by their vernacular name, while their scientific names were obtained from the published literature (Bollen, 2003; Ingram & Dawson, 2006; Ganzhorn et al., 2007; Donati et al., 2007; 2011; 2020).

While this section did not include many sensitive themes, I still wanted to ensure that all questions were asked in a culturally sensitive way, and were clear and easy to understand. Before starting the data collection, I had a meeting with each translator, during which we discussed the details of the study and I explained to them what specific kind of information I was looking to obtain and why. This way, the translators were able to contribute to data collection by providing their input on how the questions should be formed and asked. They were also able to use nonspecific prompts (Albequerque et al., 2014) when participants would not offer the kind of answer we were looking for initially (i.e., when they said they did not use or any plants as medicine, construction material, or fuelwood). While my translators were local to the area in which I conducted my research, my positionality as a foreigner in undeniable. It is possible that it could have led the participants to form expectations about me upon meeting, which would have been based on their previous encounters with other foreigners of similar age, gender, race or culture. This can create biases, which would be impossible to completely remove. However, I acted to minimise them by not conveying any expectations about participants' answers, receiving all information with interest and empathy, creating a pleasant atmosphere, and ensuring they were always aware that no matter what they reveal, it would remain confidential. Ethical approval for the study was granted by the University Research Ethics Committee of Oxford Brookes University.

1. Medicinal plants

Participants were asked whether they used medicinal plants, and if their answer was positive, I asked them to list each species they used, along with the details of its use - i.e., which part of the plant was used (e.g., leaves, bark, roots, etc.), how the medicine was prepared, and which illness or condition it treated. To better understand the relationship between medical conditions and medicinal plants that treat them, all the mentioned illnesses were assigned a category, depending on the body system to which they belong. I created eleven categories - circulatory system, digestive system, immune system (e.g., fevers, as well as autoimmune disease, such as rheumatism), body pain, reproductive system, respiratory system, skin conditions, spirit possession, wounds and injuries, other, and *hevo* - a culturally understood childhood illness, consisting of a range of symptoms such as diarrhoea, dehydration, stomach ache, high temperature, prickly oral cavity, soft fontanel and a general state of weakness (*Assessment of Maternal and Child Health in Fort Dauphin, Madagascar,* SEED Madagascar, 2012). I also asked where the medicinal plants were obtained from, and whether the participants were still able to find them since the establishment of the protected areas. In addition, I inquired about the participants' use of western medicine. If they used both types of medicine, I asked which they preferred, and why.

2. Plants used as construction materials (timber)

In this section, participants were asked to list all the plants they used for construction of their homes, and to identify which of those they found most important. Additionally, I asked them whether the timber species they use, and the area from which they obtained them have changed since the establishment of the protected areas.

3. Plants used as fuelwood

Finally, I surveyed the participants' use of firewood or charcoal as cooking fuel. I asked each participant whether they used firewood, and if the answer was positive, I asked them to list all the species they used, and the area from which they collected firewood. In addition, I asked them whether or not they use charcoal. I also asked people who reported using firewood and charcoal which they preferred, and why.

Results

1. Medicinal plants

The use of plants for medicinal purposes is present in Sainte Luce and Mandena, but while each of the surveyed participants from Sainte Luce reported using at least one medicinal plant, the same was the case for only 80 % of the Mandena sample (N=24). Between the two areas, participants reported using a total of 123 species for medicinal purposes, 49 of which I was able to identify to the species level. The number of reported species was higher in Sainte Luce (n=92) than in Mandena (n=51). Of all plant species used as medicine, 15 were introduced species.

Despite the high overall number of medicinal plants reported by the participants (n=123), only 21 (17.07 %) are used in both Sainte Luce and Mandena. The most often reported species in both areas was the Madagascar periwinkle (*Catharanthus roseus*), from the Apocyaceae family, locally known as tonga. This flowering plant is used by a third of both Sainte Luce and Mandena participants, to treat stomach problems (Table A1, Appendix IV). In Sainte Luce, another plant was equally important, locally known as fagnota (*Monathotaxus* sp.). Tea made from its leaves is used to alleviate stomach problems and heart problems, while a paste made from its powdered roots and water is believed to help with bad spirit possession. As one participant explained, “Fagnota has a bad smell. If you put it under the person’s nose, the bad spirit goes” (woman, 33, Ambandrika). The same participant also used fagnota to relieve bad luck: “If you are unlucky, mix the powder with water and put it all over your body to lose the bad luck”. In both Sainte Luce and Mandena, most medicinal plants were used for treating digestion issues (Sainte Luce: n=34; Mandena: n=15). Conservation status and population trend information were available for only twenty medicinal plants. (Table A1, Appendix IV).

The use of western medicines

Despite the prevalence of medicinal plants' use, most participants also reported using western medicine (N=29, or 96.7 % of each sub-sample). 37.9 % of the Sainte Luce participants and 58.6 % of participants in Mandena stated they prefer to use western medicines, mostly because they were perceived to be more effective than medicinal plants (75.0 % in Sainte Luce, 45.5 % in Mandena). Western medicines are available in their village, or from the travelling salespeople who visit their villages. Not all the villages have doctors or hospitals, but both are reportedly available in the nearby villages and towns. As one participant explained, "I can get it here, I do not have to go far." (woman, 28, Manafiafy). However, people state that western medicines are expensive, and at times their only option is to sell their chickens to raise money to pay for them. As one participant illustrated, "I prefer medicinal plants because I do not have to buy them. If I have a stomachache, I spend 50,000 ariary to buy medication for it." (man, 64, Betaligny). Participants who preferred to rely on medicinal plants (26.0 % in Sainte Luce, 20.0 % in Mandena) defended their choice by explaining that medicinal plants constitute their heritage and using them is a tradition. Furthermore, they are a cheaper option - collecting them from the unprotected areas is free, whereas their collection is still allowed even from the protected area (with a permit). Finally, some participants (33.3 % in Sainte Luce, 20.0 % in Mandena) explained that their preference depends on the illness: "When a doctor cannot treat me, the witch doctor recognises that it is a bad spirit." (man, 66, Ambandrika). One participant who used both options explained that he uses medicinal plants "for simpler illnesses, like stomach pain." (man, 65, Mangaiky). Another stated that "plants are the first aid" (man, 40, Mangaiky), in situations when the western medicines are not instantly available. There are also culturally understood ailments that the participants felt cannot be treated with western medicines. As one participant revealed, "Doctors do not have any medication to treat *hevo*" (woman, 35, Mangaiky). Medicinal plants are also considered more practical, and do not have any side effects. As one participant explained: "Medicinal plants can treat a lot of diseases, and western medicines have a bad impact on me – if I take too many, I get stomach problems." (man, 67, Ambandrika). Sainte Luce participants reported using a total of 25 western medicines, the most common being paracetamol (N=24) and amoxicillin (N=17). Participants mostly reported using western medicine as painkillers (n=34) to alleviate headache, toothache, and other body pain. Participants from Mandena reported using 13 types of western medication, with the most common again being paracetamol (N=15) and amoxicillin (N=7).

2. Plants used as construction material

Using forest species as construction materials is highly prevalent among the surveyed population. The majority of participants in both Sainte Luce and Mandena reported using plants as construction materials (96.7 % of each sub-sample) (Figures 1 and 2). As one participant disclosed, "It can take up to 80 trees to build a house." (woman, 45, Ampanasatomboky). In both cases, the only participants who did not use plants in this way (and who also did not know any timber species) were women.

Figure 1. Timber and firewood collection in Sainte Luce. Both mainly come from unprotected areas. Photographs taken at the edge of one of the protected fragments (i.e., S9) by R. Dalton (September 2019) and E. Račevska (July 2018).

In Sainte Luce, plants used as construction materials belonged to 38 species, while in Mandena, the surveyed participants used 36 species (Table A2, Appendix IV). The most frequently reported species in Sainte Luce was traveller's palm (*Ravenala madagascariensis*; Strelitziaceae) used by 79.12 % of the sample). The majority of the houses use dry leaves of this plant to build the roof, while its trunk is sometimes used as timber. Species of high prevalence were also the Pacific teak (*Intsia bijuga;* Fabaceae), locally known as harandrato (75.68 %) and *Plectronia densiflora* (Rubiaceae), locally known as fantsikahitry (72.24 %) (Table A2, Appendix IV). When asked which species they considered the most important, participants' most frequent answer was the Pacific teak (68.8 %), followed by *Phylloxylon xylophylloides* (Fabaceae), locally known as sotro (44.2 %). These were the plant species which they believed to be of the highest quality and durability.

Many participants (17.24 % in Sainte Luce and 27.59 % in Mandena) mentioned that not being able to access timber species in the protected area negatively impacted them. A few participants (6.90 % in Sainte Luce, 10.34 % in Mandena) stated they were unable to find elsewhere the native species they used to obtain from the now protected areas. In Mandena, they relied more on the introduced, faster growing species planted as a replacement (i.e., *Eucalyptus* sp.) despite their reportedly perceived lower quality and longevity. The species used most often are the *Eucalyptus citriodora* and *E. robusta* (Myrtaceae) locally known as kinini bonaky (72.24 %) and kinini mena (34.40 %), respectively, along with *Humbertia madagascariensis* (Humbertiaceae) (34.40 %), locally known as endrangendra. As one participant described, “Kinini bonaky lasts long. It is good for roof, but not for the floor because it is too soft.” (woman, 31, Mangaiky). When asked about the species they considered to be the most important, the two most frequent answers given by the Mandena participants were endragedra (24.08 %) and sotro (24.08 %).

Since the establishment of the protected area in Sainte Luce, all participants who used trees for timber (N=29, or 100 %) stated that they obtain timber trees from one of the unprotected fragments (i.e., S7). Additionally, three participants also reported occasionally obtaining wood from another unprotected fragment (i.e., S10), or an area around protected fragments (i.e., S9, and the privately owned S17), while two reported also acquiring timber from a protected fragment (i.e., S8). Participants stated that, to collect wood (from the unprotected fragment), they needed a permit, which can cost between 2,000 and 4,000 Malagasy Ariary (0.43 to 0.86 GBP) for enough wood to build a new house. In Mandena, all but one participant reported obtaining wood from the unprotected forest patches (N=28, or 96.55 %) - i.e., east of the MCZ (N=10), around the mountains (N=10), west of MCZ (N=2), near the mining project (N=1), around their villages (N=4), while one stating collecting wood from the protected area.

3. Plants used as fuelwood

Dead wood collected from the forest was the most prevalent fuel used for cooking in Sainte Luce and Mandena. Every participant confirmed that they relied on this resource. A total of 71 species were used as firewood, but only six species (9.85 %) were used in both areas. More species were named by participants from Sainte Luce (n=48) than those from Mandena (n=26). However, it is important to note here that many participants, especially in Mandena (N=12, or 40%; compared to N=4 or 13.3 % in Sainte Luce) did not name particular tree species stating that the species does not matter, and they would use any dead wood they found (Figure 2). The most frequently reported species in Sainte Luce were *Asteropeia multiflora* and *A. micraster* (Asteropeiaceae), locally known as fanola fotsy and fanola mena, respectively (both used by 65.45 % of the sample). Mandena participants were less uniform in their use of firewood than the Sainte Luce participants, but the most frequently reported species was *E. citriodora* (Myrtaceae) locally known as kinini bonaky (used by 38.85 % of the sample) (Table A3, Appendix IV). In Sainte Luce, most participants stated that their firewood comes mainly from an unprotected forest fragment (i.e., S7; N=25 or 83.3 %). Seven of those participants noted that they buy firewood but were confidently able to trace its origin to the same fragment. A couple of participants collected their firewood from protected fragments (i.e., four from S8, and three from S17), stating that they are allowed to do so. Finally, two participants said they collect firewood from around the village they live in. In Mandena, most of the firewood comes from what participants described as the unprotected forest patches in the mountains (N=12), but it is possible that what they referred to could be Tsitongambarika Protected Area (G. Donati, personal communication), which is not as monitored as Mandena Conservation Zone. Several participants also mentioned obtaining firewood from the areas surrounding their villages (N=8), and the areas around the protected fragments, or around the mining site (N=5). One participant said that they occasionally collected firewood in the protected area, but that they were allowed to do so, provided they pay 200 Malagasy

Ariary (0.043 GBP) each time. Another participant indicated they buy their firewood, but did not know its origin.

Only four Sainte Luce participants used charcoal (Figure 3), and only one of them reported a preference for it, due to them perceiving it as an easier method (i.e., no need to tend the fire). The reasons why the majority preferred to use firewood were mostly related to it being a custom in Sainte Luce (N=9), and "the way of their ancestors". As they explained, “I do not need to blow in the fire. It is easy, I can leave it” (woman, 28, Manafiafy). “You can leave the stove and do something else.” (man, 66, Ambandrika). The reasons why the majority of participants preferred to use firewood were mostly related to it being a custom in Sainte Luce (N=9). As one participant explained, “It is a habit inherited from the ancestors.” (man, 32, Manafiafy). On the other hand, charcoal, along with the stove needed for its use, is expensive (N=9). “A bag costs 3,000 ariary.” (0.64 GBP) (man, 78, Manafiafy). Other reasons were mostly connected to charcoal use, for example not knowing how to use the stove (N=2), seeing no need to cut down trees to make it (due to an abundance of dead wood) (N=5), or not being allowed to do it (N=1), as it takes many trees to produce charcoal (N=1). As one participant explained, “Charcoal requires living wood to be made, I do not like it. You need to chop down living trees.” (man, 42, Ambandrika). Finally, some participants stated that firewood is a quicker and easier way to cook (N=2), while one also mentioned that cooking on firewood makes the food taste better.

Mandena participants who preferred to use firewood (N=23, or 76.66 %) explained that their reason was firewood being cheaper (N=11), while a bag of charcoal costs around 6,000 Malagasy Ariary (1.28 GBP). One participant explained that, to cook a single meal, he would need around five pieces of charcoal, which would cost him around 200 Malagasy Ariary (0.038 GBP) (man, 76, Ampanasatomboky). Other reasons listed by participants who preferred to use firewood were that this is a quicker way to cook food (N=4), that using firewood was their habit (N=3), or that firewood was easy to collect (N=1), while one participant attributed their preference to issues with their charcoal stove. Participants who preferred to use charcoal (N=7) explained that cooking is easier using charcoal (N=3) due to the lack of smoke and the fact that they do not need to collect wood for it (N=1). Participants who reported making charcoal themselves said they make it in the village, and mainly use introduced species, such as *E. citriodora* (n=5), *E. robusta* (n=1), or fruit trees such as *Litchi chinensis* (n=3), *Mangifera indica* (n=2) or *Artocarpus heterophyllus* (n=1).

Figure 2. Timber and firewood collection in Mandena Conservation Zone. According to the participants of this study, both are largely collected in the unprotected areas. However, these photographs were taken in the protected area. Photographs by E. Račevska (August 2018).

Figure 3. Charcoal production in Ampasy Nahampoana (Mandena), and charcoal sold on the market in Mahatalaky. Charcoal is now produced in villages from introduced species and fruit crops, and not native forest plants. Photographs by E. Račevska (July 2018).

Other uses of plants

Besides collecting dead wood, participants (namely women) also reported collecting sedge (*Lepironia mucronata*; Cyperaceae), locally known as mahampy, with which they weave mats, hats and baskets (Figure 4). Sedge is cut and collected from marsh and swamps, dried in the sun, and covered with a whitish clay (also collected from the swamps), or occasionally, grass strands are dyed. It is traditionally woven using the so-called "over/under" technique. Final products are typically sold to increase livelihoods. Women from both Sainte Luce (N=10, 33.3 %) and Mandena (N=6, 20 %) reported collecting sedge to weave different types of products. Collection of sedge from the protected areas is banned in both Sainte Luce and Mandena. Sainte Luce women collect this plant from the areas around one of the protected fragments (i.e., S9) - namely the swamps in the east of the fragment (N=9), the northeast (N=1) and the west (N=1), as well as from the swamps around an unprotected fragment (i.e., S7) (N=6), typically two-three times a week. They mainly sell their products in

Mahatalaky, located 10-12 km from the surveyed villages. Women in Mandena mostly get sedge from the unprotected area east of the MCZ (N=7) or buy it in the village (N=1). Similar to the Sainte Luce, women typically collect it two-three times a week. The products they make are sold in Fort Dauphin.

Figure 4. Sedge (*Lepironia mucronata*), locally known as mahampy, is a plant of high local importance. Many women in both Sainte Luce and Mandena use it to weave mats, baskets, and hats. These products are sold as a way of increasing income. The photographs show sedge growing in a swamp east of a protected fragment (i.e., S8) in Sainte Luce, women carrying their daily yields back to their village, and a close up of the collected plants. Photographs by S. Hyde Roberts (2018).

Utilitarian species found in the diet of *Eulemur collaris*

Out of 191 species used by the participants of this study, 52 species were previously found in the diet of *Eulemur collaris* population in Sainte Luce and Mandena. This is the largest currently extant lemur species in the littoral forest. Species level identification was available for 45 of them. Of the 52 total species, *Eulemur collaris* ate fruit of 42 species. The highest number of species are used as construction materials (N=34), followed by firewood (N=29) and traditional medicine (N=20) (Table 1). While not all of the species' conservation status is known, several (19.23%) are classified as Vulnerable or Endangered (IUCN Red List 2021).

Table 1. Utilitarian species found in *E. collaris* diet. Species from which the fruit is eaten are presented in **bold**.

Scientific name	Local name	Conservation status and population trend	Use	Area	*Eulemur* diet data
Anthostema madagascariensis	**bamby**	LC (decreasing)	construction	SL	6
Asteropeia multiflora	fanola fotsy	LC (decreasing)	medicine; construction;	SL, MND; SL, MND; SL	2, 6

			firewood		
Beilschmiedia madagascariensis	**resonjo**	LC (decreasing)	firewood	SL	1, 2, 6
Bembicia uniflora	bemalemy	LC (decreasing)	firewood	SL	1, 2, 6
Brochoneura acuminata	**mafotra**	LC (decreasing)	construction	MND	1, 2, 6
Burasaia madagascariensis	**farisaty**	LC (decreasing)	medicine	SL	6
Buxus madagascariensis	**haramboanjo**	LC (decreasing)	construction; firewood	SL	1, 2
Cabucala madagascariensis	**tandrokosy**	LC (decreasing)	medicine	SL	6
Campnosperma micranteium	**roandria**	LC (decreasing)	medicine	SL, MND	1, 2, 6
Scolopia erythrocarpa	**lampivahatry**	EN (decreasing)	construction; firewood	SL, MND; SL	1, 2, 3, 4, 6
***Clerodendrum* sp.**	**fantsikohy**	-	construction	MND	1, 2
Cynometra cloiselii	mampay	-	firewood	SL	1, 2, 3, 4, 6
Dillenia triquetra	**varikanda**	LC (decreasing)	construction	SL	1, 2, 4
Diospyros myriophylla	**hazomainty**	LC (decreasing)	construction; firewood	SL, MND; SL	1, 2, 6
Dracaena reflexa var. nervosa	**falinandro**	LC (stable)	medicine	SL	6
Dypsis prestoniana	**boaka**	VU (decreasing)	medicine	SL, MND	3, 6
Dypsis sp.	**raotry**	-	medicine; construction	SL; SL, MND	6
Embelia incumbens	**taratasy**	-	medicine	MND	6
Saldinia littoralis	**mangavoa**	-	construction	SL	1, 2, 6
Erythroxylum sp.	fangora	-	medicine	SL	2
Ficus megapoda	**aviavi**	-	medicine	SL	1, 2
Ficus pyrifolia	**nonoky**	-	medicine	MND	1, 2
Ficus guatteriifolia	**fihamy**	-	medicine	SL, MND	6
***Grisollea* sp.**	**zambo**	-	firewood	SL	1, 2
Homalium albiflorum	**voakazoala**	LC (decreasing)	construction; firewood	SL	2, 3, 4
Homalium louvelianum	**ramirisa**	VU (decreasing)	construction; firewood	SL	1, 2
Intsia bijuga	harandrato	NT (decreasing)	medicine; construction; firewood	SL, MND; SL, MND; SL	1, 2
Leptolaena pauciflora	**fonto**	LC (decreasing)	construction	SL, MND	1, 2
Homalium planiflorum	**hazofotsy**	LC (decreasing)	construction	MND	6

***Macaranga* sp.**	**makaranga**	-	firewood	MND	1, 2, 6
Neotina isoneura	sagnira	LC (decreasing)	medicine; construction	MND	2
Noronhia emarginata	**belavenoky**	LC (decreasing)	construction; firewood	SL	1, 2, 6
Noronhia ovalifolia	**zorafotsy**	EN (decreasing)	construction; firewood	SL	3
Ocotea racemosa	**varongy**	LC (unknown)	construction	MND	4, 6
Phyllarthron licifolium	zahambe	EN (decreasing)	construction; firewood	SL	6
Plectronia densiflorum	**fanstikahitry**	LC (decreasing)	construction; firewood	SL	1, 2, 6
Poupartia chapelieri	**sisikandrongo**	LC (decreasing)	construction	SL	3, 6
Psidium guayave	**guavy**	-	medicine; construction; firewood	SL, MND; MND; MND	1, 2, 5
Psorospermum brachypodum	**haronga**	VU (decreasing)	medicine; firewood	SL, MND; MND	1, 2
Ravenala madagascariensis	**ravenala**	LC (decreasing)	construction; firewood	SL, MND; SL	1, 2, 3, 4, 5
***Sarcoleana* sp.**	**vondroza**	-	construction; firewood	SL, MND; SL	1, 2
Neocussonia rainaliana	**vonsilana**	EN (decreasing)	firewood	MND	1, 2
Schizolaena elongata	**fotondahy**	LC (decreasing)	construction, firewood	SL	3, 6
Scolopia orientalis	**zoramena**	VU (decreasing)	construction, firewood	SL	6
Suregada baronii	kalavelo	-	medicine	SL	2
Symphonia verrucosa	hazingy	LC (decreasing)	construction	SL, MND	1, 2
Syzygium emirnense	**rotry**	LC (stable)	medicine, construction, firewood	SL; SL, MND; SL, MND	1, 2, 3, 4, 5, 6
Tambourissa purpurea	**ambora**	LC (stable)	construction, firewood	SL; SL, MND	1, 2, 4
Terminalia fatraea	**katrafa**	LC (decreasing)	medicine, construction, firewood	SL, MND; SL; SL	3, 6
Uapaca sp.	**voapaky**	-	construction, firewood	SL, MND; SL, MND	1, 2, 3, 4, 5, 6
Vepris elliotii	**ampoly**	LC (decreasing)	medicine, construction, firewood	SL; SL, MND; SL	1, 2, 3, 4, 5
Vitex tristis	nofotrakoho	EN (decreasing)	construction, firewood	SL; SL	1, 2, 5, 6

1: Račevska, this thesis; 2: Račevska, unpublished data; 3: Donati et al., 2007; 4: Donati et al., 2011; 5: Donati et al., 2020; 6: Bollen 2003

Discussion

Sainte Luce participants reported a higher diversity of all examined utilitarian plant species, which might be related to the differences between the two areas in the plant species' abundance, due to difference in forest degradation prior to forest protection (Bollen & Donati, 2006). As plants become rarer, the knowledge about them and the culture associated with them decline (Grenier, 1998). Both medicinal plants and western medicines are more prevalently used than previously documented, but participants' preference between the two choices often depends on the medical issue. While people in Sainte Luce used native species as construction materials, many participants from Mandena reported a switch to introduced species, such as *Eucalyptus* sp. Species' availability and accessibility were previously shown to increase their socio-cultural value (Thomas et al., 2009; Brandt et al., 2013). This suggests that these exotic species might become more valued in Mandena, as their use becomes more prevalent. All participants reported using firewood as cooking fuel, and were less selective of plant species used for this purpose. The majority preferred firewood to charcoal, mostly due to it being the more affordable option. The importance of local traditions and ancestors was evident in many participants' choices throughout. Of all the plant species used by the participants of this study, *Eulemur collaris* fed on 52 species. The common use of utilitarian plants by people and wildlife should inform these plant species' conservation efforts (Gérard et al., 2015; Steffens, 2020; Konersmann et al., 2021).

Medicinal plants

Medicinal properties of many plants used by the participants of this study are already known in the literature (e.g., Ingram et al., 2005b; Norscia & Borgognini-Tarli, 2006; Hou & Harinanteaina, 2010), but some have not been previously recorded. The species most frequently used among both sub-samples is the Madagascar periwinkle (*Catharanthus roseus*), locally known as tonga. Medicinal plants are widely used in Sainte Luce and Mandena, but despite the prevalence of their use in both areas, their use was more frequently reported by the participants from Sainte Luce than the participants from Mandena. Sainte Luce participants also reported using a more diverse selection of plants than their Mandena counterparts. The reasons listed by the Mandena participants who did not use medicinal plants were most often related to their religious beliefs. As many of them explained, they do not use medicinal plants because they practice Christianity. While the traditional (indigenous) Malagasy religion is practiced by 46 % of the population (Madagascar country report, 2002), almost half of the population are practitioners of Christian faiths (Catholicism – 26 %, and Protestantism – 23 %), one of which (i.e., Protestantism) is well known to discourage the use of medicinal plants, labelling them as traditional magic (Caniago & Siebert, 1998). Fort Dauphin has been the headquarter for missionaries of the American Lutheran Church since 1888 (Vigen, 1992), so although the details of participants' religious beliefs were not collected in this study, it is likely that they were practicing Protestantism. Moreover, as Catholicism does not prohibit medicinal plant use, it is most likely that the participants in question were of the Protestant faith.

The findings of this study show that rural communities are reliant on western medicine much more than the previous studies had suggested (QMM, 2001).Most participants stated they prefer to use western medicine, as they believe them to be more effective than the medicinal plants. Western medicines appear to be readily available even in the rural areas. This leaves their price as one of the only hurdles to their use, along with the fact that using medicinal plants is the cultural heritage of the area, and is therefore of high importance. Medicinal plants can also be used free of charge when collected from the unprotected fragments, or around village areas, which seems to typically be the case. This finding is in line with previous research, which demonstrated that medicinal plants were a cheaper alternative to western medicine (Neudert et al., 2017). According to the surveyed population, medicinal plants remain abundant, despite (or perhaps because of) it still being legal to collect them from the protected fragments. The uses of western medicine and traditional healing seem well integrated, but while both are widely used, their use is not interchangeable. Many participants explained that their choice will depend on the condition they need to treat. This findings suggests that even if western medicines were more affordable, local people might still choose to use medicinal plants to treat certain illnesses. Some conditions, such as issues with the reproductive system, skin burns, culturally understood illnesses (i.e., *hevo*) and situations that are believed to be the result of possession by a bad spirit are only treated using medicinal plants. Regardless of their faith, most Malagasy people believe in spirit possession. They believe that spiritual forces guide and govern their lives, and serious illnesses are seen as resulting from violation of spiritual rules (Lyon & Hardesty, 2005). Traditional healers use a holistic approach in their treatment and the importance of ancestors is also evident here, as healers will often consult the ancestors' spirits, in hope to guide diagnosis and treatment. While Antanosy believe that everyone is susceptible to spirit possession, regardless of their religion or nationality, those with non-traditional religious beliefs believe that their religious faith will protect them from it (Lyon & Hardesty, 2005).

<u>Plants used as construction material (timber)</u>

Using trees as construction materials was equally prevalent in Sainte Luce and Mandena, and nearly all participants stated they have used them. The number of species listed in both areas was very similar. Fifty-nine plants were mentioned as used for construction, but only 14 of those species (23.73 %) were used both in Mandena and Sainte Luce. While some of the species are only present in one of the areas, the reason for this difference could also be because of variable availability across the sites.

The protected areas have been established in both Sainte Luce and Mandena, and the majority of the participants from both sub-samples reported harvesting timber species from the non-protected areas.

However, the mining of ilmenite from the sandy soil from which these littoral forests grow has already begun in Mandena, decimating some of the (albeit heavily degraded) areas outside of the MCZ. Whether or not a plantation of non-native trees (i.e., *Eucalyptus* and *Acacia* species) has met the daily needs of the local people is unclear, as people's perspectives on this differ. For older people, planting exotic species is a reminder of the colonial past, and their unpaid work on tree plantations, while the younger people's concerns are mostly focused on the lower durability and quality of the introduced species, in comparison to the native ones (Harbinson, 2007). This issue was also raised by the participants in this study, who reported that the (perceived) quality and longevity of *Eucalyptus* sp. is inferior to the native species they previously used, and which they are no longer able to find. Some of the species they mention in this context are *Phyllocylon xylophylloides* (locally known as sotro) and the Pacific teak (*Intsia bijuga,* locally known as harandrato), which are incidentally the most esteemed timber species in Sainte Luce. Instead, Mandena participants now mostly use two of the introduced *Eucalyptus* species (*E. citriodora* and *E. robusta*), locally known as kinini bonaky and kinini mena, respectively. *Eucalyptus* species are broadly used as construction material, and are often considered hardwood. However, durability of any timber is influenced by many factors, such as climate conditions or structural design, making it very difficult to talk about durability as an absolute value (Brischke et al., 2013). Despite Mandena participants emphasising the loss of their tradition, switching to introduced species is perhaps the only way to conserve the littoral forests, while at the same time increasing the sustainability of local communities' lives and forest-related livelihoods. Cultural heritage is of an immense importance in the region, and as the QMM is locally run by Malagasy people, they are certainly aware of that. Coping with change is inevitably complex, and experiencing nostalgia towards the previously used unsustainable techniques is expected. The fact that people of Mandena have switched to the introduced species is a reason for hope in the longevity of forest protection, especially considering that many of the Mandena participants are aware that without this change, the forest would have been gone by now (Chapter 8). Conservation education and outreach may be necessary to help smooth the transition and bridge the difference between nostalgically viewed traditions, and what is realistically possible. While it may seem like the approach of easing the transition onto the use of introduced species is conflicting with the idea of ensuring that local people are included in developing conservation strategies and that their wishes and concerns are addressed, conservation education could play an important role in bridging the gap. Based on the answers received from the Sainte Luce participants, awareness of forest protection as a strategy to increase the likelihood of the forest (i.e., native tree species) being there for the future generations, who might then be able to use their resources, was related to the participants' more positive perception of the forest protection and its restrictions (Chapter 8). This strategy might safeguard the possibility for the tradition, and the ancestral ways, to continue into the future generations. I believe that employing this approach would result in Mandena community accepting the transition onto the introduced plant species with more ease, than if the approach focused on reassuring them of the quality and longevity of *Eucalyptus* species as construction materials.

Plants used as fuelwood

Firewood is the most commonly used type of cooking fuel in both Sainte Luce and Mandena, but once again, Sainte Luce participants disclosed a higher number of species. A total of 71 species are reportedly used as firewood between the two areas, which suggests a higher diversity than was the case for species used as construction materials. This is not surprising because the extraction of non-timber forest products tends to include multiples species (Dovie et al., 2002; Shackleton et al., 2002). Moreover, this lack of selectivity is also evidenced by the participants themselves, as many of them readily stated they use any dead wood that is available. Despite the overall diversity, the overlap between Sainte Luce and Mandena is relatively small, as less than 10 % of the species (i.e., 9.85 %) are used in both areas. As with differences in timber species selection, these differences could also be explained by the difference in species availability. While many of the participants collected firewood from the unprotected areas, a small number of them still acquired it in the protected areas. The latter practice has been banned by the local law (*dina)* in Sainte Luce, but is still legal in Mandena, provided people obtain a permit from the community-level forest association (Communautés de Base, or *COBA*). While a number of people were observed collecting firewood from the protected fragment (i.e., S9) during the duration of this study, all were seen entering or exiting the forest by alternative transects, as the main entrance is typically guarded by *TBSE (Tropical Biodiversity & Social Enterprise)*. This is a Malagasy-run consultancy, created in 2016 by five biologists previously employed by Rio Tinto (QMM), who administer the fragment. This suggests that better control of fragment entrances may be needed if *dina* is to be enforced. Judging from the participants of this study, firewood is collected by both women and men.

Despite fewer people using charcoal in both Sainte Luce and Mandena, this practice is significantly more common in Mandena. The effects of forest use restriction are once again evident, not only in the higher incidence of charcoal use, but also in charcoal production being limited to fruit crops and introduced tree species. This finding is in contrast with that about the species used for charcoal production by the Antandroy immigrating to the area. They were reported to use mainly forest species, and produce charcoal in the forest (QMM, 2001; Ingram et al., 2005b; Rasolofoharivelo, 2007). However, according to the participants of this study, charcoal production typically takes within the village (Figure 3). As those studies were conducted between 12 and 18 years ago, and before the beginning of mining, the circumstances may have substantially changed since then.

What prompted this change needs more research attention. Participant accounts suggest the lack of authority of local forest management, due to them being community members (Chapter 8). My data also suggest that a change in behaviour may not have been accompanied with a change in attitude, as the old ways are, for the most part, still discussed with nostalgia. Due to the importance of tradition, restricting people's ability to continue securing their livelihoods in a way inherited from their ancestors is unlikely to be accepted with ease. While changes take time, this could also be related to them not having had a say in the changes of rules concerning their forest-based livelihoods (Chapter 8). The majority of participants prefer to use firewood, stating that using firewood is their heritage, as well as a more affordable option. Charcoal seems to be reserved for the comparatively more well-off urban population (QMM, 2001). As one of the Mandena participants disclosed, it is not uncommon for charcoal producers to sell all of the charcoal, and use firewood themselves, in an attempt to increase their income.

Participants from Sainte Luce reported a higher diversity of medicinal plants, plants used as construction materials, and plants used as firewood. While this can be attributed to the higher intactness of Sainte Luce forest (Bollen & Donati, 2006), due to the correlation between natural resource' abundance and knowledge about it (Joa et al., 2018), some studies show that knowledge about plants (specifically, those used as firewood) persists even after contact with them has diminished (Oliveira et al, 2019). As authors explain, however, knowledge about the natural resource use might still be lost by future generations: this is because although it is maintained, due to the lack of resources use, it is no longer transmitted (Oliveira et al., 2019).

<u>Utilitarian species used by *Eulemur collaris*</u>

Using several data sets, I showed that red-collared brown lemurs feed on 52 (27.23%) utilitarian plant species used by the participants of this study. Furthermore, this lemur consumed fruit of 42 of those species, and could therefore play a role in their dispersal. Overall, lemur diet significantly relies on plants. Previous research showed that the diet of 56 lemur species, published over 64 studies, includes fruits and leaves of 1,026 plants, or 9.14% of all vascular plants in Madagascar (Steffens, 2020). Many of those plant species might be facing extinction: a 2021 report by the Botanic Gardens Conservation International revealed that 1,840 tree species Madagascar are threatened, 1,828 of them endemic (BGCI, 2021). The same report showed that 53% of all endemic tree species have at least one use to local people: most of them are used as timber, while other common uses include plant use as fuel and medicine. Of the utilitarian species documented in this study, conservation status and population trend information were available for only 27 medicinal plants, 42 species used as construction materials, and 43 species used as firewood. The majority were classified as Least Concern (IUCN Red List, 2021)

Out of all the species whose use by both people and lemurs I documented in this study, and for which their conservation status was available (73.08%), less than 10% (i.e., 7.899%) have stable population trends (IUCN Red List, 2021). These numbers are quite high, so emphasising plants' common uses by people and other animals might be a beneficial contribution to their conservation. One such strategy are forest restauration projects (Konnersmann et al., 2021), which would also benefit people and other wildlife relying on these species, or others growing in the same habitats. However, preserving naturally growing plants might be more important than their artificial planting – at least when the local people are concerned. One study conducted in India showed that people did not want to use cultivated medicinal plants because they believed they did not have medicinal properties (Kasagana et al., 2011). Whether a similar belief is present in Sainte Luce and Mandena needs to be investigated. As main seed dispersers in Madagascar, lemurs might be especially important in this context.

Previous studies conducted elsewhere showed that an overlap between plant species eaten by primates and used by people is not uncommon. Woolly spider monkeys (*Brachyteles arachnoides*) in Intervales State Park, São Paulo state of Brazil were found to feed on 24.5% of medicinal plants used by people living nearby (Petroni et al., 2017). The diet of chimpanzees (*Pan troglodytes*) in the Kibale National Park in Uganda included 21.4% of plants used in traditional medicine locally (Krief et al., 2005). Plants typically harvested for timber in La Chonta (Bolivia) were found to make up 50% of the diet of Peruvian spider monkeys (*Ateles chamek*) inhabiting the unlogged area (Felton et al., 2010). As *Eulemur collaris* diet includes species used as medicine, construction materials and firewood, emphasising this lemur's interdependence with local communities could benefit its conservation. While the conservation status of the majority of utilitarian plants documented in this study is yet to be examined, it is clear that even their local extinction would affect both lemurs and people, as well as their traditional livelihoods).

Conclusion

Diversity of plants used as medicine, construction materials and fuelwood is higher in Sainte Luce than in Mandena. Use of western medicines is common, but the choice between medicinal plants and western medicine often depends on the medical issue. Native tree species are preferred in construction, but Mandena participants also rely on the introduced species. While charcoal is more commonly used in Mandena, firewood is preferred as cooking fuel in both communities. Littoral forests of southeastern Madagascar are home to a diversity of plants of unparalleled global importance. The extensive ethnobotanical knowledge of the people living in this region, and their reliance on plants in many aspects of their daily lives is to be expected, especially considering how important their tradition and cultural heritage are to them. While economic developments move the country forward, they also place a constraint on the daily lives of people who were directly reliant on the natural resources that are being used for said development. A way to improve the local situation could perhaps be through emphasising the global importance of the species present in those forests, and through promoting their sustainable extraction, both locally and globally. A switch to introduced species and the accompanied change in lives and livelihoods of the local people may have been unwelcome, but it may also be a necessary measure that could improve the chances for a more sustainable future for the local communities, as well as the preservation of littoral forests, and conservation of all the unique flora and fauna that inhabit them.

CHAPTER 8

Life with forest protection - the lives and livelihoods in Sainte Luce and Mandena, and perceived conservation, social and economic impacts associated with the protected area

Introduction

For many developing countries, protected areas are a vital component of forest biodiversity conservation (Brechin et al., 2002; Lele et al., 2010; Ervin, 2013; Singh et al., 2013). Nonetheless, this conservation measure can impose considerable socio-economic costs onto the local people (Coad et al., 2008), especially when implemented without the provision of alternative livelihood sources (Lele et al., 2010; Van-Vliet, 2010). In some cases, protected areas remain under anthropogenic pressures (Silva et al., 2005). It is therefore necessary to study and monitor how the local communities are coping with and adhering to forest protection policies, how the actions of the relevant stakeholders are perceived, and to what extent are the local communities included in the decision making. That way we can ensure that environmental protection is working, but in a way that does not diminish local communities' quality of life.

Establishing a protected area can have both positive and negative effects on the people living in its vicinity. Positive effects usually include protection of ecosystem services (Ferraro & Kiss, 2002; Grieg-Gran et al., 2005), and since many rural areas with livelihood insecurity are rich in culture and biodiversity, the development of tourism projects. Tourism is often viewed as a desirable venture, as it brings direct income to the local population (Adams & Infield, 2003; Bedunah & Schmidt, 2004; Bajracharya, 2006), generates jobs, and enhances community infrastructure (Bowden, 2005; Butcher, 2011; Snyman, 2012). It can, however, also impose social costs (King et al., 1993; Ashley & Roe, 2002; Bowden, 2005; Butcher, 2011) and inflate the cost of living (Muganda et al., 2010). Additionally, it is vulnerable to external forces, such as civil wars, global economic processes, tourism trends, and pandemics. Negative effects of protected areas typically comprise a restricted use of natural resources, an interference with indigenous communities' traditional livelihoods and local economy, and in some cases, an involuntary relocation from ancestral lands (Coad et al., 2008). When a protected area is established, biodiversity offsets are often created as well, to achieve no net loss of biodiversity, either through increasing biodiversity or mitigating its future loss (Maron et al., 2012; Sonter et al., 2017). An analysis of a global database on biodiversity offset projects found that 34 % of them displaced local people and negatively affected their livelihoods (Sonter et al., 2018). Continuous and open two-way communication is essential for making sure that socio-economic development is in line with what impacted communities want for themselves. However, this goal is not always achieved (Rao & Geisler, 1990; Coad et al., 2008). Coping with high socio-economic pressures and diminishing natural resources can lead to antagonistic attitudes towards the protected areas (Anderson, 1990), as well as towards those who manage them (Infield, 1988; Newmark et al., 1993). If the local communities are not included in decision-making, they can instead of being empowered, become further marginalised, which can result in social conflict (Castro & Nielsen, 2001).

While understanding local people's wishes, perceptions and attitudes towards forest protection is important, it can be difficult to assess objectively the polarity of the impact that a protected area has had on the local communities, as it would require the before and after data, as well as monitoring over a period of years post implementation (Coad et al., 2008). The most common methods used are therefore attitudinal surveys. Some studies have revealed positive perceptions of the protected areas (Sekhar, 1998), while negative perceptions are usually a result of restrictive forest management policies (Tshamie, 1994; Allendorf, 2006). It is important to consider that protected areas do not necessarily affect all community members in the same way. For example, they can have different effects on men and women, due to traditional land tenure (Sundberg, 2003) or the difference in the natural resources around which they centre their livelihood activities. Restricting them can differ depending on the protected area management strategy - for instance, activities like hunting (typically the responsibility of men) can be banned, while firewood collection (typically the responsibility of women) may be permitted (Sekhar, 1998; Allendorf et al., 2006). Furthermore, people whose livelihoods are not dependent on the extraction of forest resources, or who have alternative income sources might not be impacted in the same way as those whose livelihoods entirely rely on the forest resources. Impacts can also differ between subgroups of different socioeconomic statuses, age, education, wealth, location (in relation to the protected area), or ethnicity (i.e., ethnic minorities) (Infield & Namara, 2001; Ferraro, 2002; Allendorf et al., 2006; Kideghesho, 2007; Griffiths et al., 2019). People living in poverty or without land, elderly women, and child-headed households (i.e., households with no adult carers), and ethnic minorities are more vulnerable (International Finance Corporation, 2012).

Madagascar is among the economically poorest countries in the world, with more than 75 % of its population living below the poverty line (World Bank, 2019). However, when it comes to biodiversity richness, Madagascar is one of the world's hotspots (Myers et al., 2000; Ganzhorn et al., 2001). One of the biggest threats to Madagascar's ecosystems is the traditional agricultural practice - the so-called slash-and-burn agriculture, locally known as *tavy* (Ganzhorn et al., 1997). Around 80 % of this country's 27.2 million inhabitants base their livelihoods in agriculture (World Bank, 2019). While they depend on natural resources for practical reasons, Malagasy people are also known for their intrinsic attachments to nature, and the significance it holds in their ancestral traditions (Middleton, 1999). Therefore, in addition to economic importance, the land in Madagascar also has socio-cultural significance. It represents ancestral inheritance, and it is the ancestors' burial place (Evers, 2002;

Graeber, 2007). The Malagasy typically bury their dead in sacred forests (Ramilisonina, 2003), and ancestors hold an important part in traditional religious services (Cole & Middleton, 2001). Losing land is therefore not only a loss of livelihood strategies, but can be related to a loss of ancestral ties, cultural heritage, and identity (Evers & Seagle, 2012).

The littoral forests of Sainte Luce and Mandena located in Anosy region are rich in biodiversity (Ganzhorn, 1998; Dumetz, 1999; Ramanamanjato, 2000; Watson et al., 2005). In addition, the region is known for being exceptionally rich in mineral resources. Since 1986, the QMM mining company (QIT Madagascar Minerals), owned by the Rio Tinto corporation (80 %) and the Malagasy government (20 %), has been active in the area, where it is expected to continue its operations for the following forty years (Rio Tinto, 2017). The QMM's arrival also led to an economic expansion in Fort Dauphin and the smaller surrounding villages. This included establishment of new businesses, as well as city services (for example, subsidized electricity), all of which were completely funded by the QMM (Rio Tinto, 2017). While economic development can be beneficial and lead to increased income (McMahon & Remy, 2001) and employment opportunities (Matlaba et al., 2017), mining can also have negative impacts. Previous studies reported increased living costs, diseases, conflicts and insecurity (Stoudmann et al., 2021), especially from those who were directly involved with mining. Some among them even felt more financially vulnerable, which is contrary to the expected increase of income often anticipated from such enterprises. In addition to negative social impacts, mining can also create environmental problems (Kitula, 2006). The QMM mining company initially set out to operate with a net positive biodiversity impact. As a result of their environmental studies, which commenced in the 1990s, some of the littoral forest fragments became protected areas. Mandena Conservation Zone (MCZ) was established in 2002, and Sainte Luce Conservation Zone was designated in 2005. In addition, around 2,400 ha were set aside as biodiversity offset sites, to compensate for the biodiversity loss and restricted access to the protected areas (Rio Tinto, 2008).

QMM is not the only stakeholder involved in environmental conservation or local livelihoods in the region. SEED Madagascar (previously known as ONG Azafady) is a British conservation charity based in Fort Dauphin and operating in Sainte Luce, where they have had a long-term presence in the form of a conservation camp located at the edge of a protected fragment (i.e., S9). TBSE (Tropical Biodiversity and Social Enterprise) is a Malagasy-run consultancy, created in 2016 by five biologists previously employed by Rio Tinto (QMM). TBSE administer Mandena Conservation Zone, as well as the protected areas in Sainte Luce, where they also operate in the same protected fragment as SEED Madagascar (i.e., S9). Both Sainte Luce and Mandena communities have also benefited from tourism. Manafiafy Beach and Rainforest Lodge is a tourism resort located close to Manafiafy village in Sainte Luce, opened in 2010. Nahampoana Reserve is a privately-owned reserve located close to the Ampasy

Nahampoana village, which was formerly a French colonial garden until becoming a reserve around 20 years ago.

In this study, I combined a qualitative and quantitative approach to investigate how establishing a protected area has affected the lives and livelihoods of people living in the rural communities of Sainte Luce and Mandena, who traditionally depended on local natural resources. I was interested in identifying the positively and the negatively perceived impacts of the QMM mining company, several tourism ventures, and one NGO operating in the region, and to understand how their activities affected the local communities. I did not aim to compare directly the local perceptions of these stakeholders, as their main purposes are too different, despite some of the shared objectives. Instead, I use my findings to compare the two communities (Mandena and Sainte Luce). To understand fully the impacts of forest protection, I compare how the current situation differs from the time before the protected areas were established. In this study, I address the following questions:

1. How are the forest protection, mining, tourism and the NGO activity perceived by the local communities of Sainte Luce and Mandena? What are their perceived impacts?
2. What is the quality of communication between all stakeholders included in this survey? Have the changes in forest management been implemented with cultural sensitivity?
3. Are there any differences in participants' perceptions that are related to their demographic characteristics (i.e., gender and age)?
4. How has forest protection affected the local livelihood strategies in Sainte Luce and Mandena?

Methods

Study area

The study took place in the Anosy region, located in the southeast of the country, which is Madagascar's poorest and most isolated region (Vincelette et al., 2007). It is home to an estimated 807,418 inhabitants (Institut National de la Statistique Madagascar, 2020). The majority of people living in rural communities earn their living as subsistence farmers (ALT & Panos 2009), but agricultural productivity is seasonal and often low. As a result, many are heavily reliant on forest resources for both sustenance and livelihoods (Ingram et al., 2005; Razafindraibe et al., 2013) - a practice that has led to substantial destruction and degradation of the littoral forests over the last 50 years (Dumetz, 1999; QMM, 2001). The littoral forests of Sainte Luce and Mandena located in Anosy region are home to numerous endemic plant and animal species (Ganzhorn, 1998; Dumetz, 1999; Ramanamanjato, 2000; Watson et al., 2005), including several lemur species. Red-collared brown lemur (*Eulemur collaris*), southern woolly lemur (*Avahi meridionalis),* southern bamboo lemur (*Hapalemur meridionalis),* Thomas's dwarf lemur *(Cheirogaleus thomasi)* inhabit both Sainte Luce and Mandena. Ganzhorn's mouse lemur *(Microcebus ganzhorni)* and greater dwarf lemur (*Cheirogaleus major)* are also present in Mandena*,* while Anosy mouse lemur (*Microcebus tanosi)* is among the species found in Sainte Luce. Other threatened species include the Malagasy flying fox (*Pteropus rufus*), the fossa (*Cryptoprocta ferox*), both classified as Vulnerable (Bollen & Donati, 2006). The littoral forests are also home to several threatened species of plants (Chapter 7). This biodiversity made them a national conservation priority (Ganzhorn et al., 2001).

In addition to its rich natural heritage, the region is known for the high level of its exploitation. The extraction of timber and non-timber forest products (i.e., firewood and medicinal plants) is common throughout the littoral forests (Lowry et al., 1999; Vincelette et al., 2003; Ingram et al., 2005b; Norscia & Borgonini-Tarli, 2006; Razafindraibe et al., 2013; Holloway & Short, 2014), while marine fishing is often the primary income source for the coastal community of Sainte Luce (SEED Madagascar Household Survey, unpublished). By contrast, in the more inland community of Mandena, livelihood strategies typically revolve around forest resources and agriculture. Men primarily rely on extraction and selling of timber and non-timber products (Ingram et al., 2005b), farming crops (such as rice and sweet potatoes), and raising cattle (Evers & Seagle, 2012; Kraemer, 2012), while women generate their income from weaving sedge into mats, baskets and hats (Kraemer, 2012). Although local people have used the littoral forests for many purposes, the slash-and-burn agriculture and charcoal production are among the most prominent threats to these forests' biodiversity (Bollen & Donati, 2006). In the past, these practices led to the complete destruction of some of the smaller forest fragments in Mandena (Rasolofoharivelo, 2007).

Mining began in Mandena in 2009, after which it is planned to extend mining activities in Sainte Luce and Petriky (Smith et al., 2012). Preliminary steps for developing the mining site in Sainte Luce began in 2012, but it remains unclear when mining will commence there (Holloway & Short 2014). Since their arrival in the area, the mining company's main purpose is extracting and exporting around 75 million tonnes of ilmenite, titanium ores and zirconium. Their activity is expected to bring benefits in the view of economic influx and development, both to the local population and Madagascar as a whole. The QMM has created 4,000 job positions during the mine construction period, as well as another 600 direct and 2,000 indirect positions that will remain filled during the years of production (Rio Tinto, 2017). Additionally, their economic contributions nationally include taxes and royalties, of which the company is expected to pay US$ 50 million. In terms of social development, QMM has stated its aim as an improvement of households' well-being and quality of life. The QMM supports the Business Centre for the Anosy Region (CARA), responsible for entrepreneurial training of over 4,500 people and a creation of over 200 small businesses. They also support several local associations working towards improving livelihoods through fishing, weaving, and cultivation of red pepper and honey (Rio Tinto, 2017). Rio Tinto stated their recognition of the importance of cultural heritage, as well as the necessity of local communities' active participation through all the stages of their activity (Rio Tinto, 2011). The mining company previously (until at least 2014) held monthly meetings of the Mandena management committee (COGEMA) and members of the local community. Therein they discussed various aspects of the protected area (including access to and use of resources within the protected area), and the larger mining footprint (T. Eppley, personal communication). However, it is unclear whether these meetings still take place.

The local impacts of other stakeholders are diverse. In addition to their Conservation Research Programme, running since 2010, SEED Madagascar also manages several sustainable livelihoods projects, focused on embroidery, beekeeping, sustainable lobster fishing, and weaving (SEED Madagascar, 2019), as well as a community health project (SEED Madagascar, 2019b) and conservation education lessons for children (SEED Madagascar, 2019c). Similarly, TBSE, which are based in Fort Dauphin, specialise in environment and biodiversity management (TBSE, 2017), and instigate "sustainable development", in the view of job creation, beekeeping, and fish farming. Manafiafy tourist lodge mainly contribute through tourism. Their guests typically visit the protected area (i.e., S9 fragment), for diurnal and nocturnal forest walks. However, the lodge operators help the local community by offering local employment, contributing to the local schools, and road maintenance. They also contribute to species conservation through a system of forest fees paid by visitors who are taken on daily educational forest walks, and through a turtle conservation project they run outside of the tourist season (S. Hyde Roberts, SEED Madagascar, personal communication). Finally, Nahampoana Reserve receives around 3,000 tourists a year (Donadieu, 2016), and employs members of the local community as tourist guides.

Data collection

I collected data between April and October 2018. A sample comprising 60 adults (30 women and 30 men) participated in one semi-structured interview (Bernard, 2017) per participant. The study included participants from six villages, three in the Sainte Luce area: Ambandrika (24°46'57.75" S, 47°10'23.99" E), Ampanasatomboky (24°46'48.4" S, 47°11'35.9" E), and Manafiafy (24°46'34.4" S, 47°11'53.5" E), and three in the Mandena area: Ampasy Nahampoana (24°58'51.24" S, 46°58'53.73" E), Betaligny (24°59′28.2" S, 46°58′43.1" E), and Mangaiky (24°56′09.0" S, 46°59'20.1" E). Participants were heterogeneous in respect to their age, while each subsample comprised of equal numbers of women and men. All interviews were conducted in Malagasy with help of a local Antanosy translator (N=3).

Many of the themes investigated in this study could be perceived by the participants as sensitive in their nature. For this reason, I made a conscious effort to assure them of data confidentiality, as well as the anonymous and voluntary nature of their participation. I assured the participants that they had the option of not replying to any question they did not want to reply to without having to provide an explanation, and if this would happen, we would simply move on to the next one. I worked to create a pleasant atmosphere in which the participants would feel comfortable discussing even the more sensitive aspects of their lives. However, my positionality might have still affected the data collection process, by impacting how I was perceived by the participants. As a person of different racial and cultural background, I could have been perceived as similar to foreigners of similar characteristics, which they had previously encountered. Examples include researchers who had previously worked in their area, foreigners delivering conservation education or outreach activities, working in wildlife conservation or developing community sustainable development programs. As this might have led the participants to expect me to hold specific beliefs about aspects of their lives discussed in the study (i.e., a belief that forest and wildlife protection is of outmost importance), they could have subconsciously wanted their answers to reflect their agreement with me. Another factor that could have affected how the participants perceived us was my translator who worked with me in Sainte Luce being employed by a local NGO (i.e., SEED Madagascar). I reflect on the implications of this for the study results in the Discussion of this chapter. While biases are expected, I acted to minimise them by ensuring that neither myself nor the translator conveyed any specific expectations about their answers, and that we always used neutral language. Whenever a participant provided an answer which might be perceived as "less desirable" (i.e., dismissing the benefits of forest protection), I would communicate understanding and empathy, and ask follow up questions. Ethical approval for the study was granted by the University Research Ethics Committee of Oxford Brookes University.

In the interviews, I explored how participants have experienced forest protection and the socio-economic development resulting from it, as well as how these changes affected their lives and livelihoods. I surveyed the perceived positive and negative effects of the protected area, mining and the QMM mining company, tourism projects (i.e., Manafiafy Beach & Rainforest Lodge in Sainte Luce, and Nahampoana Reserve in Mandena), and NGO presence (SEED Madagascar in Sainte Luce). While my questions directly focused on the perceptions and impacts of forest protection and mining and the QMM, my findings about the tourism and an NGO are a product of the more general inquiries about the perceptions of foreigners' presence in the area (General Appendix). As participants' answers focused around the previously mentioned tourist projects, and in Sainte Luce, an NGO operating locally, I was able to assess their perceptions separately in a meaningful way. Positive and negative reports were categorised as conservation impact, social impact, and economic impact. Categorisation was based on themes the reports focused on – for example, preserving forest and wildlife, or protecting the ecosystem services were listed as positive conservation impacts, while destruction of forest or harming wildlife were recognised as negative conservation impacts. Positive social impact category comprised reports of community investment or knowledge and skill development, while negative social impacts included fearful responses and health and safety concerns. Finally, positive economic impacts included job opportunities, tourism, or buying local products, while negative economic impact category comprised reports of unfairness, resource restrictions and livelihood insecurity. The QMM mining company is responsible for forest management, therefore inquiring about them might be perceived as a sensitive question. For this reason, I made sure that all participants were aware that I was in no way associated with the mining company, and that their replies will not be reported to the mining company. To comprehend any potential change in local livelihoods better, I inquired about participants' income sources, with attention given to previous and current use of natural resources (i.e., hunting, fishing).

Results

1. *Forest protection*

Forest protection impacted the surveyed participants differently. Most commonly, participants reported both positive and negative impacts of this conservation measure. A solely negative perception of forest protection was more commonly reported in Mandena (Table 2).

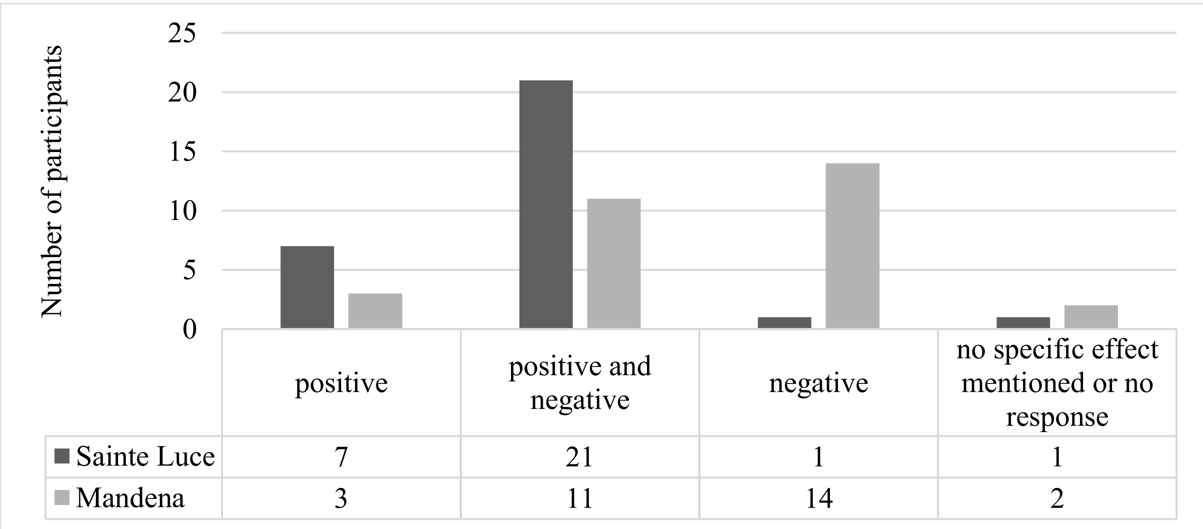


Figure 1. Perceptions of the protected area of the participants from Sainte Luce (N=30) and Mandena (N=30).

If the number of effects mentioned by the participants is considered, positively perceived effects of forest protection were reported by more participants in Sainte Luce than in Mandena (Table 1). They were mainly associated with the positive conservation impact of forest protection, such as forest and wildlife preservation, or protection of the ecosystem services. As one participant from Sainte Luce explained, “I like the protected area, and I have had no negative impact from it. The forest brings the rain. I want the new generation to see the forest, I want it to be conserved.” (man, 56, Ampanasatomboky). Another stated that without forest protection measures, the forest might have been gone already: “My grandfather told me there used to be a lot of forest in Sainte Luce. Primary forest. But now, only some of it is left. Without forest protection, all would disappear.” (man, 32, Manafiafy). Albeit to a lesser extent, Mandena participants also recognised the implications of forest protection for the preservation of natural resources: “Without the protected area, everything would have been gone now as a result of hunting and logging.” (woman, 36, Mangaiky). “It is good to conserve the wildlife, like chameleons, snakes and tortoises. They are preserved for the new generations in the future. They would not be able to see them otherwise, they would be gone without the protected area. But it is also bad because I cannot get firewood and timber.” (man, 70, Betaligny).

The negative effects were reported to a similar extent by Sainte Luce and Mandena participants (Table 1). Some participants discussed the diminishing resources in the unprotected areas due to growing anthropogenic pressures and selective logging: “There are a lot of people using the unprotected area and there is no more of the strong wood there because everyone wants to use it for building their houses. It is difficult not being able to go into the protected area. Other types of wood only last 4-5 years.” (man, 66, Ambandrika). Many participants often focused on the negative economic impact of this conservation measure on their livelihoods, resulting from the restriction of their use of natural resources (Figure 2). As one Sainte Luce participant revealed, “It is good for conservation, but not for me. I cannot go in the protected area to collect firewood, timber, medicinal plants.” (man, 80, Manafiafy). Another added that “Before forest protection, everything I needed was free and close. Life is more stressful now. I am older, but I have to go far away to get firewood, and I can only carry a little bit from so far. It takes longer and I cannot get as much.” (woman, 61, Ampanasatomboky). A participant from Mandena explained, “The protected area is good for the future. At the moment it looks bad, but it will be good for the future generations. It keeps the forest for them. We are poorer now, the income is lower. It was stopped by the QMM because they protected the forest.” (woman, 43, Mangaiky). Others felt that there were too many rules: “I would feel like I was stealing if I went to the protected area.” (woman, 27, Ampasy Nahampoana). A single participant from each area gave no response to the question.

Figure 2. One of the activities now banned in the protected area is zebu grazing. However, zebus can still occasionally be observed grazing in the Mandena Conservation Zone. Zebu grazing is not to be confused with them being escorted through the protected area (shown above), which is allowed. Photographs by E. Račevska, July 2017 and October 2017.

Table 1. Positive and negative effects of forest protection, as reported by the participants from Sainte Luce (N=29) and Mandena (N=29).

Forest protection		**Frequency of response**	
Positive effects		**SL**	**MND**
Conservation impact	Preservation of forest and wildlife for future generations.	8	5
	An increase in species' population sizes.	3	-
	Prevention of forest destruction, e.g. for agriculture.	2	-
	Healthy forest attracts the rain.	5	1
	Forests purifies the air.	1	-
	Forest can regenerate, increase in size.	1	-
	Forest and animals would otherwise disappear.	3	5
Social impact	Children and tourists like seeing the lemurs.	2	-
Economic impact	Protected forest attracts tourists.	1	-
	Jobs provided by the researchers. Jobs in the protected area management.	1	1
	Forest attracts the rain, which is good for agriculture.	-	2
Negative effects			
Economic impact	Restriction of forest resource extraction. Increased difficulty of securing livelihoods.	22	20
	No suitable/enough alternatives.	5	1
	Unfair distribution of money between communities.	2	-
	Livelihood strategies (i.e. fishing) banned in the MCZ.	-	2

2. Mining and the QMM mining company

Sainte Luce and Mandena participants most commonly reported the negatively perceived effects of mining (Figure 3). “Mining will destroy the forest, and I do not have the money to buy cement. There is also a bad smell associated with mining, it makes people sick.” (man, 32, Manafiafy). Two participants in Sainte Luce and four in Mandena did not answer this question, and one participant in Sainte Luce stated they did not know anything about mining or the QMM, and could not respond.

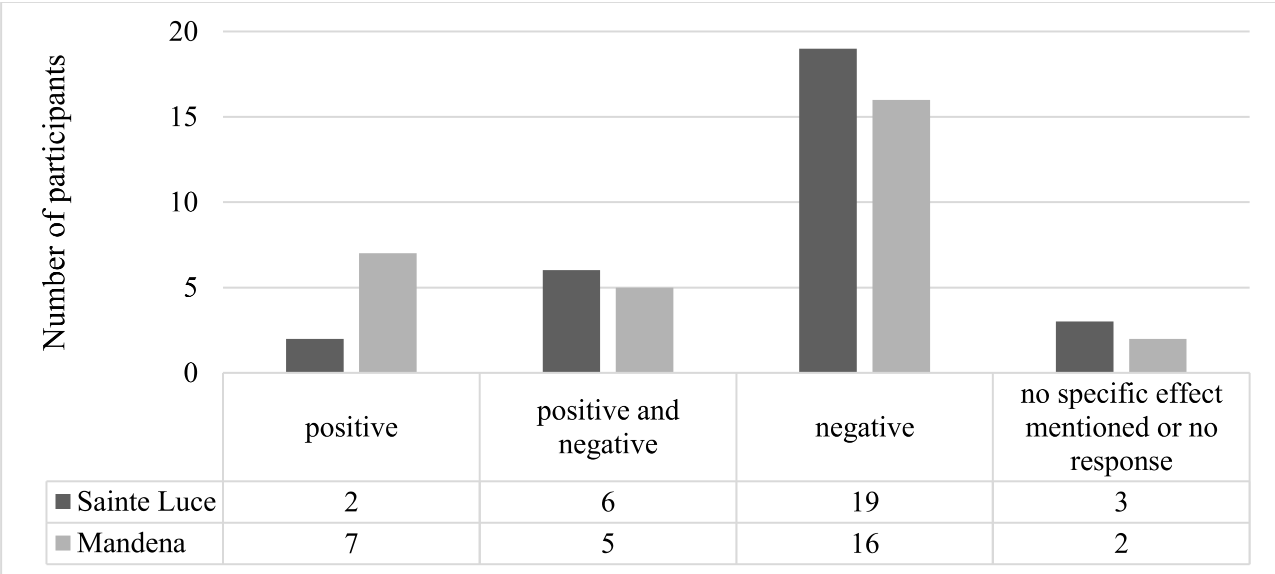


Figure 3. Perceptions of mining and the QMM company, as reported by participants from Sainte Luce (N=30) and Mandena (N=30).

Sainte Luce participants anticipated positive economic impact of mining (Table 2). As one participant explained, “I do not mind if the QMM get here if I get a job there.” (woman, 42, Ambandrika). Others hoped that job opportunities will extend to their children: “I like the QMM and want them to come here. Maybe my children will get a job with them.” (woman, 64, Ambandrika). Mandena participants praised the mining company most notably for their investment in community infrastructure, and job opportunities. One participant explained that “The QMM bring development. They also built the school and help the local people.” (man, 48, Betaligny). Another stated that “The QMM have done social work, like forming an association in Ampasy Nahampoana for beroz farmers. They buy the fruits from the people. Also, the QMM employees buy their products in the market in Fort Dauphin.” (man, 28, Betaligny).

Participants from both areas listed many more negative than positive effects of mining. In Sainte Luce participants’ responses largely focused on the anticipated future negative conservation impact, which they often explained as a result of seeing what happened in Mandena. “The forest has disappeared in

Mandena. People who live close are not healthy." (man, 78, Manafiafy). "They will destroy everything, similarly to in Mandena. When they come, farmers will not be able to grow crops. They promise to do good things, but at the moment, there is still nothing." (woman, 61, Ampanasatomboky). Sainte Luce participants voiced their concerns about mining destroying the forest, but also recognised the importance of economic development associated with mining: "I could say that it is good, but they are destroying the forest. I could say it is bad, but we need the jobs and the money." (man, 77, Manafiafy). They were also worried about the bad impact that mining would have on their health, as well as potential relocation. "I do not want them to come to Sainte Luce because they will create a lot of problems here, for example health problems. People will get sick from radioactivity, and the water will become dirty. I do not know where we will move when the mining company gets here, the village will have to leave." (woman, 28, Manafiafy). In many cases, the relocation concerns were related to livelihood strategies: "If they come, I will have to move, and I do not want that. My life depends on fishing, and I would not be able to fish if I move." (man, 48, Ampanasatomboky). "The QMM will destroy the land, and my life depends on growing crops. I also have a tomb in the area that will be mined, I will have to move the bodies." (man, 42, Ambandrika).

Mandena participants most frequently listed the factors associated with the (negative) economic impact. As one participant stated, "Mining has affected our life. The area used to be natural, a good source of income from selling natural resources like timber or fish, which were free. We earn less money now." (woman, 35, Mangaiky). Another explained that the QMM salary is not sufficient to compensate their previous income: "My husband works for the QMM, but the salary is not enough. We have problems because we cannot collect natural resources." (woman, 25, Mangaiky). One participant explained that, as mining has affected every family, the company should employ at least one member of each family. Some participants voiced their sense of helplessness, explaining that there is nothing they can do since the government had already made their decision without regard for their opinions. "Mining will destroy all of the forest, the animals and the people. But the problem is that the Malagasy government likes the money." (man, 41, Ampanasatomboky).

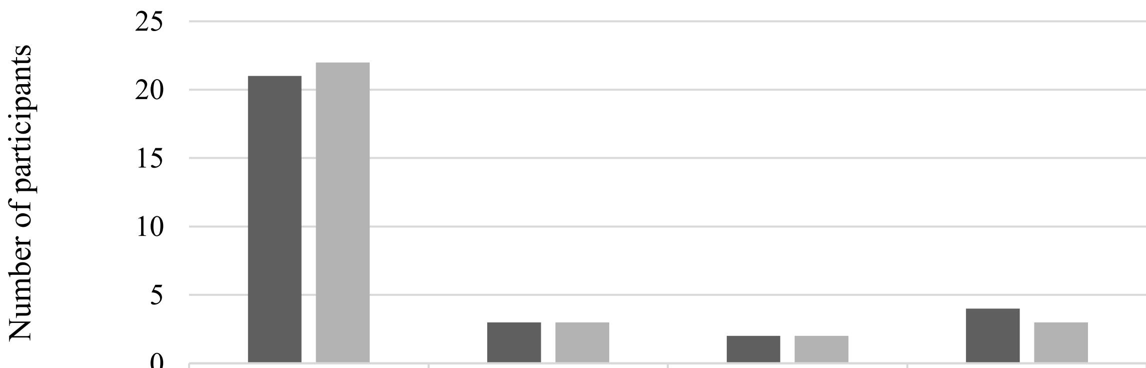
Table 2. Positive and negative effects of mining and the presence of QMM mining company, as reported by the participants from Sainte Luce (N=27) and Mandena (N=26).

QMM Mining Company		**Frequency of response**	
Positive effects		**SL**	**MND**
Conservation impact	Creating the protected area. They are one of the stakeholders in charge of protecting the forest.	2	1
Social impact	Community investment (they built a bridge, a school, a hospital).	1	2
	Bringing skills (i.e. bee keeping).	-	1
Economic impact	They (will) bring job opportunities, provide compensations.	6	4
	It is the biggest project in the area.	-	1
	Starting a farmers' association and buying their products.	-	2
Negative effects			
Conservation impact	Destruction of the forest and/or the swamps. Holes in the ground, the land unstable.	13	3
	Air and water pollution.	3	-
	Harmful to wildlife.	2	-
Social impact	Fear. An organised strike resulted in arrests.	-	2
	Too many rules, people feel like thieves for breaking them.	-	2
	No access to their ancestral land.	-	1
	Fear of tomb relocation.	1	-
	Destruction of the forest, and people need wood to build houses.	1	-
	Fear of village relocation.	6	-
	Health concerns. Radioactive particles carried by wind and polluted water making people sick, impacting pregnancies, causing death.	8	4
	More cars, making the area unsafe for children.	1	-
Economic impact	Concerns over soil fertility, and the negative consequences for agriculture, leading to diminished livelihoods.	10	10
	Impact of forest destruction on the forest-based livelihoods.	2	-
	(Fear of) no compensations or no jobs. Salary too low.	2	6
	Only gave money to the mayor.	-	2
	Only hire migrants (i.e. from Antananarivo), people with university degrees.	-	4
	Not enough development - people still live in wooden houses.	-	1
	Fear for livelihoods in case of village relocation.	2	-

Interestingly, although the QMM mining company has created the protected areas and is responsible for their management, this was pointed out by only one participant in Mandena, and two in Sainte Luce. One only mentioned it in passing while discussing a different question, while the other stated that the QMM only protected the forest because they wanted something from it. Some participants were also dissatisfied about the lack of response from the QMM when they tried to voice their concerns: "We wanted to talk to the QMM and ask for help, but the police came, and people went to jail." (man, 62, Ampasy Nahampoana). Others were unhappy about the perceived insufficient development in the area: "Nothing changed in FD since they came, people still live in wooden houses. I do not like that." (woman, 27, Betaligny). Some participants also felt that their community was insufficiently compensated for their loss of land and impact on livelihoods: "The QMM destroyed the area where mahampy used to grow. And the forest. Local people have land there – the QMM took it and did not give them money as compensation. The QMM made a deal with the mayor, and if he accepted it, the QMM do not care about the local people." (man, 70, Betaligny).

3. Tourism and foreign visitors

Sainte Luce and Mandena participants most frequently reported positively perceived impacts of tourism (Figure 4). One participant from Sainte Luce stated that they had no experience with either tourists or the tourism project, and therefore did not know how to respond.



	positive	positive and negative	negative	no specific effect mentioned or no response
Sainte Luce	21	3	2	4
Mandena	22	3	2	3

Figure 4. Perceptions of tourism by participants from Sainte Luce (N=30) and Mandena (N=30).

Participants from Sainte Luce and Mandena mainly listed the positive effects of tourism. In Sainte Luce, a third of the participants reported the community support demonstrated by the local tourism venture. "The Manafiafy lodge give their car to people in emergency." (man, 32, Ampanasatomboky).

"The Manafiafy lodge gave fishermen jackets." (man, 76, Ampanasatomboky). I In Mandena, the most frequently reported positive social impact was tourists' engagement with members of the local community. "Tourists bring knowledge, skills and development." (man, 65, Mangaiky). Others noted that local tourist guide discouraged tourists' contact with the local people. "Tourists used to be kind when I was a child. They would give us pens, books and clothes. Now, the guide (at Nahampoana Reserve) has stopped them. Only the rich benefit from the tourists, people who have restaurants. They get the money." (woman, 52, Betaligny). Other reported negative effects mostly focused on the lack of positive economic impact (Table 3). As one participant explained, "The tourists just take a photograph and go home. I have no benefit from them." (woman, 27, Betaligny)

Table 3. Positive and negative effects of tourism, as reported by the participants from Sainte Luce (N=29) and Mandena (N=30).

Tourism		**Frequency of response**	
Positive effects		**SL**	**MND**
Social impact	Community investment (they built a bridge, provide jackets for the fishermen, lend vehicle in emergencies, provide school supplies).	10	-
	Tourists are friendly. Happy to see/engage with them.	3	6
	Tourists curious about their way of life, respectful of their culture.	1	2
	Tourists bring knowledge and skills.	1	1
	Tourist presence is good for the children, they can learn English.	1	1
	Tourists can spread their voice to others who can help. They can show photographs, attract more tourists.	-	2
Economic impact	Tourists help their income, buy local products, bring presents.	7	6
	Tourists take their photograph, and give money or presents in return.	-	1
	Development and job opportunities for community members.	5	4
Negative effects			
Social impact	Not enough. They should build a hospital for the fishermen.	1	-
	They do not the help the community, only think about themselves.	1	1
	They do not provide as much development as SEED Madagascar.	1	-
Economic impact	Only the rich profit from tourists.	-	1
	No benefits for the participant personally.	1	-
	Tourists discouraged from giving presents.	-	2
	Not enough job opportunities.	1	-
	Donations from abroad do not always reach them.	-	1

4. NGO (in Sainte Luce)

The perceptions of the NGO operating in Sainte Luce (i.e., SEED Madagascar) predominantly included positive effects (Figure 5). SEED Madagascar was mostly praised for the positive effects of its presence. Most arguments focused on their positive social impact, mainly in the form of community development projects and educational efforts. "SEED Madagascar help the community. *Project Tatirano* provides many water tanks so people can have clean water. Before we only had wells. They also do conservation work." (man, 32, Ampanasatomboky). "They help people with tree planting, and they help the children through conservation education." (woman, 61, Ampanasatomboky). Their conservation work and positive economic impact (i.e., job opportunities) were also reported, while the negative effects were limited to the lack of job opportunities (Table 4). "SEED Madagascar help with conservation. Because of them and other researchers, there are more trees regenerating, and tenrecs and lemurs have increased in numbers because of the conservation zone." (man, 67, Ambandrika). "If there are jobs for the local people, they do not hire many people. They should employ people from all villages and from different families." (woman, 68, Ampanasatomboky).

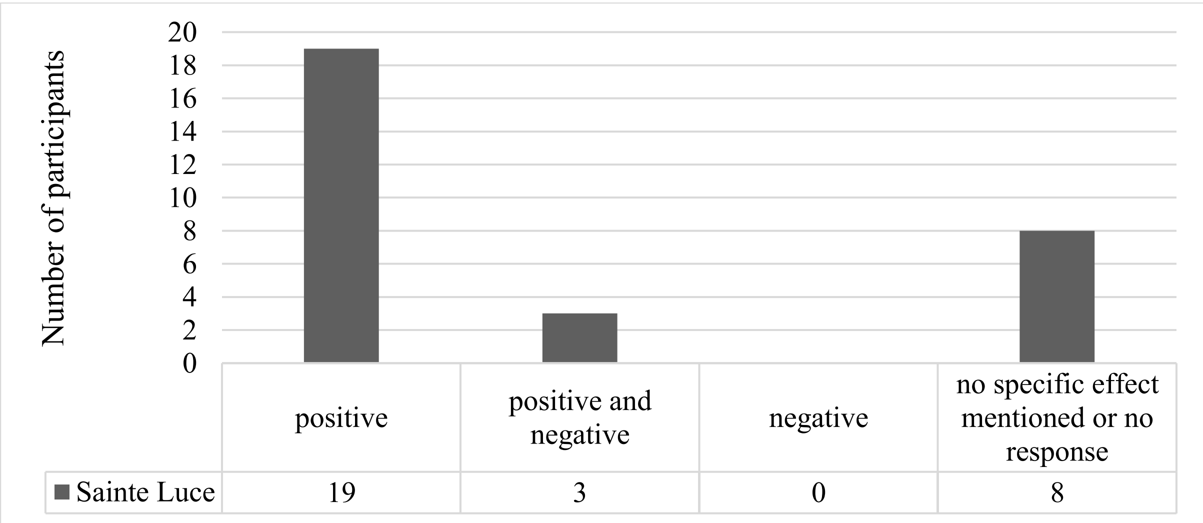


Figure 5. Perceptions of SEED Madagascar among participants from Sainte Luce (N=30).

Table 4. Positive and negative effects of NGO presence (i.e., SEED Madagascar), as reported by the participants from Sainte Luce (N=30).

SEED Madagascar		**Frequency of response**
Positive effects		
Conservation impact	Conservation projects and planting trees.	6
	Increased wildlife population sizes (e.g. tenrecs, lemurs), and tree regeneration.	1
Social impact	Investment into community (English lessons, school building, provision of clean water).	7
	Knowledge and skills.	3
	Conservation lessons for children.	5
	Staff participate in important ceremonies.	1
	Volunteers bring toys.	1
	They make this place special and are well liked.	3
Economic impact	Job opportunities. Setting up local enterprises that yield economic benefits.	10
	Their staff and volunteers buy local products.	4
Negative effects		
Economic impact	Not enough job opportunities.	2

5. *Impact of forest protection on local livelihoods*

In Sainte Luce, the main livelihood strategies showed a strong gender division: women most often earned their income from weaving sedge (mahampy) into various products (most notably mats, baskets, and hats) (36.66 %), while men most commonly reported fishing as their main livelihood strategy (36.66 %) (Table 5). Some men also provided a secondary income source, most often agriculture (10 %). In Mandena, agriculture was the most prevalent livelihood strategy (56.66 %) regardless of participants' gender. Income sources re-categorised as *other* included embroidering (*Stitch Sainte Luce*), working as a guard at a tourist lodge, and being a teacher in Sainte Luce, and working at a shop and maintaining others' rice paddies in Mandena.

Table 5. The main income sources of the participants from Sainte Luce (N=30) and Mandena (N=30).

	Sainte Luce			**Mandena**		
	Women	**Men**	**Total**	**Women**	**Men**	**Total**
Charcoal production	0	0	**0**	1	1	**2**
Farming	0	3	**3**	7	10	**17**
Fishing	0	11	**11**	0	0	**0**
Timber collection	0	1	**1**	0	3	**3**
Weaving	11	0	**11**	0	7	**7**
Other	2	1	**3**	2	0	**2**
No income	2	2	**4**	0	2	**2**

Many of the participants of both sub-samples reported growing crops (N=29, or 96.6 %). The most commonly grown crop in both communities was cassava (N=30 in Sainte Luce, N=26 in Mandena) (Table A1, Appendix V). Participants reported growing between two and nine different crops in both Sainte Luce (Median=4.5, IQR=2), and Mandena (Median=5.0, IQR=2). The most prevalent agricultural practice in both areas was slash-and-burn agriculture, locally known as *tavy* (N=58). When the harvest was good and extra crops were grown, people typically sold it. “When the trees are young, there is not enough fruit to sell, but when the harvest is good, I sell.” (woman, 35, Mangaiky).

Most participants reported keeping production animals (N=28, or 93.3 % in Sainte Luce, and N=24, or 80.0 % in Mandena). Commonly kept animals included poultry (i.e., chickens, ducks, and geese), pigs and zebu cattle (a species of domestic cattle originating from South Asia, but commonly kept in many parts of Africa) (Figure 6). In both Sainte Luce and Mandena the most commonly kept animals were chickens (Table 6). Zebu cattle and bigger poultry (i.e., geese) were sometimes shared between related households. As one participant explained, he kept the chickens, pigs and zebus because “This is the tradition” (man, 24, Mangaiky).

Table 6. Production animals kept by the participants from Luce (N=28) and Mandena (N=24).

	Sainte Luce	**Mandena**
Chickens	28	21
Ducks	13	1
Geese	10	1
Pigs	4	12
Zebu cattle	8	10

Cats were commonly kept as companion animals in Sainte Luce (N=10), but seldom in Mandena (N=2), with their value stemming from them keeping the rodents away from people's homes. Dogs were mostly kept for protection, or for tenrec hunting, but keeping dogs was considered a taboo (*fady*) by many members of the community. For this reason, dogs were kept by only a very few households in the sample from Mandena.

Figure 6. Economically important production animals (left to right): zebu cattle returning to the village of Ambandrika in Sainte Luce after being grazed in the savannah, live chickens being transported to Fort Dauphin on the side of a truck, pigs foraging on the river shore near Ambandrika. Photographs taken by E. Račevska in November 2017, and July 2017.

6. Reliance on natural resources: past and present

Hunting

According to the participants of this study, prior to the establishment of the protected areas, the prevalence of hunting was similar in Sainte Luce and Mandena: 11 participants from Sainte Luce and 13 from Mandena reportedly hunted in the past. After forest protection was implemented, however, only one participant from Sainte Luce continued to hunt, while the same was true of seven participants from Mandena. Before the protected areas were established, many Sainte Luce participants used to hunt in the now protected fragments (i.e., S8, S9, and S17), as well as the unprotected ones (i.e., S7). One participant revealed he was able to catch three or four woolly lemurs in a day using a slingshot: "They just rest, it is crazy." (man, 44, Ambandrika). Participants who still hunted at the time of my data collection did so around the protected fragments, in the area where the community cultivates crops (i.e., near S8 forest fragment), and occasionally in one of the protected forest fragments (i.e., S8). Participants who had never hunted provided different explanations. For example, some explained they "did not like to kill animals" (man, 38, Manafiafy). Others explained that "I would feel as a weak man if I hunted animals. It is embarrassing for the community if somebody's only job is hunting. It is not a real job, people would talk bad about me." (man, 32, Ampanasatomboky). Other reasons included not knowing how to hunt or build traps, as well as hunting being against their job policy – a reason provided by the participant who used to work for TBSE (man, 31, Ambandrika).

Birds were typically hunted using a slingshot, with the exception of the Madagascan crowned ibis (*Lophotibis cristata*), which just like in Mandena, used to be hunted with a trap (Figure 7). Tenrecs (Tenrecinae) were hunted with dogs, traps, or by being hit with a stick or grabbed by their necks. As one participant explained, "I hunted birds with a slingshot, and tenrecs with traps (*ampiviky*) baited with banana peel or forest crabs" (man, 32, Manafiafy). Another explained that he used to hunt tenrecs when he was younger. "If I saw a tenrec in a cassava field, I would hit it with a stick. They are hard to catch, they bite." (man, 72, Manafiafy). Lemur hunting depended on the species: bigger lemurs, such as the red-collared brown lemur (*Eulemur collaris*), or the southern woolly lemur (*Avahi meridionalis*), used to be hunted with slingshots or traps, while smaller species, such as the Anosy mouse lemur (*Microcebus tanosi*) were grabbed from their sleeping sites. One participant reported having used a gun to hunt lemurs and birds.

Similarly, Mandena participants used to hunt in the Mandena Conservation Zone (MCZ) before it became protected, as well as in the mountains. As one participant explained, "I used to hunt once or twice a week, twenty years ago. I hunted tenrecs with a dog." (man, 48, Betaligny). Another participant detailed that he only ever hunted for sustenance: "I never sold what I caught, it was only for my own food. I stopped hunting when I was 40." (man, 70, Betaligny). Those who still hunted at the time of data collection, did so in the unprotected forest fragments. Participants who have never hunted explained that this was because they were not good at it or did not know how to hunt. One participant replied that he did not hunt because he did not want to be near the snakes: "I don't like the snakes living in the forest." (man, 50, Betaligny). The majority of hunted species were birds, such as helmeted guinea fowl (*Umida meleagris*) and wild ducks (*Dendrocygna javanica)*. One participant explained he used to hunt wild ducks "In the hunting season, which is the rainy season, between April and October. I used guns." He also used to hunt tenrecs as a boy, but does not anymore because of a family taboo related to keeping dogs: "I don't have a dog anymore to help me catch tenrecs, it is *fady* for my wife to keep dogs." (man, 65, Mangaiky). In Mandena, one participant disclosed occasionally hunting lemurs (Table A2, Appendix V).

Figure 7. Hunting tools (left to right): a trap consisting of wood and fishing line, used for catching bush pigs in Ampasy Nahampoana village in Mandena; a slingshot used for hunting small birds, and lemurs (Ampasy Nahampoana); evidence of lemur hunting in a protected fragment in Sainte Luce (i.e., S9), confirmed by a member of *FIMPIA* (Association of Managers of Forests of Ambatoatsinana) - a long, sharp stick left in a tree hole. Photographs taken by E. Račevska, July 2018 and April 2018.

Fishing

Before the establishment of the protected area, fishing was more prevalent in Sainte Luce (N=30) than in Mandena (N=18). Since the protected areas have been created, fewer people fish in both Sainte Luce (N=23) and Mandena (N=11). However, fishing continuing to be more common in Sainte Luce. Older Sainte Luce participants stated that they no longer fished due to their advanced age. “I used to use a fishing line and hooks, but I no longer fish because I am too old now.” (man, 67, Ambandrika). On the other hand, Mandena participants who no longer fished, stated that this is because fishing has been banned in the MCZ, and the other areas are farther away. One participant explained that he used to fish as a child, but does not anymore because “I don’t know how to fish” (man, 40, Mangaiky). Participants also mentioned that there are now fewer fish than there used to be when they were young.

Since the establishment of the protected area, twice as many people continued to fish in the river in Sainte Luce (N=22) than in Mandena (N=11). As one participant explained, “When the weather is nice, I fish on the sea. When the weather is bad, I fish on the river.” (woman, 42, Ambandrika). A participant from Mandena revealed that “I fish on the river twice a week.” (man, 25, Ampasy Nahampoana). Another explained that he used to fish before, but has stopped because “I cannot earn enough money from it anymore.” (man, 62, Ampasy Nahampoana). One participant explained how he fishes on the river to pass the time: “When I’m too tired from working in the field, I fish while I rest to pass the time.” (man, 24, Mangaiky).

Similarly, just over half of Sainte Luce participants (N=16) and none of the participants in Mandena fished in the ocean. In addition to fishing, 12 of Sainte Luce participants also collected lobsters, and 14 collected prawns. Fishermen typically used a canoe, locally called a *pirogue*, both on the river and on the ocean. Fishing equipment included fishing lines with hooks for fishing in the ocean, while lobster traps were built using different types of wood, tied together with vines. One participant explained he used “fishing line and hooks, and worms for bait” (man, 70, Betaligny). Fishing in the river traditionally involved a fish trap woven from sedge (mahampy), locally known as *antsidy*, but the most prevalent equipment still in use were old mosquito nets (Figures 8 and 9).

Figure 8. Fishing in Mandena (left to right): fishermen on the river outside of the Mandena Conservation Zone, and a day's catch of a different fishermen, encountered after fishing in the Mandena Conservation Zone. For this amount of fish, he would typically charge 2,000 Malagasy Ariary (0.42 GBP). Photographs by E. Račevska, September 2018.

Figure 9. Fishing in Sainte Luce (left to right): *pirogues* on the beach in Manafiafy village, a fisherman carrying a shark to be sold on the market in Mahatalaky, and a demonstration of using a mosquito net for fishing on the river by a woman in Ambandrika. Photographs by E. Račevska, March 2018 and September 2018.

Discussion

Findings of this study show that livelihood strategies of the two communities traditionally dependent on natural resources reportedly remained unchanged, but securing them became harder. Mandena participants mostly perceived the restrictive side to forest protection, which also led to negative perceptions of the mining company. The company was praised for job opportunities, but their perceived unfair distribution was reported as negative. Sainte Luce participants more frequently recognised positive aspects of forest protection, but their perceptions of (upcoming) mining were similar to those of Mandena participants. Perceptions of the NGO and tourism were overwhelmingly positive in both communities, due to their community investment and support.

Perceptions of forest protection

Sainte Luce and Mandena participants differed in their perception of forest protection, namely in terms of their solely negative perceptions of this conservation measure, which was higher in Mandena. While the majority of Sainte Luce participants also reported its negative impacts, they were more frequently paired with positive impacts. Sainte Luce and Mandena participants also differed in the frequency of giving specific responses. For example, while the argument that forest protection will lead to the preservation of natural resources for the future generations was given by participants from both communities, it was more commonly voiced in Sainte Luce. This could be related to the fact that only the Sainte Luce community have had regular and extensive exposure to conservation education, implemented by SEED Madagascar. Although their lessons are directed at children, it is likely that children share their acquired information with their parents, thereby increasing parents' knowledge. This is a common strategy for enhancing conservation awareness in adults (Duvall & Zint, 2007; Damerell et al., 2013; Rakotomamonji et al., 2015). Sainte Luce has also had a more continuous presence of researchers from various institutions since 1999. However, these findings should not be interpreted as the lack of importance of forest conservation among Mandena participants, especially since several have, for example, reported that without forest protection, forest and animals would have disappeared by now. This also does not mean that members of either community would have not recognised the importance of forest preservation without the aid of conservation education, or researchers' presence in the area. Furthermore, other aspects of participants' lives, which might be impossible to separate from the establishment of the protected area, could have played important roles in shaping their perspectives. The fact that Mandena is already mined (unlike Sainte Luce) could have shifted participants' focus from the positive aspects, due to the additional impacts on livelihoods. It is important to note here that thinking about the future is a luxury only available to those with adequate, stable and secure livelihoods. Long-term benefits might therefore not be a priority to those facing the more pressing issues of securing food for their families in the present or the near future.

The positively perceived economic impacts of tourist attraction were mentioned only in Sainte Luce. Although tourism ventures operate in both communities, the one in Sainte Luce (i.e., Manafiafy Beach and Rainforest Lodge) brings the tourists directly to the protected area (and requires their payment of entrance fees), while only a few international tourists visit the Mandena Conservation Zone, spending the majority of their time in the nearby Nahampoana Reserve. Certainly, fewer international tourists visit the Mandena Conservation Zone, as compared to the protected area in Sainte Luce. The fact that no participants mentioned the Mandena Conservation Zone in this context might also be related to its location. Most tourists arriving at the Nahampoana Reserve pass through the villages located along the national road, which gives them an opportunity to later explore the area and come in contact with the locals. However, tourists coming to the Mandena Conservation Zone arrive thorough the mine gate, by-passing the villages, which decreases their chances of being seen by and interacting with the local population. Interestingly, while the tourism project in Sainte Luce is a private enterprise, and Mandena Conservation Zone is managed by the local community (and entrance fees are instated as well), the former is perceived as more positive despite it not being community based.

Negative attitudes towards a protected area are often related to the restriction of natural resource use or restrictive forest management policies (Anderson, 1990; Allendorf, 2006). This especially refers to people with less diversified income sources, who only base their livelihoods in the forest resources (Ratsimbazafy et al., 2012). Similarly, a lack of compensation for loss of (traditional) livelihoods, negative economic impact and a perception of no direct benefits from the protected area can lead to negative attitudes towards it. On the other hand, more positive attitudes are related to a better understanding of conservation issues. These are often associated with higher education (Marcus, 2001; Allendorf, 2006; Ratsimbazafy et al., 2012): more educated people are often more knowledgeable about forest conservation issues. A study of local perceptions of protected areas in Ghana and Tanzania showed that attitudes towards forest protection are mostly influenced by the conservation governance of the two countries (Abukari & Mwalyosi, 2020). Participants of that study reported that a more inclusive governance would increase the positive perceptions and attitudes towards conservation goals. The same study reported a possible lack of understanding of the ecological outcomes of a protected area, which the authors believe might change with implementation of educational activities. Local communities' positive attitudes are important for conservation success, but caution is necessary when interpreting such seemingly overly positive results, as they may be a result of participant bias. People who have received conservation education might simply be more likely to report what they think the researcher wants to hear, while their thoughts or actions might not have actually changed. I acted to minimize this by emphasising data confidentiality, while also creating a judgement-free atmosphere during data collection and receiving all answers with interest and gratitude.

Concerns about the negative effects of forest protection on traditional livelihoods are also not uncommon (Ite, 1996; Ratsimbazafy et al., 2012). Even when many respondents express positive attitudes, they tend to not want to be the ones directly (negatively) impacted by the change (Marcus, 2001). In this study, the establishment of the protected area has reportedly increased the difficulty of most participants' efforts to secure livelihoods, but the new policies are not adhered to by all. The issue may be more serious in Mandena than in Sainte Luce, where some of the banned activities (i.e., fishing, grazing zebu cattle) were observed several times in the protected area during the data collection. Although fishing may not have a big impact on the forest, the presence of cattle is likely detrimental to forest regeneration, and its incidence should be examined in more detail in the future. Zebu cattle grazing was not observed in the protected forest by other researchers who previously worked in the area (G. Donati, personal communication; T. Eppley, personal communication), so it is possible that zebu cattle grazing is a recent habit, or something that happens infrequently. It is also not clear which villages the people disregarding the ban were from - they might not belong to the communities included in this study. To address these issues, it is necessary to understand why they happen, and to what extent. It is not uncommon that new management policies are respected out of fear of punishment, rather than a sense of importance of conservation (Marcus, 2001). In the current study, this was exemplified during an informal post-interview conversation with a Mandena participant, who stated he no longer hunted red-collared brown lemurs (*Eulemur collaris*), especially those wearing radio collars, out of fear of the consequences he might receive from the mining company. This information is interesting considering that radio-collars are not placed by the mining company, but by the researchers working in the area. The mining company had previously radio collared the red-collared brown lemurs and the southern bamboo lemurs (T. Eppley, personal communication), so it is possible that this is the reason for the confusion. Moreover, forest protection rules are enforced by the community members, and not the mining company. This finding therefore shows the perceived authority of QMM, while also signalling the urgency of exploring the relationships with and the attitudes towards the local staff in charge of enforcing the forest protection rules. While the majority of people enforcing forest protection are community members (in both Sainte Luce and Mandena), it is also possible that their lack of authority could stem from the socioeconomic imbalance between them and the rest of the community (Ormsby & Kaplin, 2005). Power struggles over economic benefits or decision-making authority can lead to intra-community conflict (Moscardo, 2008). People obtaining the most benefits from having a protected area are sometimes those that already have a socioeconomic advantage (Ormsby & Kaplan, 2005; Ratsimbazafy et al., 2012; although such finding was not confirmed in all studies – Marcus, 2001), and this was also reported by some of the Mandena participants.

Perceptions of mining and the QMM mining company

Sainte Luce and Mandena participants did not differ in their perceptions of mining and the QMM mining company, despite the two areas being in different stages of mining. In fact, several arguments stated by the Mandena participants were echoed in the concerns of Sainte Luce participants, some of whom explained that their worries stem from seeing what has happened in Mandena. It is interesting that negative conservation impacts were reported more frequently in Sainte Luce, despite this area not having yet experienced mining. This is possibly due to participants' higher awareness of conservation issues, due to conservation education or nearly continuous presence of researchers over the past 20 years. Mandena participants might be less concerned about the negative conservation impact of mining than Sainte Luce participants due to the habitat restoration programme implemented by the QMM over the last decade, but this was not mentioned by any participants. Moreover, only one Mandena participant mentioned the mining company's creation of the protected area as a positively perceived conservation impact.

Another emerging worry reported in Sainte Luce was the relocation of villages that may be in the mine's trajectory. While I categorised relocation as a social impact due to the cultural importance of ancestral land for the Malagasy people (Middleton, 2001; Evers & Seagle, 2012), it also constitutes a potential cost in terms of livelihood strategies – especially fishing if the community was forced to relocate further inland. Involuntary relocation is the most disruptive social consequence of forest protection, known to cause severe psychological stress and illness (Scudder & Colson, 1982). Sainte Luce community members are reportedly already stressed, as it is still not known whether or not the villages will be relocated, and if so, when and where. It is clear that a more direct and open communication is needed between the Sainte Luce community and the mining company.

Several participants reported a sense of apathy in the face of governmental decisions about allowing the mining project to operate in the area, stating that they were not involved in the decision making. Rio Tinto states their recognition of the necessity of local communities' active participation through all the stages of their activity. This includes regular consultations and involving community members in milestones and ceremonies (Rio Tinto, 2011), and regular meetings between the mining company representatives and the community members were reportedly held at least between 2008 and 2014 (T. Eppley, personal communication). In these, various aspects of the protected area (including the access to and use of resources within the protected area) were discussed, along with the larger mining footprint (T. Eppley, personal communication). Nevertheless, in the past years, this dissatisfaction led to several disputes over the land compensations and employment policies, mitigated by the QMM's social assistance programs (World Bank, 2015). The same document states that the tensions lingered, and that ongoing monitoring and more engagement from the QMM with individuals who still felt unfairly compensated was required (World Bank, 2015). According to some of our participants, communication may currently be limited to the village chiefs and mayors, which, if true, seems to leave at least some community members uninformed. If this is the case, it may be beneficial to (re)instate meetings of increased inclusivity, during which all interested community members would have a chance to receive information directly from the mining company (and other stakeholders in the area). This would also allow them to actively participate in the dialogue, which may help alleviate their concerns, and resolve any misunderstandings. Alternatively, if local representatives better reflected the social diversity of their community, it would allow for more community members' voices and concerns to be heard and addressed, as was also suggested by other authors (Ratsimbazafy et al., 2012). I believe that the mining company would be open to this, especially since they have already held community meetings in the past.

While the arrival of the QMM mining company instigated economic development in the form of local employment opportunities (among other), several Mandena participants argued that it was not enough. They perceived the jobs designated for local people as too few (explaining that many new employees came from the capital), and according to the participants, the salaries constituted insufficient compensations for their loss of traditional livelihoods. While it is not uncommon for outsiders to move into a community and outcompete locals for jobs (Rao & Geisler, 1990), the participants' main concern were the job requirements, which seemed better suited to the more highly educated. According to participants, high qualifications, which are rarely acquired in the Mandena community, were not previously mentioned in this context. It is possible that many of the local people had unrealistic expectations about job opportunities or the degree of compensation they would receive for loss of land. According to Rio Tinto's 2013 report, the QMM company employs 658 people, 73 % of which are local hires (Rio Tinto, 2013b). While it is possible that these numbers have somewhat changed over the past years (for which I was unable to procure reports, despite several attempts), it is reasonable to expect that the ratio of local and migrant workers would not have changed dramatically. It is therefore justifiable to conclude that a dissatisfaction of those not hired by the mining company may be clouding their opinions. Although this disparity could also be improved with enhanced communication efforts between the local communities and the QMM, people who do not work for the mining company may still feel the "injustice" over those who do, and see them as more highly compensated. It would be unreasonable to expect, however, that every member of each community affected by mining will be compensated through a direct hire. Another possibility to alleviate their concerns would be to refocus their attention on the social measures implemented by the QMM.

Despite not being an organisation primarily focused on social development, the QMM have invested in health services and education (Rio Tinto, 2014). They also created and provided continual support for local cooperatives focused on several areas, from agriculture to fishing (Rio Tinto, 2014). The fact that these were mentioned by few participants in this study again suggests there may be a lack of awareness of these measures, or that they are tied to the QMM. It is also possible that some of the participants may resent these measures if they have not personally benefited from them. Additionally, other aspects of people's daily lives that still need improvement may be more salient in their memory, and therefore have a higher impact on their attitudes towards the mining company, which they hold responsible for the change. It is worth noting here that the QMM may have implemented more social development programmes than have been mentioned in their reports or by our participants. As many other Malagasy-led companies, businesses or NGOs, they rarely publicise their work or discuss it with outsiders, seeing it as proprietary. The QMM are also a for-profit business, and their priority is therefore understandably achieving their goals, and not publishing the results of their social programs or scientific studies. Due to the nature of their work, this behaviour can be misinterpreted as covertness of their lack of positive impact. However, as previously mentioned, their investment into the region, in terms of both economic and social assistance, has been wide-reaching and diverse (Rio Tinto, 2014; World Bank, 2015).

While the local community's traditional way of life was impeded, it is people's general understanding that they were expected to maintain the same lifestyle, but with fewer resources. This situation is similar to other cases described in the literature (e.g., Rao & Geisler, 1990; Castro & Nielsen, 2001; Evers, 2002; Graeber, 2007; Coad et al., 2008), as well as previous accounts of the situation in Mandena (ALT & Panos, 2009; Evers & Seagle, 2012; World Bank, 2015). This suggests that little has changed since the situation was last assessed, and that concerns raised before still remain. The need for a constructive dialog between the QMM and the local communities persists, and its urgency increases as the commencement of mining in Sainte Luce approaches. While Mandena events are seen as a cautionary tale in Sainte Luce, they should also serve as a lesson for the QMM, highlighting the aspects of their work that people may find problematic.

The concerns about mining raised by the participants of this study share several similarities with those voiced by participants of a study focused on documenting the impacts of artisanal and small-scale mining in the Alaotra-Mangoro region of Madagascar (Stoudmann et al., 2021). The positive impacts largely focused on the increased income and employment, while the recognised negative impacts included insecurity, conflicts, increased living costs and diseases. Participants who were directly involved in mining recognised more negative impacts than those who were indirectly affected by it, including the deterioration of their quality of life. They felt more vulnerable, which shows that mining does not always bring financial security. The opposite was the case in Tanzania, where a study found that despite serious environmental and social impacts of mining, significantly more respondents from the mining communities reported benefits resulting from mining (Kitula, 2006). These primarily included employment, positive social impact (improved road network, water access, and school construction) and increased crop sales. While direct income benefits were reported by participants who worked for the mine, the income of the non-miners increased through different socio-economic activities. This is similar to the situation in Bolivia (McMahon & Remy, 2001) where miners spent their wages on the locally produced goods, thus increasing the income of the local population. A similar trend was mentioned by the participants of this study as well, who said that the mining company employers buy the products of local farmers. Positive perceptions of the mining also focused on the employment benefits among the people of Canaã dos Carajás municipality in the Pará state of Brazil (Matlaba et al., 2017). Similar to the results of this study, the negative perceptions often focused on the environmental degradation.

Perceptions of tourism/NGO

The participants from both communities primarily listed the positive effects of tourism. They largely focused on the community development, or the positive interactions and respect of local customs. Economic benefits associated with tourists also received frequent praise, which is in line with numerous studies that showed the positive economic impacts of tourism (Adams & Infield, 2003; Bedunah & Schmidt, 2004; Bajracharya, 2006). However, the situations in which visitors are encountered seem to be different: in Mandena, tourist interactions and gifts are reportedly limited and even discouraged by the tourist guides working for the Nahampoana Reserve, which was viewed as negative. As the opposite outcomes were frequently reported as positive effects, it is clear that both social and economic effects are important in both communities, and constitute pertinent criteria on which assessments (positive or negative) are based. As mentioned earlier, Mandena Conservation Zone was not mentioned in this context by any of the participants. Whether this is due to their lack of awareness of the conservation zone being open to visitors, or it being further away from the surveyed villages is unclear at present. Tourism can also erode traditions and cultural diversity (West & Carrier, 2004), but this was not mentioned in this study. However, some participants mentioned that only rich people benefit from tourism, which is in line with studies reporting how tourism can lead to social inequality (e.g., Pi-Sunyer & Thomas, 1997; Leatherman & Goodman, 2005).

Sainte Luce participants mainly reported the positive effects of the NGO (SEED Madagascar). As their work focuses on nature conservation and community development, those aspects of their activity were frequently mentioned. Job provision was commonly reported as a positive economic effect, but the desire for more such positions was the only negative effect reported in the study. The most commonly mentioned project was *Stitch Sainte Luce*, a business venture focused on embroidery training and production, which currently employs over 100 women, and supports an estimated 948 people in the community (SEED Madagascar, 2019). The perceived negative effect of not employing enough people might reflect the resentment of the currently not hired participants, or their wish to be hired in the future. Managing expectations and explaining the hiring process could resolve this issue. However, no participants reported solely negative impacts. This suggests a higher awareness of conservation and social impacts of SEED Madagascar.

The participants were eager to discuss their way of life, and it was clear that they remain hopeful that their opinions may yet be considered. They emphasised that development is welcome, but that their communities do not want to lose their traditions. Socio-economic development and conservation are not incompatible, but for their coexistence to be successful, communication channels should be open and local people integrated in the decision making (Gadgil, 1992; Danielsen et al., 2007; Gardner et al., 2008; Lotter & Clark, 2014). As the Malagasy define development as being in harmony with the ancestors (Evers & Seagle, 2012), it is clear that integrating the socio-economic development with traditional aspects of culture and livelihood strategies is necessary for successful, long-term forest protection.

Impact on local livelihoods

Sainte Luce is known as a fishing community (Holloway & Short, 2014), but many households supplement their income by subsistence farming. This is consistent with previous research (SEED Madagascar, unpublished), which found that 84 % of families engage in agriculture, but only 4 % consider it their primary source of income. On the other hand, agriculture was the predominant livelihood strategy in Mandena, as previously reported (Evers & Seagle, 2012; Kraemer, 2012). The most prevalent crop cultivated in both communities was cassava. The most commonly kept production animals were the chickens, but they are reportedly often kept only to be sold if the family needs money for medical care. This leaves those whose chickens had perished especially vulnerable. Pigs are typically only eaten for celebrations such as Madagascar's Independence Day, or New Year. The importance of zebu cattle surpasses that of a staple food or farm work tool, as they are also markers of socio-economic status, and have a key role as sacrificial animals in many important rituals, from births and circumcisions to weddings and funerals. Both crops and production animals are cuisine, but their surrounding livelihood strategies are quite different. While both are produced for household consumption and to be sold to generate income, crops are primarily used as the former, and production animals as the latter.

Reliance on natural resources

Despite the decrease in both fishing and hunting, the former remains more common in Sainte Luce, and the latter in Mandena. However, while hunting was a common practice in the fragments that now form protected areas (most likely due to their proximity to human settlements), it has since largely taken place in the unprotected forest fragments and crop fields. Hunting now mostly targets smaller bird species, while lemurs are almost exclusively caught opportunistically. The reasons for not hunting include a lack of skill or habit, or its negative perception. With the exception of participants who did not hunt because they were employed on conservation projects or forest management positions, and for whom it is reasonable to assume they had an understating of the impacts of hunting on wildlife diversity and abundance, it is possible that these answers may be a result of the demand effects - experimental artifacts where participants form an interpretation of the experiment's purpose and subconsciously change their behaviour to fit their interpretation (Orne, 2009). A precautionary measure was taken in the view of emphasising the independence of the research project from the mining company and the NGO (operating in Sainte Luce). However, as the participants were generally happy to discuss their hunting, I believe they did not feel that it was a sensitive issue.

Despite most participants reportedly no longer hunting lemurs, I documented what was later confirmed by a member of *FIMPIA* as evidence of Thomas's dwarf lemur (*Cheirogaleus thomasi*) hunt in the protected area in Sainte Luce (i.e., S9). It was attributed to the community located North of the fragment, but I am unable to confirm if this was true. Alternatively, it may be evidence of people from Sainte Luce hunting in the protected area, possibly due to the lack of *FIMPIA*'s authority. As one participant explained, people are more respectful of the authority of QMM or SEED Madagascar. This is reportedly because many *FIMPIA* members have relatives and friends within the community, and are therefore likely to disregard their rule breaking. In Mandena, the participants seemed to comply hunting restrictions, mostly limiting their hunting to animals caught damaging their crops.

While fishing remains more prevalent in Sainte Luce than in Mandena, the decrease in river fishing prevalence in this community is related to demographic characteristics of the sample (i.e., their advanced age). On the other hand, the decline in fishing in Mandena is reportedly a result of the ban. However, people were observed fishing in Mandena Conservation Zone on several occasions during this study. While I cannot confirm which communities each fisherman belonged to, some of them have been recognised as members of the surveyed villages by my local guides who live in those same villages. It appears that not all bans are (equally) observed or enforced.

An aspect of my data collection that might have affected my findings is that my translator for the Sainte Luce interviews worked for an NGO that was mentioned by some participants (i.e., SEED Madagascar), and the perceptions of which I subsequently analysed. I cannot be certain whether participants mentioning this NGO when responding to a question about their perceptions of foreign presence was related to me working with this particular translator, or whether local people generally associate this NGO with foreign presence (in addition to the tourism, which was analysed separately). While it is possible that employing this translator might have affected participants' reports and led to an overall positive perception, over a third of Sainte Luce participants (36.66 %) did not mention SEED Madagascar at all, or reported a negatively perceived impact. Furthermore, if participants were (unintentionally or intentionally) dishonest, this would have also been evident from their other replies collected at the same time, some of which of an equally (or more) sensitive nature (i.e., local hunting practices). I believe participants were honest due to the content of their replies, and their general behaviour. Instead, I believe that using a familiar and locally well-respected translator resulted in a better rapport and trust, and enabled me to collect reliable data. Additionally, while my own social and racial identity might have influenced how I was perceived, ensuring that I had a well-respected community member as a local translator was a way to minimise its effect on the data. At the start of my project, I met with my translators and explained to them the purpose of my study, as well as the kind of information I would like to obtain from the participants. By understanding these, the translators were able to ask the questions in a way that the participants were familiar with, and provide additional prompts when necessary, to guide the discussion. Another potential issue comes from my sampling method. I was not able to achieve random sampling, and my sample might be biased towards people who were available at times of data collection. However, as most of the interviews were conducted on weekends, any bias against participants with more formal employment is inadvertent.

Conclusion and recommendations

Despite the differences between Sainte Luce and Mandena present at the time of data collection, there were numerous similarities in the way that forest protection, and the different stakeholders associated with it were perceived by the surveyed members of the two communities. Nearly all participants stated that their daily life and livelihood security were made more difficult by the establishment of the protected areas. However, the comparison between Sainte Luce and Mandena showed that the experienced difficulties seemed even more significant when there was a lack of understanding of the benefits that forest protection policies were likely to bring for the future generations.
Although local perceptions of different stakeholders and their actions differ in both communities, the aim of this study was not to compare them to one another (as this would not even be possible, due to their numerous differences), but instead to investigate how their local perceptions might differ between Sainte Luce and Mandena. This is particularly important when considering the perceptions of the measures implemented by the mining company and the NGO. While NGO's measures were implemented locally, targeting the households within Sainte Luce, many of the QMM's measures were implemented on a much larger geographical scale. This fact could have contributed to participants being less aware of the latter.

These findings do not represent assessments of conservation measures or developmental policies, but instead their perception among the local populations of Sainte Luce and Mandena. As many of the implemented measures were not mentioned by the participants, I believe there is room for improvement when it comes to communication between the local communities and those in charge of protected area management. Based on the results of this study, I make the following recommendations:

1. Many of the social measures implemented by the QMM mining company were not reported by the participants of this study, therefore it is likely they are not perceived as related to and created by the mining company. Whether this omission was a result of the lack of awareness, or was deliberate, it suggests a clear need for improved communication between all stakeholders. It would be beneficial if the mining company communicated directly with community members, as reportedly used to be the case. Efforts should be made to establish a two-way communication channel, so that community members' concerns could be heard and addressed directly by the QMM representatives. In Mandena, this approach would allow the resolution of the ambiguities concerning the received compensations. In Sainte Luce, such meetings might alleviate some of the community members' worries and adjust their expectations of positive and negative outcomes alike. Other aspects of communication (i.e., communication with researchers, publishing) should be enhanced as well.

2. At the time of data collection, some of the restrictions brought about by forest protection were seemingly not adequately enforced. Research efforts should be implemented to examine why this is the case. Moreover, as the current study only included six villages, similar projects should be extended to more villages surrounding the protected areas in Sainte Luce and Mandena. This approach will likely resolve the confusion about which communities are not adhering to the rules and bans associated with forest protection, and why, providing important information about how to resolve this issue in the best way. A sensitive approach is necessary, so as not to alienate any of the local communities. Finally, a study of attitudes towards community members responsible for managing the protected areas and enforcing the new rules would enable an understanding of additional underlying reasons that might be hindering the enforcement of forest protection measures.

3. Conservation education seems to result in higher perception of positive effects of forest protection in Sainte Luce. For this reason, similar initiatives should be implemented in Mandena. Even shorter-term outreach activities could be a good start, and potentially result in an improved understanding of the importance of forest protection. The effects of these activities should be regularly assessed, for better-tailored outreach and education programs in the future.

4. As there are several positive effects of tourism, more attention should be given from the locally present stakeholders in Mandena to attract tourists to the Mandena Conservation Zone. Local people's perceptions of Mandena Conservation Zone as a tourist destination should be surveyed to understand whether its omission by the participants of this study is due to the lack of awareness (perhaps due to its geographical location and modes of entry), or might be caused by other factors. Participant reports that contact with tourists visiting Nahampoana Reserve is restricted should be given more attention.

5. As tourism is dependent on many external forces – from politics to economics and pandemics, we also propose further investigation of other possibilities of self-supportive and locally effective practices. Current agricultural practices could be modified in a way that would not require further land clearance, but would instead extend the market reach of the sustainably grown products.

6. The situation in both Sainte Luce and Mandena should continue to be monitored regularly, as the mining project progresses from Mandena to Sainte Luce. A similar survey should be done with Petriky communities (where the mining project is planned to continue after Sainte Luce), to enable more wholesome understanding of the conservation, social and economic impacts of mining through all of the phases.

CHAPTER 9: General discussion

The main aims of this doctoral study were to investigate how the presence of the red-collared brown lemur (*Eulemur collaris*) – a species classified as Endangered by the IUCN Red List (Donati et al., 2020), and a frugivorous primate of particular ecological importance as a seed disperser – affects the regeneration of the littoral forest fragments of Sainte Luce and Mandena, and how this in turn affects the lives and livelihoods of people relying on forest resources. The botanical similarity (Dumetz, 1999) of Sainte Luce and Mandena, the differences in the degree of their anthropogenic use prior to the formation of the protected areas (Rabevohitra et al., 1996; Dumetz, 1999; Bollen & Donati, 2006), and the differences in the abundance of red-collared brown lemurs (Bollen & Donati, 2006; Donati et al., 2007) made their comparison interesting. The study species and its habitat are ecologically unique and threatened (Bollen & Donati, 2006), thereby warranting research attention and conservation action (Ganzhorn et al., 2001). A unique aspect of the current study comes from extending the research scope to the local human communities and their cultural practices relating to their ecosystem uses and local ecological knowledge. As several forest fragments in both Sainte Luce and Mandena became protected in the early 2000s, these areas provided an excellent setting for testing the predictions about the potential influences of forest protection on the red-collared brown lemur ecology (Chapters 3, 4, and 5) and the lives and livelihoods of local human communities (Chapters 6, 7, and 8). This study therefore represents an assessment of the changes brought about by forest protection measures, from the perspective of both the lemurs and the local people.

The arrival of the Rio Tinto Corporation several decades ago, and the subsequent start of the mining operations (QMM, 2001; Rio Tinto, 2017) led to substantial changes for Sainte Luce and Mandena, the implications of which concern the lemurs, the forests and the people. The **establishment of protected areas**, as well as the associated **socio-economic development** created a distinct context for which I developed my predictions. This included reframing some of the previously explored research questions, such as those relating to this lemur's habitat use, activity budgets, diet, and seed dispersal, and considering them in a new light – in the context of forest protection measures. Additionally, I developed several new research questions, which primarily concerned the people-forest dynamic instigated by the new circumstances. At the time of data collection, Sainte Luce and Mandena differed in respect to the mining pressure: Sainte Luce was in the pre-mining phase, while mining was well underway in Mandena. The two areas also differed in the degree and structure of community development projects, such as conservation education programs, or projects focused on sustainable livelihoods. These were more encompassing, more numerous and longer lasting in Sainte Luce. This created further bases for the comparison between the two areas. In the following pages, I will demonstrate and discuss the connections between the principal findings of each of the sub-topics of this doctoral thesis, identify the challenges faced during the project, outline the limitations as appropriate, and propose guidelines for the future.

Prior to the beginning of this project, my expectation was that the changes in forest management and protection status would have affected the now protected forest fragments, enhancing their regeneration. I anticipated that these changes would also affect the red-collared brown lemurs, impacting their habitat use, activity budgets and diet. Finally, I expected that forest protection measures would have affected the local people, through impacting their forest-based traditions and livelihoods. Several variables may moderate how these changes are experienced. Most notable of them are likely to be the adherence to the new policies (which will have manifested as increased forest regeneration, and consequently, more efficient habitat use by the lemurs), and the internalised understanding of the importance of adhering to them (which will have manifested as better coping with the resource use restrictions by the local people).

Red-collared brown lemur ecology

To test my predictions concerning the effects of forest protection measures on the ecology of the red-collared brown lemur (i.e., its habitat use, activity budgets, and diet), I collected behavioural and spatial data across seasons and across the 24-hour cycle. I gave particular attention to the ranging behaviour and diet composition and diversity, as changes in these ecological aspects would have indicated a change in the quality of this species' habitat. Comparing my findings to those of previous studies (Donati, 2002; Donati et al., 2007; 2007b; 2011; 2011b; Campera et al., 2014; 2019), it is easy to see some differences, most of which are in line with my expectations. For example, the **home ranges were smaller**, and in the case of Mandena, **less fragmented** than previously reported. Taken together with the recently published NDVI data (Donati et al., 2020b), this suggests an improvement of habitat quality and resource availability. *Eulemur* ranging patterns are generally affected by resource availability (Scholz & Kappeler, 2004), and show seasonal variation (Overdorff, 1993; Scholz & Kappeler, 2004; Sato et al., 2013; Campera et al., 2014). Seasonality of resource abundance also contributes to changes in activity patterns of lemurs and other primates (Clutton-Brock, 1977; Oates, 1987; Yamagiwa & Mwanza, 1994; Overdorff et al., 1997; Korstjens et al., 2006; 2010; Hill et al., 2004; Hill, 2006; Guo et al., 2007; Asensio et al., 2009; Dunbar et al., 2009; Masi et al., 2009; Donati et al., 2011b; Sato, 2012b; Campera et al., 2014). In this study, the lemurs were **more active during the day** than at night, but showed no difference in activity between the two seasons, or between the two study sites. Their higher daily activity confirmed my prediction, and was in line with previous studies of a few other *Eulemur* sp. (Overdorff, 1996; Kappeler & Erkert, 2003). While the species' diet remained largely frugivorous throughout the year, as expected (Overdorff, 1993; Donati et al., 2007; Erhart & Overdorff, 2008; Donati et al., 2011; 2020), lemurs ate **more fruit in the wet**

season than in the dry season. This finding was also in line with my prediction, and several studies of frugivorous primates' diet (Asensio, 2009; Felton et al., 2009; Masi et al., 2009; Campera et al., 2014). The lemurs **spent more time feeding in the dry season** than in the wet season, which coincided with lower percentages of fruit in the diet. During this season, lemurs consumed more nectar, mostly from a few key species flowering at these times. This result is not atypical, as an increase in nectar consumption was previously shown to increase during peak flowering times of the same species whose nectar lemurs largely consumed in this study (Campera et al., 2014). **Dietary diversity** was **lower than expected**, but **larger in the wet season** than in the dry season **and larger during the day** than at night, confirming my predictions. The relatively low overlap between currently reported most common plant species in this lemur's diet, and those reported in previous studies (Donati et al., 2007; 2020b) can be explained by the fluctuation of plant species' availability over time (Donati et al., 2020b) as a result of irregular seasonality (Wright, 1999; Dewar & Richard, 2007). To understand the reasons behind significant variation in the number of species consumed across the 24-hour cycle, it is necessary to examine other possible correlates of preferential feeding tree selection (e.g., tree height, lemur feeding height). These would help allow conclusions about whether other aspects of red-collared brown lemur ecology (such as predator avoidance) may be causing these differences. In the context of forest protection, surveying the population sizes and ranging patterns of known red-collared brown lemur groups in the littoral forests may provide helpful information on possible predation levels that the lemurs are facing. This could also help understand how predation pressure affects their own ranging and diet.

One of the ecologically most important reasons to study red-collared brown lemur's diet is this lemur's seed dispersal. It is highly unlikely for a plant species to be dispersed by only a single disperser (Howe & Smallwood, 1982; Howe, 1984; Herrera, 1985; Gautier-Hion et al., 1985; Fisher & Chapman, 1993; Chapman, 1995; Erikkson & Ehrlen, 1998; Lambert & Garber, 1998; Bollen et al., 2004). However, exactly that appears to be the case for a number of tree species growing in the littoral forest fragments of Sainte Luce and Mandena. Due to the size of their seeds, large-seeded plants can only be dispersed by frugivores of a sufficiently large body size (Leighton & Leighton, 1983; Janson, 1983; Kitamura et al., 2002; Zanne et al., 2005). Due to its body size, red-collared brown lemur is the only extant species inhabiting these littoral forests that is able to disperse the seeds of species with seeds exceeding 12.5mm in diameter (Bollen et al., 2004; Bollen & Donati, 2006). Its uniqueness as a seed disperser of large-seeded plants, and the associated implications for forest regeneration made this aspect of red-collared brown lemur's ecology one of the central focuses of this doctoral study. I examined this species' defecation locations and their microhabitat characteristics, as these may have repercussions for seed predation, secondary seed dispersal or even seedling germination (Schupp, 1988; Forget, 1997; Wenny, 2000; Gomez, 2003; Gross-Camp & Kaplin, 2005; Russo, 2005; Gross-Camp, 2009). My findings indicate that red-collared brown lemurs defecate in areas of **relatively**

closed canopy, but I found no difference between defecation locations and randomly selected locations in this aspect. My results also show that defecation locations have **lower forest density** than random locations within the same habitat. This finding did not confirm my prediction, but it may be a consequence of decreased hunting pressures since forest protection. Forest density was higher in the defecation locations of Mandena lemurs. Lemurs gravitating to the denser parts of their habitat to spend time in, and subsequently defecate in, would be in line with my observation of higher human presence in Mandena Conservation Zone than in the protected fragments of Sainte Luce (i.e., S9). Of course, it is also possible that lemurs might be spending more time in denser areas due to their higher food richness (Balko & Brian Underwood, 2005), or as a predator avoidance strategy. A study of forest phenology, and a survey of known red-collared lemur predators previously confirmed in the area, such as fossa (Lewis Environmental Consultants, 1992) and diurnal raptors (Donati et al., 2007; 2007b), as well as estimating their predation levels would help towards understanding if this might be the case. Likewise, a thorough analysis of human activities and a comparison between Sainte Luce (i.e., S9 fragment) and Mandena (Mandena Conservation Zone) is needed to fully understand the current level of anthropogenic disturbance in the protected areas, and to inform the discussion about its possible impact on the lemurs.

The analyses of spatial and temporal patterns of this lemur's defecation suggest that the red-collared brown lemur typically **defecates after resting**, especially during the day. On the other hand, lemurs defecated closer to the most recently used feeding trees in the wet season. These relationships between defecation, feeding and resting could be affected by the activity pattern, as well as the temporal distribution of different food items in lemurs' daily diet (Westcott et al., 2005; Russo et al., 2006), as diet affects gut passage times (Tsuji et al., 2010). It is also not uncommon for primates to rest near or within their feeding sites (Champman, 1988; Heymann, 1995; Julliot, 1996b; Gilbert, 1997; von Hippel, 1998), as this is a way to maximise foraging efficiency. Connecting the red-collared brown lemur's gut passage times to the temporal distribution of its fruit consumption could allow predictions of when and where the seeds will be dispersed. These are important to understanding seedling recruitment (Chesson et al., 2005), and to modelling the effects of this endangered (Donati et al., 2020) lemur's potential extirpation on the regeneration of species in its diet (Wright et al., 2000). Although I did not find evidence of latrine behaviour in the red-collared brown lemur, several other aspects of its seed dispersal ecology may be worth examining. Among them is **sequential defecation** of multiple group members observed during data collection, as this likely impacts the quantity of seeds disposed in a particular area. As proximity to other conspecifics, and especially parent trees, negatively affects seedlings' germination (Overdorff & Strait, 1998) and establishment (Janzen, 1970; Connell, 1971; Howe & Smallwood, 1982), this might have implications for forest regeneration.

Regeneration of the littoral forest is a topic that unites the lemur-related and people-related aspects of this study, showcasing the unique role of the red-collared brown lemur in *protecting* not only the future of the littoral forests, but indirectly also many of the local people's traditions and traditional livelihood resources. My findings show that **red-collared brown lemurs feed on 52 utilitarian species**, which are used by the local people as medicines, construction materials and cooking fuel. For 42 of them, this lemur might be a seed disperser, as it consumes the fruit, but this should be examined in the future studies. Previous studies elsewhere showed that an overlap between plant species eaten by primates and used by people is not uncommon. Woolly spider monkeys (*Brachyteles arachnoides*) in Intervales State Park, São Paulo (Brazil) feed on 24.5% of medicinal plants used by people living nearby (Petroni et al., 2017). The diet of chimpanzees (*Pan troglodytes*) in the Kibale National Park (Uganda) included 21.4% of plants used in traditional medicine locally (Krief et al., 2005). Plants typically harvested for timber in La Chonta (Bolivia) were found to make up 50% of the diet of Peruvian spider monkeys (*Ateles chamek*) inhabiting the unlogged area (Felton et al., 2010). Lemurs consume a high variety of plant species (Steffens, 2020), including the endemic ones, many of which are threatened with extinction (BGCI, 2021). As over a half of threatened endemic species are also used by the local people (BGCI, 2021), cross-referencing the lists of species used by both people and lemurs, and emphasising their commonality might be beneficial to these plant species' conservation. As the diet of red-collared brown lemurs includes species used as medicine, construction materials and firewood, emphasising this lemur's interdependence with local people could benefit its conservation. While the conservation status of the majority of plants documented in this study needs examining, even their local extinction might impact both the lemurs and the people who share their landscape.

While all the steps of the seed dispersal process carry the potential to have a significant effect on the germination of seedlings, which – if successful and uninterrupted – contributes to the regeneration of the forest, the most essential among them is primary seed dispersal. According to my findings, total regeneration (i.e., regeneration of all tree species in the forest) differs between the levels of seedlings and saplings. The former is higher in the protected forest fragment of Sainte Luce (i.e., S9) and in Mandena Conservation Zone (MCZ) than in the unprotected forest fragment (i.e., S7), but this difference does not persist to the latter. When saplings are considered, the two Sainte Luce fragments no longer differ, while MCZ has a lower average number of saplings than S7. The initial difference (i.e., seedling regeneration) might be the result of forest composition – specifically, the number of adult trees of the same species or tree density (which is higher in S9 and MCZ than in S7). However, the likelihood of successful establishment below the parent trees is lower, as explained by the Janzen-Connell hypothesis (Janzen, 1970; Connell, 1971). This hypothesis can explain why S7 has higher establishment rates (i.e., more saplings) than MCZ.

An especially important finding is that the presence of the red-collared brown lemur is significantly related to **higher regeneration** of seedlings of the fruiting species of which this lemur is, due to its body size, believed to be the only disperser in this ecosystem (Bollen et al., 2004; Bollen & Donati, 2006). This is a strong argument in favour of this species' conservation, and one that could be very useful in conservation education and outreach activities. Furthermore, this finding supports previous confirmations of relationships between large-bodied lemurs and the large-seeded plants they disperse (Ganzhorn et al., 1999; Federman et al., 2016). This relationship, however, is only significant at the level of seedlings. This suggests that other factors (for instance, number of adult trees, forest density, presence of other frugivores, and anthropogenic pressures) play important roles in the likelihood of successful establishment. The red-collared brown lemur's abundance in the fragments in which it still occurs (i.e., S9, MCZ) does not relate to higher regeneration at either regeneration level. There are no differences between the fragment in which this lemurs occurs in higher numbers (i.e., S9) and the one in which its abundance is lower (i.e., MCZ) (Bollen & Donati, 2006; Donati et al., 2007), but as the population estimates used in this study are based on censuses conducted over a decade ago (Bollen et al., 2006; Donati et al., 2007), population sizes in both areas should be reassessed to ensure the validity of any conclusions that might be based on them I also found no difference between the two fragments when I considered the regeneration of the randomly selected locations, suggesting their similar regeneration. What is important to consider is that a single variable on its own will rarely influence the entire dynamics of the ecosystem of which it is a part. An appreciable amount of regeneration also comes as a result of seedling germination from the fruits fallen from their maternal plants. Moreover, many plants in the littoral forests are also dispersed by other vectors, and some of them do not need the red-collared brown lemur at all. Consequently, I believe that, to understand the dynamics of any ecosystem, it is necessary to consider the entire context in which the observed interaction takes place.

Characteristics of all three fragments included in this study (such as canopy closure and tree density) are affected by both the lemurs and the people, but the two may act in opposite directions. While the beneficial effect of brown lemur activity (i.e., forest regeneration) may take decades to be observed, the effects of human activity (i.e., timber extraction) may change the forest landscape a lot quicker. For example, only one of the studied fragments is currently unprotected, and its resources are being extracted at an increasing rate since the other fragments, previously more highly used due to their closer proximity to local human settlements, became protected. As the red-collared brown lemur has been hunted out of this fragment (M. Aimeé, personal communication), and the anthropogenic pressure on the forest resources has increased, there is little hope for the regeneration of the *Eulemur*-dispersed tree species there. Sadly, this is of no real concern, as this fragment has been designated for community resource extraction. Despite its large size, its resources are likely to deplete in the upcoming years, as the local human population increases.

Local people

Prior to this study, there was a huge imbalance of the available information (in the view of peer-review publications, available unpublished data or NGO reports) on the red-collared brown lemurs and the littoral forests in the southeast of Madagascar on the one side, and the local human communities on the other side. Furthermore, the area in which the study took place is at a crossroads between the traditional way of life and the time-honoured (if often unsustainable) practices surrounding the use of forest resources and livelihood provision, and the socioeconomic development, which the area has been experiencing (at a seemingly increasing rate) in recent decades. This dynamic situation created a great set up for examining how these changes, which are not unique to southeastern Madagascar (Quinn et al., 2003: Naughton-Treves et al., 2005; Mukul et al., 2010; Abukari & Mwalyosi, 2020), affect the lives and livelihoods of people who have traditionally developed their livelihood strategies around the (declining) forest resources. Understanding this relationship can help create guidelines for successful conservation programmes (Müller-Böker & Kollmair, 2000) and alleviate the issues that often accompany forest protection, such as the socio-economic costs for the local people (Coad et al., 2008). Some of the most severe costs include loss of infrastructure, restricted natural resource use and the resulting loss of livelihoods, loss of land tenure, and community displacement (Cernea, 1997; West & Brockington, 2006; Coad et al., 2008). Forest protection also protects ecosystem services (Ferraro & Kiss, 2002; Griet-Gran et al., 2005), as well as creates socio-economic benefits and opportunities for income diversification (Twyman, 2001), most commonly in the form of tourism. These ventures bring income to the local population (Adams & Infield, 2003; Bedunah & Schmidt, 2003; Bajracharyja, 2006; Coad et al., 2008), and might change their perceptions and knowledge of local wildlife (Vannelli et al., 2019; Waylen et al., 2019).

One of the hugely important factors in wildlife conservation is the significance of a species to the people living in its proximity. This brings into focus knowledge, perception, attitudes, and practices that comprise people-wildlife relationships. Red-collared brown lemurs and people living in the rural communities surrounding the littoral forest fragments of Sainte Luce and Mandena have a long history of interactions. Until the creation of conservation zones in the early 2000s, this lemur was a prominent hunting target across the region, and other parts of its range (Campera et al., 2019). As this species is the largest extant lemur in these forests, its appeal as a food source for the impoverished communities (Vincelette et al., 2007) is easily understandable – albeit concerning from the conservation perspective, due to its unique ecological importance. Alongside habitat fragmentation and loss, to which large frugivores such as the red-collared brown lemur are particularly vulnerable (McEuen & Curran, 2004; Lahann, 2007), hunting led to this species' local extirpation from several forest fragments across Sainte Luce (Bollen & Donati, 2005; Donati et al., 2007) and Mandena (Donati et al., 2007b). In recent years, some of those fragments were repopulated by this species, either as a result of human-instigated translocation of smaller groups from the more degraded, insufficiently sized fragments, into the Mandena Conservation Zone (Donati et al., 2007b; 2020), or due to a natural recolonisation across an open savannah (Hyde Roberts et al., 2020). Both examples constitute extraordinary cases, and in the case of the latter, will require more research attention to understand their long-term success, in terms of ecological consequences for the lemur and its reclaimed habitat.

According to my findings, forest protection and a change in forest management were adequate in ensuring **a cessation of hunting of the red-collared brown lemur** in both Sainte Luce and Mandena. It may be difficult, however, to separate the relative roles of past hunting habits and the more recent conservation education efforts in the **ecological knowledge** of the local people. The relationship between past hunting and current knowledge has proved to be significant, which is in line with previous studies that showed people who hunt demonstrate better ecological knowledge of the species they hunt (Boud et al., 2013; Kolb, 2014; Miard et al., 2017). However, I advise caution in the interpretation of this result. Firstly, correlation does not imply causation. Secondly, the significance of this relationship was confirmed only in Sainte Luce, which is incidentally the community with an almost continuous presence of researchers over the last 20 years, and a much greater exposure to conservation education. Thirdly, this finding could also be related to the higher population density of this species in Sainte Luce (Bollen & Donati 2006; Donati et al., 2007), which could have theoretically increased its chances of being observed by an average community member (as noted above, however, populations sizes need to be reassessed and the difference between them confirmed). As red-collared brown lemurs are fairly conspicuous in terms of their behaviour (Donati, 2002; Donati et al., 2007), it is not surprising they are widely recognised in both Sainte Luce and Mandena. The species also appears to be **well-liked**, especially in Sainte Luce. Some of the arguments stated by participants in both areas reflected a **utilitarian attitude** (Kellert, 1985), stemming from this lemur's practical or material value, both in the past and currently. These participants described the brown lemurs as a food source, a desirable pet, and a tourist attraction, while also mentioning its lack of unwelcome qualities (i.e., it constituting an unlikely forager of the human-grown crops). Others emphasised **local pride** in having this lemur in the forest, and its **ecological importance** for forest regeneration, thus expressing an ecologistic and scientistic attitude (Kellert, 1985) (i.e., emphasising lemurs' biological functions – i.e., seed dispersal, respectively). Some participants also expressed a negativistic attitude, comprising indifference or dislike for it (Kellert, 1985). Among the participants with a positive attitude towards this species, the argument about its ecological importance was more frequently heard in Mandena, despite the participants from this area having had less contact with researchers and fewer conservation education opportunities than their Sainte Luce counterparts. On the other hand, Sainte Luce participants more frequently praised this lemur's physical appearance, possibly as a result of researchers' and tourists' perception of this lemur as beautiful or cute, thus expressing an aesthetic attitude (Kellert, 1985). The finding that Sainte Luce participants were also less likely than Mandena participants to note that the red-collared brown lemur is a good food source might be related to them learning over time that outsiders (such as researchers and foreign tourists) often perceive hunting and eating lemurs as negative, which could have decreased the likelihood of giving this answer. The fact that this lemur is seemingly locally already valued for its contribution to the propagation of resources that people themselves find both necessary and desirable creates an engaging context in which to present and advocate for this species conservation. Consequently, the red-collared brown lemur can truly be considered, as previously suggested, a symbol of forest conservation (Donati et al., 2007b).

Of course, biocultural knowledge and practices extend beyond the human-wildlife interactions, and onto the equally notable interplay of people and plants. In some ways, this particular aspect of local people's lives and livelihoods has experienced an even more substantial alteration by the forest protection measures. Livelihood strategies based on forest resources, which had been embraced for generations and are regarded as very important (Middleton, 1999; Evers, 2002; Graeber, 2007; Evers & Seagle, 2012) became restricted. At the same time, resource extraction was re-directed to more inconvenient locations, thus **increasing the difficulty of acquiring resources** that had already been depleted by an extensive anthropogenic pressure. As a result, people were prompted to switch to the previously unused species for construction of their houses. In Sainte Luce, people resorted to, in their own words, **less durable native species**. The perception of some species as less durable may need further attention and clarification, as timber durability is influenced by climate and structural design (Brischke et al. 2013), but such plants were still widely available due to their perceived lesser quality. In contrast, the Mandena community switched to **the introduced exotic species** (primarily *Eucalyptus*), some of which were elsewhere ranked high as construction materials (Krog et al., 2005; Lavialle et al., 2015). While the use of native species has proven to be unsustainable in both communities, a switch to the exotic species may be the only way to conserve the littoral forests in the current socioeconomic context. It relives the pressure on natural resources (Sedio & Botkin, 1997), while simultaneously helping towards a higher sustainability of the traditional forest-based livelihoods (i.e., timber extraction). It is not uncommon for the native species to be considered of higher wood quality than the exotic ones (Lavialle et al., 2015), other studies showed that sociocultural value of timber increases with the availability and accessibility of particular species (Thomas et al., 2009; Brandt et al., 2013). This means that the exotic species might become more highly valued as their use becomes more prevalent. However, as changes in the ecosystem are reflected in the changes of knowledge of its species (Joa et al., 2018), by preserving the forest and the native species, local ecological knowledge about them is preserved as well.

The abundance of traditionally used (and preferred) timber species has reportedly declined over time, but this does not appear to be the case for medicinal plants. An **array of medicinal plants** are used in Sainte Luce and Mandena, which supports the findings of previous studies (Lyon & Hardesty 2002;

Ingram et al., 2005b; Norscia & Borgonini-Tarli, 2006; Razafindraibe et al., 2013; Hogg et al., 2013). They have **wide applications**, from fever or a heart condition to spirit possession, often associated with traditional religious beliefs, superstitions, or perceived divine interventions. This finding is in line with literature (Smith-Hall et al., 2012), which highlights the importance of medicinal plants in most countries' culture and tradition (Quansah, 2005). In many developing countries, medicinal plants are the primary source of medicine (Tabuti, 2003; Muthu et al., 2006; Gurib-Fakim, 2006; Bhattarai et al., 2010; Abdullahi, 2011; Maroyi, 2013). Interestingly, while the medically more intangible cases (e.g., spirit possession) were treated exclusively with medicinal plants, **western medicine** was decidedly preferred for the treatment of the scientifically more tangible maladies. This finding reveals not only the extent of the comparative reliance of the local people on the forest resources and modern medicine, but provides a valuable insight into people's cultural ways, and how they are changing as a result of exposure to western ones. However, the preferred type of medicine is decided by more than the medical condition. For example, in Mandena, a personal belief system has proved important, while individual socioeconomic circumstances seem to affect the medical choices of both communities. On the one hand, despite the traditional importance of medicinal plants, some people deliberately refrain from using them, as that would be against their (non-traditional) religious beliefs, known to discourage use of medicinal plants (Caniago & Siebert, 1998). On the other hand, despite modern medicines being more prevalent than previously thought (QMM, 2001), they generally remain financially out of reach for many community members. Western medicines are often more expensive than medicinal plants (Sofowora, 1996; Neudert et al., 2017). It is evident that tradition and modernisation can act in different (if not opposite) directions. This example illustrates the importance of lending scientific attention to the study of both types of variables.

A compelling finding is the much **higher diversity of plants used by the Sainte Luce community** regardless of the purpose of their use. As knowledge about biodiversity is related to the degree of biodiversity (Grenier, 1998; Joa et al., 2018), one of the possible reasons for the difference in knowledge about species may be in the greater intactness of the Sainte Luce forests – if the plants are no longer found in the forest, they can no longer be used. Throughout the chapters of this thesis, Sainte Luce has *scored higher* on aspects such as forest regeneration, lemur diet diversity, or the diversity of used forest plants. Knowledge of plants and their traditional uses being higher in Sainte Luce is also in line with the direction of the between-site differences in the local ecological knowledge of the red-collared brown lemur – the abundance of which is also higher in Sainte Luce (Bollen et al., 2006; Donati et al., 2007). In future studies, it would be interesting to assess the relationships between knowledge of plants and lemurs in greater detail, connecting them to the relevant variables (such as involvement in conservation education programs, previous contact with researchers, and a more detailed account of their forest-related behaviours and experiences) at an individual level. This approach would allow for a deeper understanding of these differences and result in more definitive conclusions.

One of the most important findings of this doctoral study is that **the local way of life**, especially in Sainte luce, has changed very little since the protection measures were implemented. To a large extent, people still use the same type of resources for fulfilment of the same needs. The houses in which they live are still built from wood and leaves, and only in rare cases, cement (which is used solely for flooring). Most people survive off the **crops** they grow, while **hunting** (especially of lemurs) has decreased. Although many people keep production animals, meat is rarely on the menu, as these animals are often seen as currency and kept mostly to be sold in times of need (i.e., illness). As all of the research questions investigated in this doctoral study related to the forest protection, and the changes that this conservation measure has brought about, the project would not have been complete without an understanding of how this transition was experienced by the local people. An investigation of the perceived impact of the establishment of the protected areas in Sainte Luce and Mandena, mining and the mining company, tourism, and NGO presence (in Sainte Luce) revealed both the positively and the negatively perceived effects.

The analysis of the local perceptions of forest protection revealed a nearly unanimous recognition of the **negative economic impact of the protected area** in the form of considerable challenges and increased impracticability of resource extraction. This finding is not surprising, as restrictive forest management is often related to negative attitudes towards a protected area (Anderson, 1990; Allendorf, 2006). Due to their impact on the traditional, forest-based livelihoods, resource restriction can also lead to social tensions, and have a negative impact on local people's diet and health (Ferraro, 2002). Forest protection and resource restrictions do not impact all people the same, which is why attitudes towards forest protection can be predicted by a number of socio-demographic variables, such as age, gender, ethnicity, occupation, education, wealth, or land ownership (Infield & Namara, 2001; Allendorf et al., 2006; Kideghesho, 2007). However, it is wondrous to recognise that the negatively perceived effects were more likely to be accompanied by a perceived **positive conservation impact** by those participants who voiced their understanding of the importance of forest conservation. This was more often the case in Sainte Luce, and therefore may be easy to attribute to the between-site difference to the continuity of researchers' presence and conservation education efforts, both of which are high in Sainte Luce, and limited in Mandena. However, this finding does not mean that forest conservation is not important in Mandena, as other aspects of participants' lives in both communities may have also played important roles in shaping people's perspectives, or making specific concerns easier to express. Moreover, a separation of the perception of forest protection from its impact on one's livelihood strategy and the perception of other stakeholders might not be possible despite the distinct questions I used to assess them. The fact that the conservation education program in Sainte

Luce is directed primarily at children is of no consequence, as it is a well-established fact that such practice enhances not only the knowledge of children, but also their parents (Duvall & Zint, 2007; Damerell et al., 2013; Rakotomamonji et al., 2015). The positive correlation between better understanding of conservation issues and positive attitudes towards the protected areas (Fiallo & Jacobson, 1995; Marcus, 2001; Allendorf et al., 2006; Ratsimbazafy et al., 2012) emphasises the importance of development and implementation of conservation education and outreach activities.

When assessing the likelihood of long-term success of conservation actions, it is essential to investigate the reasons surrounding their current acceptance or opposition in as much detail as possible. In this study, this approach revealed the intricacies of conservation policies' implementation. Firstly, the QMM mining company, whose initial arrival in the 1980s triggered the discussion that resulted in the establishment of the protected areas (among other), was perceived in a negative way by the majority of the participants. However, while Sainte Luce participants were more worried about the perceived **negative conservation and social impacts** of mining, Mandena participants reported the perceived **negative economic impact**. This perception was mostly due to insufficient job opportunities, and being outcompeted by outsiders, which is not uncommon (Rao & Geisler, 1990), but also a result of mining negatively affecting their harvest. The community believes they were expected to maintain their lifestyle despite the negative impact on their traditional livelihoods, which is similar to other published cases (Rao & Geisler, 1990; Castro & Nielsen, 2001; Evers, 2002; Graeber, 2007; Coad et al., 2008), but also to the previous reports of the situation in Mandena (ALT & Panos, 2009; Evers & Seagle, 2012). On the other hand, the perceived **positive economic impact** was most often reported in the context of job opportunities. This finding is supported by Rio Tinto's own report, stating that the QMM hires 658 people, 73 % of which are local hires (Rio Tinto, 2013b). This suggests that participants not employed by the QMM might feel the injustice over those who are. To alleviate their dissatisfaction, it might be helpful to refocus their attention to by the mining company.

Interestingly, the mining company's positive conservation impact was seldom reported, despite their important role in the creation and management of the protected areas. The same was true of their social development measures (Rio Tinto, 2014). **The need for improved communication** between all involved parties is evident. If there is confusion about what aspects of forest protection are whose responsibility, and if members of the local communities are not able to identify properly which parties have the authority *vis a vis* the different facets of forest protection and management, that is a clear signal that they are not being adequately involved in the decision making process, or the implementation of the decided protocols. This is a dangerous situation, as studies in other sites showed that it can lead to negative attitudes towards the protected areas (Anderson, 1990), or even escalate into a social conflict (Castro & Nielsen, 2001; Ferraro, 2002), which could hurt the success of conservation efforts in the long term. (Coad et al., 2008) A more comprehensive dialogue would hopefully alleviate their overwhelmingly negative perception, reportedly shared by the majority of both Sainte Luce and Mandena inhabitants.

Furthermore, a different type of potential conservation-action subversion may come from within the community - or more specifically, from the dynamics between the community members who have, after the establishment of the protected area, found themselves on seemingly opposing sides. As explained by some of the participants from Sainte Luce, the degree to which people take heed of the various different policies is closely linked to their respect for individuals or agencies charged with enforcing said policies. What this emphasises is that suitable attention should be given to who is selected for these positions. However, the social dynamics embedded in the local culture could undermine or strengthen the likelihood of the desired outcome, depending on whether or not they are recognised, and used as an advantage. In the case of southeastern Madagascar, older community members (and particularly men) are typically respected more than the younger ones (Thomas, 1995; Tonheim, 2006)). Conflict between community members can often come as a result of power struggles for the control of natural resources (Abakerli et al., 2001), economic benefits or decision-making authority (Moscardo, 2008). True efficiency of policy enforcement can be less than obvious at first glance, and there can be a disparity between nominal obedience and the actual state of things. This is evidenced by the observations of community members using less direct routes into the protected fragments (i.e., not the main entrance, which was guarded most of the time (personal observation)) and extracting the resources. Whether or not those in charge of enforcing forest protection are aware of this happening is something that will need further clarification in subsequent research. Conclusions offered by the present study are not entirely optimistic, as it seems that outsiders are more likely to be respected than the community members – rendering the efforts unsustainable in the long term.

The overwhelming majority of both Sainte Luce and Mandena participants reported a **positive social and economic impact** of tourism, primarily as a result of the community support received from the tourism ventures. This finding is in accordance with several previous studies that showed a positive economic impact of tourism (e.g., Adams & Infield, 2003; Bedunah & Schmidt, 2004; Bajricharya, 2006). The very few participants' reservations towards tourism detected in this study were based in the lack of those benefits. In the case of the locally run NGO (i.e., SEED Madagascar) operating in Sainte Luce, the majority of participants reported **positive social, conservation and economic impacts**. They were mostly based in the perceived support received from the NGO, and their investment in the community. However, foreign presence may create social and economic inequalities (Pi-Sunyer & Thomas, 1997; Leatherman & Goodman, 2005), or strengthen the existing marginalisation within a community. This was also mentioned by one of the participants, who stated that foreign presence only benefits those who may already have the upper hand. Furthermore, the relationship with the mining company, and to a lesser extent with the tourism projects and the NGO is affected by the perceived cost-benefit ratio of the effects their presence has had on the individual.

Final remarks

In this study, the overarching aim of connecting the red-collared brown lemur, the littoral forest and the people through the effects of ecological and socioeconomic aspects of the forest protection on their interrelationships runs through all the chapters. In regard to red-collared brown lemurs, it is evident that their ecology has changed since forest protection. There are, of course, some caveats when considering these findings. These are due to the differences in study design, and the challenges I experienced during data collection (and which limited the data collection process). Firstly, there is a certain degree of asymmetry of data collected during the two seasons, as well as one between diurnal and nocturnal data. While the latter was to some extent incorporated into the study design from the beginning (due to the diurnal observations being a more efficient way to collect good quality data), the difference became larger after the nocturnal data collection had to be discontinued altogether due to local social developments (i.e., tomb robbery and the theft of human remains), which prompted a police curfew. As data collection continued on an altered schedule, I developed health issues, which led to a suspension of data collection for several months. Unfortunately, this development had implications for my analyses, in which nocturnal data are less well represented than the diurnal data. While the protected forest fragments continue to regenerate, simultaneously incurring less disturbance than prior to forest protection, the lemurs may continue to respond by modifying the aspects of their ecology which are known to relate to the external factors – namely, their ranging patterns, diet, and activity budgets (Curtis et al., 1999; Halle & Stensteth, 2000; Hill et al., 2003; Hemingway & Bynum, 2005; Lambert & Rothman, 2015). It is therefore important to continue to study these variables, and perhaps add new ones (for example, the variation in home range use between the different seasons and between day and night) to understand better how this lemur can be affected by the forest protection in the littoral forest environment. The conclusions of this study might also be useful in developing similar ones on other primate species inhabiting fragmented forests or protected which had previously experienced strong anthropogenic pressures.

In regard to the local communities, the acquired insights into how their lives and livelihoods have been affected by both the positively and the negatively perceived consequences of forest protection and the associated development should be used as guidelines in planning conservation actions. I deliberately emphasise the *perception* of the inferred consequences, as this is likely to be more important to people's overall satisfaction than the implemented measures themselves, and should therefore guide the approach to resolving any issue that arises. Sainte Luce and Mandena differ in several ways, from the past and present state of the littoral forest (Rabevohitra et al., 1996; Dumetz, 1999; Bollen et al., 2006; Donati et al., 2007; Rabenantoandro et al., 2007), to the differences in the traditional and current livelihood strategies of their people (Evers & Seagle, 2012; Kraemer, 2012; Holloway & Short, 2014; SEED Madagascar, unpublished) and social measures available for them (SEED Madagascar, 2019). However, there are also plenty of similarities, primarily in their needs for a better dialogue with the powerful stakeholders. As evidenced by several inconsistencies in the adherence to some of the forest protection policies, there is also a need for their more comprehensive enforcement.

In both communities, economic factors play a significant role when it comes to deciding which resources are used, and they often overpower the conservation-related aspects, even in cases where there is a good understanding of why the alternative would be optimal in the long term. This finding demonstrates what we already know about conservation, and that it is a slow process that takes not only effort, but also time. Even when people's knowledge and attitudes have changed, this shift may not always become immediately observable in their behaviour (Waylen et al., 2009). Poverty, illiteracy, and the lack of infrastructure and sanitation are all likely to impede progress of conservation measures. Although these issues are not easy to work with, it may make a big difference to start by acknowledging their existence, and compromise where possible to include even the smallest steps towards their improvement. Conservation goals should not obscure the importance of local capacity building and including the local people in administration of conservation measures (Campbell & Vainio-Matilla, 2003). Considering wishes and needs of the people whose help is absolutely paramount to successful conservation of both wildlife and their habitats may also alleviate some of the apathy caused by not being included in decision making on a larger scale (for example, in this case, whether or not both the mining project and the forest protection will be implemented in their area).

The importance of understanding the role of ecosystem in the lives, livelihoods and culture of the people living on the outskirts of the protected areas is not new to conservation science. However, although the importance of including the local communities in the decision making and policy implementation is widely recognised (Castro & Nielsen, 2001), the success of its practical application can vary. To improve the situation, it is crucial to understand the reasons behind any existing issues. Case studies like this one can be useful in this respect, as they allow for a thorough consideration of numerous factors. The limitation, however, is that some of these are likely to be locally specific. Another pitfall of conservation actions may arise if the traditional ways of indigenous populations are equated with the sustainability of natural resource extraction. As also evidenced by the example of Sainte Luce and Mandena, this is rarely the case. Similarly, characterising external pressures of the historically more recent stakeholders – as is the QMM mining company – as the antagonists is equally fallible. Without the conservation measures prompted by their very arrival, the remaining littoral forest left in Sainte Luce and Mandena might have been under even greater threat. As biodiversity is lost, so is the knowledge about its uses and the role it had in people's lives, leading to an erosion of biocultural diversity (Loh & Harmon, 2005). While it is important to preserve the ecosystem, it is also important to preserve the cultural heritage associated with it. This creates urgency to study and document the local ecological knowledge of communities at risk, to the same extent as the urgency to work towards preserving biodiversity.

The world as the rural Antanosy people of Sainte Luce and Mandena knew is changing. Although it may be difficult to predict where this change will take them in the following decades, a lot of time may pass before their traditional ways could ever be re-established. In fact, by the time when it could become possible (that is to say, if the forest is restored with all the native species it once grew), the socioeconomic development may have already moved these communities in a different direction. Their reluctance to accept an externally initiated impact is understandable, and should be respected and approached sensitively, through creating a context in which they are acknowledged and valued as equal partners. As there may come a time for all externally run conservation efforts to end, it is important for the longevity of forest protection policies to become locally run. Local people understanding the situations that directly concern them, being aware of the consequences they may personally infer (positive and negative ones), and being able to choose – and then choosing – to act in a pro-conservation way, is the only way for long-term biodiversity conservation to become reality.

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Appendix I

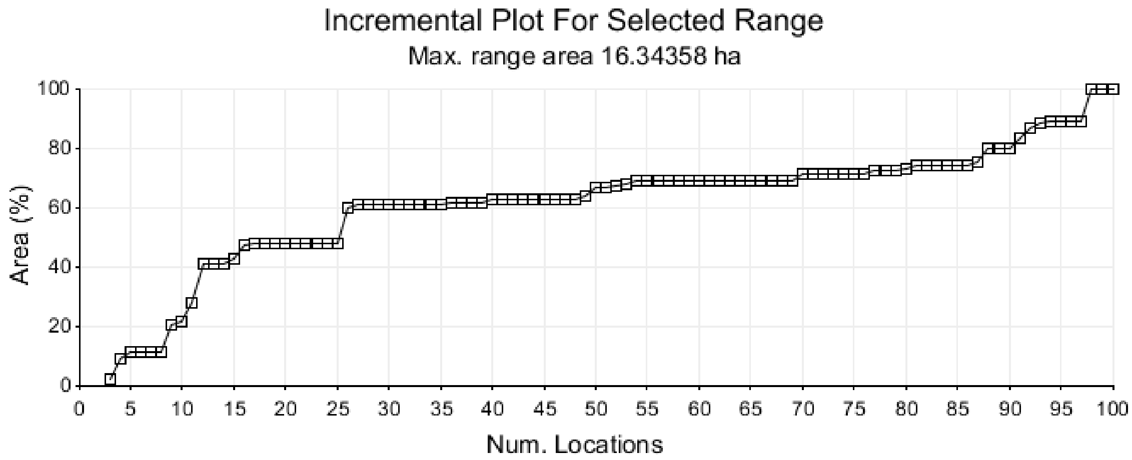

Figure A1. Incremental plot of Group A.

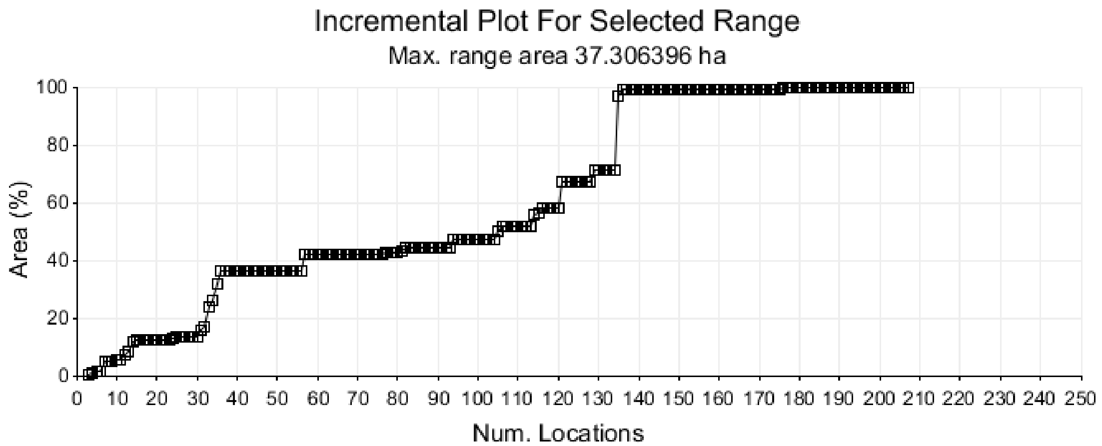

Figure A2. Incremental plot of Group B.

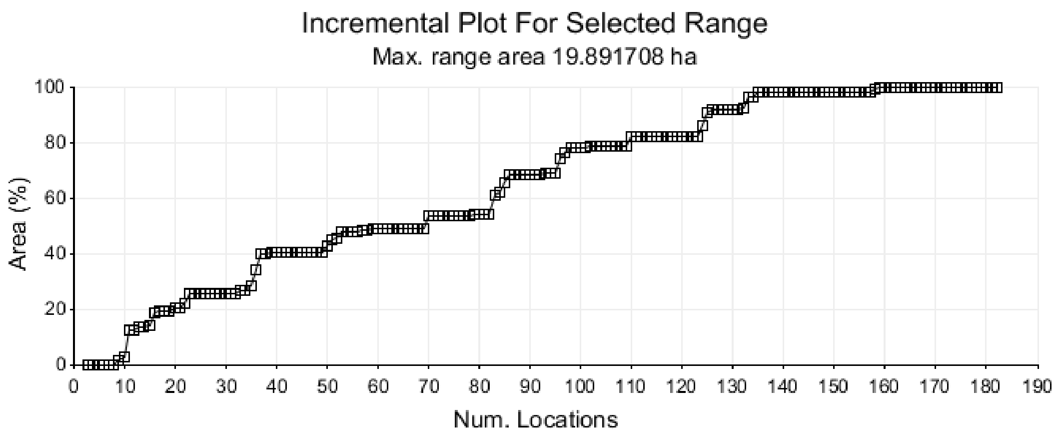

Figure A3. Incremental plots of Group C.

Table A1. Average percentages of different food items in the diet of red-collared brown lemurs (*Eulemur collaris*) in each observation session (N=44) in Sainte Luce (N=26) and Mandena (N=18), in the wet (N=22) and dry (N=22) season, and during the day (N=38) and night (N=6).

		Total	Sainte Luce	Mandena	Wet season	Dry season	Day	Night
Fruit	Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Maximum	100.0	100.0	100.0	100.0	100.0	100.0	75.0
	Median	**59.0**	**55.5**	**66.6**	**69.0**	**51.5**	**63.5**	**35.5**
	IQR	47.0	49.0	46.6	46.0	61.0	45.0	52.0
Nectar	Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Maximum	100.0	100.0	75.0	100.0	95.0	95.0	100.0
	Median	**6.5**	**17.0**	**0.0**	**4.0**	**12.5**	**45.0**	**37.0**
	IQR	50.0	62.0	47.0	43.0	69.0	49.0	89.0
Young leaves	Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Maximum	47.0	47.0	9.0	36.0	47.0	47.0	11.0
	Median	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
	IQR	0.0	0.0	0.0	0.0	0.0	0.0	0.3
Mature leaves	Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Maximum	36.0	36.0	35.0	7.0	36.0	36.0	7.0
	Median	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
	IQR	0.0	0.0	0.0	0.0	1..0	0.0	4.0
Invertebrates	Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Maximum	50.0	0.0	50.0	14.0	1.1	50.0	0.0
	Median	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**
	IQR	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table A2. List of species found in the diet of red-collared brown lemurs (*Eulemur collaris*) in Sainte Luce, in wet and dry season, and across the 24-hour cycle. Species whose fruits were consumed are presented in **bold**.

Species	Scientific name	Family	Wet season		Dry season	
			Day	Night	Day	Night
ampoly	***Vepris eliotii***	**Rutaceae**	+	-	-	-
belavenoky	***Noronhia emarginata***	**Oleaceae**	+	-	-	-
bemalemy	*Bembicia uniflora*	Flacourtiaceae	-	+	-	-
berehoky	***Dombeya mandenensis***	**Malvaceae**	+	-	-	-
beronono	***Trilepisium madagascariense***	**Moraceae**	+	-	-	-
disaky	***Garcinia aphanophlebia***	**Clusiaceae**	+	-	+	-
fandra I	*Pandanus madagascariensis*	Pandanaceae	+	-	+	-
fandra II	*Pandanus longistylus*	Pandanaceae	-	-	+	-
fanstikahitry	***Plectronia densiflora***	**Rubiaceae**	+	-	+	+
fantsikohy	***Clerodendrum* sp.**	**Lamiaceae**	+	-	-	-
fonto	***Leptolaena pauciflora***	**Sarcolaenaceae**	+	-	-	-
guavy	***Psidium guayave***	**Myrtaceae**	-	-	+	-
haramboanjo	***Buxus madagascariensis***	**Buxaceae**	+	-	-	-
harandrato	*Intsia bijuga*	Fabaceae	+	+	+	-
hazingy	*Symphonia verrucosa*	Clusiaceae	+	-	-	-
hazomainty	***Diospyrus myriophilla***	**Ebenaceae**	+	-	+	-
hazondroka*	*NA*	*NA*	+	-	-	-
lampivahatry	***Cinnamosma madagascariensis***	**Canellaceae**	+	-	+	-
mafotra	***Brochoneura madagascariensis***	**Myristicaceae**	+	-	-	-
makaranga	***Macaranga perrieri***	**Euphorbiaceae**	+	-	-	-
mampay	*Cynometra cloiselii*	Fabaceae	+	-	+	+
mangaova	***Enterospermum* sp.**	**Euphorbiaceae**	-	-	+	-
nofotrakoho	*Vitex chrysomalum*	Lamiaceae	+	-	-	-
nonoky	***Ficus* sp.**	Moraceae	+	-	+	-
pimakorova*	*NA*	*NA*	+	-	-	-
ramirisa	***Homalium louvelianum***	**Salicaceae**	+	-	-	-
ramy	***Canarium madgascariensis***	**Burseraceae**	+	-	-	-
ravenala	***Ravenala madagascariensis***	**Strelitziaceae**			+	
resonjo	***Beilschmiedia madagascariensis***	**Lauraceae**	-	-	+	-
ropasy	***Eugenia cloiselii***	**Myrtaceae**	+	-	-	-

rotry	***Syzygium emirnense***	**Myrtaceae**	+	-	-	-
sarikafe*	*NA*	*NA*	-	+	-	-
taholanga	*Hyperacanthus mandenensis*	Rubiaceae	+	-	-	-
tangatanganala	***Gaertenera arenaria***	**Rubiaceae**	-	-	+	-
varikanda	***Dillenia triquetra***	**Dilleniaceae**	+	-	-	-
voapaky	***Uapaca* sp.**	**Phyllanthaceae**	+	+	+	-
voapaky II	***Uapaca* sp.**	**Phyllanthaceae**	+	-	-	-
vondroza	***Sarcoleana* sp.**	**Sarcolaenaceae**	+	+	+	-
vonsila	***Scheflera rantsilana***	**Araliaceae**	-	-	+	-
zoralahy	*Dicoryphe stipulacea*	Hamamelidaceae	+	-	+	-

* species with no scientific names available (excluded from analyses).

Table A3. List of species found in the diet of red-collared brown lemurs (*Eulemur collaris*) in Mandena in wet and dry season, and across the 24-hour cycle. Species whose fruits were consumed are presented in **bold**.

Species	Scientific name	Family	Wet season		Dry season	
			Day	Night	Day	Night
ambora	***Tambourissa purpurea***	**Monimiaceae**	+	-	+	-
aviavi	***Ficus megapoda***	**Moraceae**	-	-	+	-
fonto	***Leptolaena pauciflora***	**Sarcolaenaceae**	+	-	-	-
harongapanihy	***Psorospermum revolutum***	**Hypericaceae**	-	-	+	-
hazomainty	***Diospyrus myriophilla***	**Ebenaceae**	+	-	+	-
mafotra	***Brochoneura madagascariensis***	**Myristicaceae**	-	-	+	-
mampay	*Cynometra cloiselii*	Fabaceae	-	-	+	-
mangavoa	***Enterospermum* sp.**	**Euphorbiaceae**	-	-	+	-
meramaintso	***Sarcolaena multiflora***	**Sarcolaenaceae**	+	+	+	-
nofotrakoho	*Vitex chrysomalum*	Lamiaceae	+	-	+	-
nonoky	***Ficus* sp.**	**Moraceae**	-	-	+	-
fandra I	***Pandanus madagascariensis***	**Pandanaceae**	-	-	+	+
ravenala	*Ravenala madagascariensis*	Strelitziaceae	+	-	+	-
ravensara	*Ravensara* sp.	Lauraceae	-	-	+	-
rondria	***Campnosperma micranteia***	**Anacardiaceae**	+	-	-	-
ropasy	***Eugenia cloiselii***	**Myrtaceae**	-	-	+	-
ropoaky	***Eugenia* sp.**	**Myrtaceae**	+	-	-	-
rotry	***Syzygium emirnense***	**Myrtaceae**	-	-	+	-

tavolohazo	***Cryptocarya oblonga***	**Lauraceae**	+	-	+	-
varikanda	*Dillenia triquetra*	Dilleniaceae	+	-	-	-
verom*	*NA*	*NA*	-	-	+	-
voangy	*Citrus aurantium*	Rutaceae	-	+	+	+
voapaky	***Uapaca* sp.**	**Phyllanthaceae**	+	+	+	+
vokarepky	*Brexia madagascariensis*	Celastraceae	-	-	+	-
zambo	***Grisollea* sp.**	**Stemonuraceae**	-	+	-	-

* species with no scientific names available (excluded from analyses).

Table A4. Overall differences in the percentages of different species consumed by the red-collared brown lemur (*Eulemur collaris*) in Sainte Luce and Mandena.

Species	Sainte Luce (%)	Mandena (%)
ambora	0.00	2.95
ampoly	0.80	0.00
aviavi	0.00	4.22
belavenoky	0.64	0.00
bemalemy	0.32	0.00
berehoky	0.48	0.00
berononο	5.63	0.00
disaky	0.48	0.00
fandra I	1.77	15.19
fandra II	0.96	0.00
fanstikahitry	4.18	0.00
fantsikohy	0.48	0.00
fonto	0.64	0.84
guavy	0.16	0.00
haramboanjo	6.26	0.00
harandrato	2.73	0.00
harongapanihy	0.00	0.42
hazingy	0.16	0.00
hazomainty	0.64	1.27
lampivahatry	0.32	0.00
mafotra	0.80	1.27
makaranga	0.32	0.00
mampay	31.19	2.11
mangavoa	0.16	0.42
meramaintso	0.00	26.16
nofotrakoho	0.16	3.80
nonoky	4.66	0.42
ramirisa	5.14	0.00
ramy	0.16	0.00
ravenala	0.16	2.11
ravensara	0.00	0.42
resonjo	0.16	0.00

rondria	0.00	2.53
ropasy	0.32	1.27
ropoaky	0.16	1.69
rotry	5.30	0.42
taholanga	0.96	0.00
tangatanganala	0.32	0.00
tavolohazo	0.00	1.69
varikanda	0.16	0.42
voangy	0.00	3.38
voapaky	10.13	17.30
voapaky II	1.93	0.00
vokarepky	0.00	9.28
vondroza	4.50	0.00
vonsila	0.16	0.00
zambo	0.00	0.42
zoralahy	6.43	0.00

Table A5. Differences in the percentages of different species consumed by the red-collared brown lemur (*Eulemur collaris*) across the two seasons, in Sainte Luce and Mandena.

	Sainte Luce		**Mandena**	
Species	**Wet season (%)**	**Dry season (%)**	**Wet season (%)**	**Dry season (%)**
ambora	0.00	0.00	2.94	3.01
ampoly	2.59	0.00	0.00	0.00
aviavi	0.00	0.00	0.00	7.52
belavenoky	2.07	0.00	0.00	0.00
bemalemy	1.04	0.00	0.00	0.00
berehoky	1.04	0.00	0.00	0.00
beronono	1.55	0.00	0.00	0.00
disaky	1.04	0.42	0.00	0.00
fandra I	1.55	2.54	0.00	27.07
fandra II	1.04	2.54	0.00	0.00
fanstikahitry	0.52	10.17	0.00	0.00
fantsikohy	1.55	0.00	0.00	0.00
fonto	2.07	0.00	1.96	0.00
guavy	0.00	0.42	0.00	0.00
haramboanjo	1.04	0.00	0.00	0.00
harandrato	3.63	3.39	0.00	0.00
harongapanihy	0.00	0.00	0.00	0.75
hazingy	0.52	0.00	0.00	0.00
hazomainty	1.04	0.42	0.98	1.50
lampivahatry	0.52	0.42	0.00	0.00
mafotra	2.59	0.00	0.00	2.26
makaranga	1.04	0.00	0.00	0.00
mampay	14.51	63.14	0.00	3.01
mangavoa	0.00	0.42	0.00	0.75
meramaintso	0.00	0.00	54.90	4.51
nofotrakoho	0.52	0.00	1.96	5.26

nonoky	13.47	1.27	0.00	0.75
ramirisa	0.52	0.00	0.00	0.00
ramy	0.52	0.00	0.00	0.00
ravenala	0.00	0.42	2.94	1.50
ravensara	0.00	0.00	0.00	0.75
resonjo	0.00	0.42	0.00	0.00
rondria	0.00	0.00	5.88	0.00
ropasy	1.04	0.00	0.00	2.26
ropoaky	0.00	0.00	3.92	0.00
rotry	7.25	0.00	0.00	0.75
taholanga	1.04	0.00	0.00	0.00
tangatanganala	0.00	0.85	0.00	0.00
tavolohazo	0.00	0.00	1.96	1.50
varikanda	0.52	0.00	0.98	0.00
voangy	0.00	0.00	2.94	3.76
voapaky	13.99	11.86	17.65	16.54
voapaky II	6.22	0.00	0.00	0.00
vokarepky	0.00	0.00	0.00	16.54
vondroza	13.47	0.42	0.00	0.00
vonsila	0.00	0.42	0.00	0.00
zambo	0.00	0.00	0.98	0.00
zoralahy	0.52	0.42	0.00	0.00

Appendix II

Table A1. Adult tree species and the frequency of their occurrence in the three study sites. Red-collared brown lemur (*Eulemur collaris*) is present in two of the forest fragments (i.e., S9, and MCZ), and absent from one (i.e., S7).

Vernacular name	**Scientific name**	**Family**	**S9**	**S7**	**MCZ**
akondronala	*Ophiocolea delphinense*	Ophiocomida	0	0	1
ambirombariky	*Plagiosypus louvelii*	Sapotaceae	1	0	0
ambora	*Tambourissa purpurea*	Monimiaceae	7	4	9
ampoly	*Vepris eliotii*	Rutaceae	3	0	7
bamby	*Anthostema madagascariensis*	Euphorbiaceae	4	5	0
belavenoky	*Noronhia emarginata*	Oleaceae	2	2	0
bemafais*	*NA*	*NA*	0	0	2
bemisa*	*NA*	*NA*	2	1	0
berehoky	*Dombeya mandenensis*	Malvaceae	0	0	1
beronono	*Trilepisium madagascariense*	Moraceae	2	1	2
boaka	*Dypsis prestoniana*	Arecaceae	0	1	0
demikaranja*	*NA*	*NA*	0	1	0
disaky	*Garcinia aphanophlebia*	Clusiaceae	0	0	3
falinandro	*Dracaena reflexa*	Asparagaceae	14	10	0
falinandro be	*Dracaena fontanesiana*	Asparagaceae	0	0	2
fandra	*Pandanus madagascariensis*	Pandanaceae	9	20	10
fandra 2	*Pandanus vacqua*	Pandanaceae	0	1	0
fangianakanga	*Polycardia phyllanthoides*	Aphloiaceae	1	3	0
fangora	*Erythroxylum* sp.	Erythroxylaceae	0	1	0
fanola	*Asteropeia* sp.	Asteropeiaceae	1	0	0
fanolafotsy	*Asteropeia multiflora*	Asteropeiaceae	0	6	6
fanolamena	*Asteropeia micraster*	Asteropeiaceae	0	9	2
fantsikahitry	*Plectronia densiflora*	Rubiaceae	6	1	1
fantsikohy	*Clerodendrum* sp.	Lamiaceae	1	0	0
farisaty	*Physena madagascariensis*	Physenaceae	2	0	0
fihamy	*Ficus* sp.	Moraceae	0	0	1
fitagianabo*	*NA*	*NA*	0	0	2
fonto	*Leptolaena pauciflora*	Sarcolaenaceae	0	0	1
forofoky	*Diospyros littoralis*	Ebenaceae	2	6	0
fotombavy	*Leptolaena multiflora*	Sarcolaenaceae	0	0	1

fotondahy	*Schizolaena elongata*	Sarcolaenaceae	4	5	5
fotsyvavy	*Polyalthia madagascariensis*	Annonaceae	0	1	4
hafyposy	*Grewia delphinense*	Malvaceae	0	0	4
haramboanjo	*Buxus madagascariensis*	Buxaceae	3	12	0
harandrato	*Intsia bijuga*	Fabaceae	8	15	1
harongapanihy	*Psorospermum revolutum*	Hypericaceae	0	0	7
hazingy	*Symphonia verrucosa*	Clusiaceae	2	0	2
hazofotsy	*Homalium axilare*	Salicaceae	1	1	1
hazomainty	*Diospyrus myriophilla*	Ebenaceae	3	14	3
hazombato	*Campylospermum obtusifolium*	Ochnaceae	1	5	8
hazomiteraky	*Mammea parviflora*	Guttiferae	0	0	2
hazondrano	*Ilex mitis*	Aquifoliaceae	0	0	2
hazondraotry	*Noronhia cf lanceolata*	Oleaceae	0	2	0
hazondroka*	*NA*	*NA*	7	4	0
hazongalala	*Canephora madagascariensis*	Rubiaceae	1	0	1
kabokala	*Cerbera manghas*	Apocynaceae	0	0	2
kalavelo	*Suregada baronii*	Euphorbiaceae	1	3	4
kambatrikambatri	*Brexia* sp.	Grossulariaceae	0	0	3
katrafa	*Terminalia fatraea*	Combretaceae	0	1	0
lalona	*Oncostenum dauphinensis*	Myristicaceae	1	1	1
lampivahatry	*Cinnamosma madagascariensis*	Canellaceae	9	0	0
lehendehemy	*Anthocleista madagascariensis*	Gentianaceae	2	1	1
mafotra	*Brochoneura madagascariensis*	Myristicaceae	0	0	1
magnara toloho	*Dalbergia martima*	Fabaceae	3	8	0
makaranga	*Macaranga perrieri*	Euphorbiaceae	2	1	0
mampay	*Cynometra cloiselii*	Fabaceae	6	0	9
mangavoa	*Saldinia littoralis*	Euphorbiaceae	0	0	11
marakoditra	*Homalium nudiflorum*	Salicaceae	0	0	1
maroando	*Blotia hildebrantii*	Euphorbiaceae	0	0	1
memboloa	*Rinorea pauciflora*	Violaceae	2	1	0
menahy	*Erythroxylon* sp.	Erythroxylaceae	3	5	1
meramaintso	*Sarcolaena multiflora*	Sarcolaenaceae	0	0	4
nato	*Faucherea hexandra*	Sapotaceae	0	0	4
nofotrakoho marecaz	*Vitex tristis*	Lamiaceae	0	0	2
nofotrakoho natiala	*Vitex bracteata*	Lamiaceae	0	2	0
ramirisa	*Homalium louvelianum*	Salicaceae	4	1	0

ramy	*Canarium madgascariensis*	Burseraceae	0	0	3
raobe*	*NA*	*NA*	0	1	0
raotry	*Dypsis scotiana*	Arecaceae	0	0	1
ravenala	*Ravenala madagascariensis*	Strelitziaceae	6	1	1
resonjo	*Beilschmiedia madagascariensis*	Lauraceae	3	8	4
robavy	*Ambavia* sp.	Annonaceae	0	1	0
ropasy	*Eugenia cloiselii*	Myrtaceae	1	2	3
ropoaky	*Eugenia* sp.	Myrtaceae	0	1	0
rotry	*Syzygium emirnense*	Myrtaceae	6	2	10
sagnira	*Neotina isoneura*	Meliaceae	6	1	3
sardobaka*	*NA*	*NA*	2	0	0
sarigoavy	*Malleastrum mandanese*	Meliaceae	0	0	4
sarihafitsy*	*NA*	*NA*	1	0	0
sarikely*	*NA*	*NA*	0	1	0
sarivotaky	*Cassine micrantha*	Celastraceae	1	0	0
sarmafotra*	*NA*	*NA*	1	0	0
sirifotrato*	*NA*	*NA*	1	1	0
sisikandrongo	*Poupartia chapelieri*	Anacardiaceae	3	4	2
sotro	*Phylloxylon xylophylloides*	Fabaceae	2	1	1
taholanga	*Hyperacanthus mandenensi*	Rubiaceae	2	1	0
tangatanganala	*Gaertenera arenaria*	Rubiaceae	0	0	7
tapinandro	*Homalium albiflorum var. Leucophleum*	Salicaceae	2	0	0
tavolohazo	*Cryptocarya oblonga*	Lauraceae	0	0	4
tomizo	*Erythroxylum corymbosum*	Erythroxylaceae	0	0	1
tsanihiposa	*Homalium involucratum*	Salicaceae	1	6	2
tsilaka	*Myrica spathulata*	Myricaceae	6	0	0
tsilantria	*Vaccinium emirnense*	Ericaceae	1	0	0
tsirimbily*	*NA*	*NA*	1	3	0
tsomsoy	*Rhodocolea racemosa*	Bigoniaceae	0	0	1
vahabahatry	*Cinnamosma madagascariensis*	Canellaceae	2	3	1
valotsy	*Breonia perrieri*	Rubiaceae	4	6	0
varikanda	*Dillenia triquetra*	Dilleniaceae	1	3	1
voakazoala	*Homalium albiflorum*	Salicaceae	0	0	3
voalaka	*Morella spatulata*	Myricaceae	0	0	1
voapaky	*Uapaca* sp.	Phyllanthaceae	12	6	8

voatsilana	*Schefflera vantsilana*	Araliaceae	2	0	3
vondroza	*Sarcoleana* sp.	Sarcolaenaceae	8	8	3
vonsila	*Scheflera rantsilana*	Araliaceae	0	2	0
zahambe	*Phyllarthron madagascariense*	Bignoniaceae	0	1	0
zambo	*Grisollea* sp.	Stemonuraceae	1	0	1
zora	*Homalium viguirei*	Salicaceae	1	0	0
zorafotsy	*Noronhia ovalifolia*	Oleaceae	3	3	0
zoralahy	*Dicoryphe stipulacea*	Hamamelidaceae	2	0	6
zoramena	*Scolopia orientalis*	Salicaceae	9	4	1

* species not included in the analyses.

Table A2. The regenerating species found in the three forests included in the study (i.e., S9 and S7 in Sainte Luce, and Mandena Conservation Zone (M15+M16) in Mandena), with their total abundance. Species dispersed solely by the red-collared brown lemur (*Eulemur collaris*) are presented in **bold**.

Vernacular name	Scientific name	Family	S9	S7	MCZ
akondronala	*Ophiocolea delphinense*	Ophiocomidae	1	1	1
ambirombariky	*Sideroxylon beguei* var. *sabouraui*	Sapotaceae	-	6	-
ambora	*Tambourissa purpurea*	Monimiaceae	23	38	31
ampoly	*Vepris eliotii*	Rutaceae	118	45	77
bamby	*Anthostema madagascariensis*	Euphorbiaceae	18	13	-
belavenoky	***Noronhia emarginata***	**Oleaceae**	72	72	14
bemafais*	*NA*	*NA*	-	-	8
bemalemy	*Bembicia uniflora*	Flacourtiaceae	-	-	15
bemisa*	*NA*	*NA*	8	-	-
berehoky	*Dombeya mandenensis*	Malvaceae	76	26	5
beronono	*Trilepisium madagascariense*	Moraceae	8	8	-
boaka	***Dypsis prestoniana***	**Arecaceae**	5	7	-
boakabe	*Dypsis* sp.	Arecaceae	2	-	-
disaky	*Garcinia aphanophlebia*	Clusiaceae	-	-	7
fagnota*	*NA*	*NA*	9	82	1
falinandro	*Dracaena reflexa*	Asparagaceae	127	124	85
falinandro be	*Dracaena fontanesiana*	Asparagaceae	4	19	41
famata	*Euphorbia tirucalli*	Euphorbiaceae	-	-	12
famoty	*Vernonia pectoralis*	Asteraceae	-	-	1
fandra I	*Pandanus madagascariensis*	Pandanaceae	68	30	3

fandrianakanga	***Polycardia phyllanthoides***	**Aphloiaceae**	35	41	1
fangiamana	*Aphloia theiformis*	Aphloiaceae	10	5	6
fangora	*Erythroxylum* sp.	Erythroxylaceae	97	48	-
fanolafotsy	*Asteropeia multiflora*	Asteropeiaceae	111	142	5
fanolamena	*Asteropeia micraste*	Asteropeiaceae	111	56	3
fantsikahitry	*Canthium* sp.	Rubiaceae	156	117	181
fantsikohy	*Clerodendrum* sp.	Lamiaceae	17	4	-
fitagiano*	*NA*	*NA*	-	-	9
forofoky	*Diospyros littoralis*	Ebenaceae	11	32	31
fotombavy	*Leptolaena multiflora*	Sarcolaenaceae	-	-	2
fotondahy	*Schizolaena elongata*	Sarcolaenaceae	8	7	-
fotsyvavy	*Polyalthia madagascariensis*	Annonaceae	1	2	-
guavy*	*Psidium guayave*	Myrtaceae	1	-	-
hafyposy	*Grewia delphinense*	Malvaceae	-	-	27
harajanboa*	*NA*	*NA*	4	-	-
harambilo	*Podocarpus madagascariensis*	Podocarpaceae	-	-	1
haramboanzo	*Elaeodendron pauciflorum*	Buxaceae	70	50	-
haramy	***Canarium boivinii***	**Burseraceae**	-	2	-
harandrato	*Intsia bijuga*	Fabaceae	26	13	43
harongapanihy	*Psorospermum brachypodium*	Hypericaceae	16	11	9
havohoa	*Dais glaucescens*	Thymelaeceae	-	-	157
hazingy	*Symphonia verrucosa*	Clusiaceae	2	-	4
hazofotsy	*Homalium axilare*	Salicaceae	20	37	23
hazomainty	***Diospyrus myriophilla***	**Ebenaceae**	100	157	43
hazomamy	*Anisophyllea fallax*	Vitaceae	-	-	2
hazombato	*Camp ylospermum obtusifolium*	Ochnaceae	4	11	63
hazondrano	*Ilex mitis*	Aquifoliaceae	9	2	1
hazondraotry	*Noronhia cf. lanceolata*	Oleaceae	18	38	-
hazondroka*	*NA*	*NA*	45	37	-
hazongalala	*Tricalysia cryptocalyx*	Rubiaceae	-	-	17
kabokala	*Cerbera manghas*	Apocynaceae	31	16	5
kaboky*	*NA*	*NA*	14	-	-
kafeniala*	*NA*	*NA*	-	-	2
kalavelo	*Suregada baronii*	Euphorbiaceae	60	32	101
kambatrikambatri	***Brexia* sp.**	**Grossulariaceae**	-	-	248

kangy	*Rhus thouarsii*	Anacardiaceae	-	-	1
katrafa	*Terminalia fatraea*	Combretaceae	12	12	-
kinini bonaky*	*Eucalyptus citriodora*	Myrtaceae	-	-	1
kokondroky*	*NA*	*NA*	-	-	5
kotofotsy	*Coffea commersoniana*	Rubiaceae	-	-	16
lalona	*Oncostenum dauphinensis*	Myristicaceae	20	3	33
lampivahatry	*Cinnamosma madagascariensis*	Canellaceae	90	84	-
lampivahatry fotsy*	*NA*	*NA*	1	-	-
lehendehemy	*Anthocleista madagascariensis*	Gentianaceae	11	4	2
lendremilahy	*Anthocleista longifolia*	Gentianaceae	1	-	-
mafotra	***Brochoneura acuminata***	**Myristicaceae**	-	-	149
magnara toloho	*Dalbergia martima*	Fabaceae	18	459	1
makaranga	*Macaranga perrieri*	Euphorbiaceae	11	16	1
mampay	***Cynometra cloiselii***	**Fabaceae**	275	23	46
mangavoa	*Enterospermum* sp.	Euphorbiaceae	-	-	12
mantsa*	*NA*	*NA*	-	31	-
maranirtatoraka	*Enterospermum aff. berieranium*	Euphorbiaceae	-	-	3
maroando	*Blotia hildebrantii*	Euphorbiaceae	-	-	1
memboloa	*Rinorea pauciflora*	Violaceae	29	25	53
menahy	*Erythroxylon* sp.	Erythroxylaceae	42	7	20
menavoa	*Erythroxylum corymbosum*	Erythroxylaceae	-	-	69
nato	***Faucherea hexandra***	**Sapotaceae**	56	23	4
nofotrakoho marecaz	*Vitex tristis*	Lamiaceae	-	-	1
nofotrakoho natiala	*Vitex bracteata*	Lamiaceae	53	47	77
pimakorova*	*NA*	*NA*	28	21	-
ramirisa	*Homalium louvelianum*	Salicaceae	6	2	1
ramy	*Canarium madgascariensis*	Burseraceae	7	6	-
raobe*	*NA*	*NA*	27	40	-
raotry	*Dypsis scottiana*	Arecaceae	126	73	119
ravenala	*Ravenala madagascariensis*	Strelitziaceae	7	2	3
resonjo	*Beilschmiedia madagascariensis*	Lauraceae	5	7	-
robavy	*Ambavia* sp.	Annonaceae	-	2	-
rondria	*Campnosperma micranteia*	Anacardiaceae	-	-	3
ropasy	*Eugenia cloiselii*	Myrtaceae	9	37	83
ropoaky	***Eugenia* sp.**	**Myrtaceae**	24	5	-

rotry	*Syzygium emirnesis*	Myrtaceae	56	75	105
rotry marecaz	*Syzigium* sp.	Myrtaceae	-	-	3
sagnira	*Astrotrichilia elliotii*	Meliaceae	133	-	141
sagnira fotsy*	*NA*	*NA*	4	-	-
sagnira mena*	*NA*	*NA*	8	-	-
sarigoavy	***Malleastrum mandanese***	**Meliaceae**	29	17	43
sarikaboky*	*NA*	*NA*	3	-	-
sarikafe*	*NA*	*NA*	-	7	-
sarikasy*	*NA*	*NA*	30	53	-
sarikely*	*NA*	*NA*	33	3	-
saripima*	*NA*	*NA*	3	-	-
sarivotaky	*Cassine micrantha*	Celastraceae	103	27	-
silambolambo*	*NA*	*NA*	-	-	1
sisikandrongo	***Poupartia chapelier***	**Anacardiaceae**	28	26	-
sivoanyo	*Croton* sp.	Euphorbiaceae	-	-	9
sivorikely	*Mammea bongo*	Clusiaceae	-	-	62
somotsoy	*Rhodocolea racemosa*	Bignoniaceae	-	-	9
sotro	*Phylloxylon xylophylloides*	Fabaceae	14	-	-
taholanga	*Hyperacanthus mandenensis*	Rubiaceae	15	11	-
takotry*	*Nepenthes madagascariensis*	Nepenthaceae	5	-	-
tanatananala	*Gaertnera arenaria*	Rubiaceae	-	-	7
tandrokosy	*Petchia madagascariensis*	Apocynaceae	2	4	8
tapinandro	*Homalium albiflorum var. leucophleum*	Salicaceae	38	31	-
tapinandro madinjavy*	*NA*	*NA*	3	-	-
tapinara*	*NA*	*NA*	1	-	-
tavolohazo	*Cryptocarya oblonga*	Lauraceae	12	8	-
tavolohazo marecaz	*Cryptocarya* sp.	Lauraceae	-	-	18
tolanosy	*NA*	*NA*	-	-	1
tomizo	*Erythroxylum corymbosum*	Erythroxylaceae	-	-	5
tsanihiposa	*Homalium involucratum*	Salicaceae	25	7	-
tsilaka	*Myrica spathulata*	Myricaceae	53	4	-
tsilantria	*Vaccinium emirnense*	Ericaceae	8	-	5
tsilavimbinato	***Rhopalocarpus coriaceus***	**Sphaerosepalaceae**	2	-	-
tsirimbily*	*NA*	*NA*	12	10	-

tsivakimbinato	*Rhopalocarpu s crassinervius*	Sphaerosepalaceae	1	-	-
vahabahatry	***Cinnamosma madagascariensis***	**Canellaceae**	117	56	2
vahyfotsy	*Anisocyclea fallax*	Menispermaceae	5	1	-
valotsy	*Breonia perrieri*	Rubiaceae	19	14	-
valypangaly*	*NA*	*NA*	3	2	-
varikanda	*Dillenia triquetra*	Dilleniaceae	36	50	-
velombariky*	*NA*	*NA*	-	1	-
vendra*	*NA*	*NA*	-	-	1
vetrotsky*	*NA*	*NA*	2	-	-
voakazoala	*Homalium albiflorum*	Salicaceae	-	-	31
voapaky	***Uapaca* sp.**	**Phyllanthaceae**	58	70	3
vokarepky	*Brexia madagascariensis*	Celastraceae	7	2	1
vondroza	*Sarcoleana* sp.	Sarcolaenaceae	25	18	-
vonsila	*Scheflera rantsilana*	Araliaceae	55	24	1
zahambe	***Phyllarthron madagascariense***	**Bignoniaceae**	50	36	-
zambo	*Grisollea sp.*	Stemonuraceae	6	22	1
zorafotsy	*Noronhia ovalifolia*	Oleaceae	114	36	1
zoralahy	*Dicoryphe stipulacea*	Hamamelidaceae	-	-	1
zoramena	*Scolopia orientalis*	Salicaceae	276	123	63

* species not included in the analyses.

Table A3. Community similarity within the three forests included in the study, expressed as Sorenson's community similarity coefficients.

	Sainte Luce		**Mandena**
	S9	**S7**	**MCZ**
Seedlings: defecation x non-defecation locations	0.890	-	0.774
Saplings: defecation x non-defecation locations	0.848	-	0.673
Defecation locations: seedlings x saplings	0.905	-	0.784
Non-defecation locations: seedlings x saplings	0.901	-	0.742
Overall: defecation x non-defecation locations	0.490	-	0.469
Overall: seedlings x saplings	0.924	0.877	0.790

Table A4. Regeneration of species dispersed by the red-collared brown lemur (*Eulemur collaris*) in the three fragments of littoral forests included in this study.

	S9 (Sainte Luce)		S7 (Saint Luce)		MCZ (Mandena)	
Scientific name	< 22 cm	> 22 cm	< 22 cm	> 22 cm	< 22 cm	> 22 cm
Noronhia emarginata	56		42	30	8	6
Dypsis prestoniana	2	3	0	7	-	-
Polycardia phyllanthoides	27	8	26	15	0	1
Canarium boivinii	-	-	2	0	-	-
Diospyrus myriophilla	42	58	105	52	25	18
Brexia sp.	-	-	-	-	222	26
Brochoneura acuminata	-	-	-	-	56	93
Cynometra cloiselii	206	69	16	7	39	7
Faucherea hexandra	42	14	16	7	0	4
Eugenia sp.	20	4	4	1	-	-
Malleastrum mandanese	11	18	7	10	36	7
Poupartia chapelier	19	9	11	15	-	-
Rhopalocarpus coriaceus	2	0	-	-	-	-
Cinnamosma madagascariensis	109	8	47	9	1	1
Uapaca sp.	32	26	51	19	3	0
Phyllarthron madagascariense	31	19	14	22	-	-

Appendix III

Table A1. Forest species mentioned as red-collared brown lemur (*Eulemur collaris*) food sources by the participants from Sainte Luce (N=26) and from Mandena (N=6).

Veracular name	Scientific name	Family	SL	MND	Confirmed in their diet
akondronala	*Ophiocolea delphinensis*	Ophiocomidae	1	0	+
ambora	*Tambourissa* sp.	Monimiaceae	1	0	+
boaka	*Dypsis prestoniana*	Araceae	1	0	+
boakabe	*Dypsis* sp.	Araceae	1	0	+
falinandro	*Dracaena reflexa var.nervosa*	Asparagaceae	1	0	+
fanga	*Pandanus dauphinensis*	Pandanaceae	3	0	+
harandrato	*Intsia bijuga*	Fabaceae	1	0	+
hazingy	*Symphonia* sp.	Clusiaceae	1	0	+
kaboky	*Cerbera manghas*	Apocynaceae	1	0	-
katrafa	*Terminalia fatraea*	Combretaceae	1	0	+
mampay	*Cynometra cloiselii*	Fabaceae	1	0	+
nato	*Fauchera hexandra*	Sapotaceae	1	0	+
nonoky	*Ficus pyrifolia*	Moraceae	6	0	+
raotry	*Dypsis scottiana*	Araceae	8	0	+
ravenala	*Ravenala madagascariensis*	Strelitziaceae	5	0	+
ropasy	*Eugenia cloiselii*	Myrtaceae	1	0	+
ropoaky	*Eugenia* sp.	Myrtaceae	2	0	+
rotry	*Syzygium* sp.	Myrtaceae	10	0	+
taholanga	Hyperacanthus mandenensis	Rubiaceae	1	0	+
tamenaky	*Magnistipula tamenaka*	Chrysobalanaceae	0	4	+
telopoloambilany *	*Dypsis saintelucei*	Araceae	1	0	+
tsilantria	*Vaccinium emirnense*	Ericaceae	11	0	+
valotsy	*Breonia perrieri*	Rubiaceae	0	2	+
voapaky	*Uapaca* sp.	Phyllanthaceae	10	2	+
voatsimatsy	*Salacia madagascariensis*	Hyppocrateaceae	3	4	+

vondroza	*Sarcoleana* sp.	Sarcoleaceae	8	0	+
anjarezo	*Trema orientalis*	Cannabaceae	1	0	-
areca palm	*Dypsis lutescens*	Arecaceae	0	2	-
lamoty	*Flacourtia indica*	Salicaceae	1	0	-
raobe	*NA*	*NA*	1	0	
tatsima	*NA*	*NA*	1	0	
varikokoky	*NA*	*NA*	1	0	
voavoany	*NA*	*NA*	1	0	
voromy	*NA*	*NA*	1	0	
vorozo	*NA*	*NA*	0	2	

*species only present in Sainte Luce

Table A2. Human crops mentioned as red-collared brown lemur (*Eulemur collaris*) food sources by the participants from Sainte Luce (N=19) and Mandena (N=26).

Crop name	**Sainte Luce**	**Mandena**
banana	12	25
guava	9	3
lychee	0	11
pineapple	2	2
mango	0	3
papaya	0	3
cassava (leaves)	0	1
pomegranate	0	1
sweet potato (leaves)	0	1
strawberry	0	1
corn	0	1
passion fruit	0	1

Appendix IV

Table A1. Plants used for medicinal purposes in Sainte Luce (N=30) and Mandena (N=24), and the details of their use.

Scientific name	Vernacular name	Family	Conservation status and population trend	Part of plant used	Type of treatment	Use	Frequency of use (%)	
							Sainte Luce	Mandena
-	ahipatra	*NA*	-	leaves	tea	after giving birth	3.33	-
-	ahipisaky	*NA*	-	leaves	tea	rheumatism	3.33	-
-	ambanivoha	*NA*	-	leaves, roots	tea	*hevo*; fever; stomach problems	9.99	-
-	ampelamengatsy	*NA*	-	leaves	tea	heart problems	3.33	-
-	bandro	*NA*	-	wood	bath, tea; powder	to avoid premature birth	3.33	-
-	basiboka	*NA*	-	leaves	bath	allergic reactions, itching	3.33	-
-	beloha	*NA*	-	leaves	tea	fever (children)	-	4.16
-	bemafais	*NA*	-	leaves	tea, bath	rash (children)	-	4.16
-	cinquate malady	*NA*	-	grass	tea	low circulation	6.66	-
-	dokotera kely	*NA*	-	leaves	tea	stomach problems	6.66	16.64
-	fagamo	*NA*	-	leaves	leaves mixed with petrol	against parasy	-	4.16
-	famoty be	*NA*	-	leaves	tea	stomach problems	-	4.16

-	fangiakatany	*NA*	-	leaves	tea	*hevo*	3.33	-
-	farfary	*NA*	-	leaves	tea	stomach problems	-	4.16
-	fitikirananfuiky	*NA*	-	leaves	tea	*hevo*	-	4.16
-	fotadrano	*NA*	-	leaves	tea	diabetes	-	4.16
-	hahatsy	*NA*	-	leaves		bad spirit possession	3.33	-
-	hazota	*NA*	-	wood	bath, tea; powder mixed with water into a paste	to avoid premature birth, stop the bleeding	6.66	-
-	hisatsy	*NA*	-	leaves	rubbed between hands, put on the eyes	eye problems	-	4.16
-	lengomantsy	*NA*	-	leaves	tea	diarrhoea with blood	3.33	-
-	madravasarotsy	*NA*	-	leaves	tea	stomach ache	-	4.16
-	madro	*NA*	-	wood	bath, tea; powder	to avoid premature birth	3.33	-
-	mahabilo	*NA*	-	leaves, bark	tea	back pain, joint pain	-	4.16
-	maharoaky	*NA*	-	leaves	tea	headache, cough (children)	3.33	4.16
-	mahasalama	*NA*	-	wood	bath, tea; powder	to avoid premature birth	3.33	-
-	mahavalia	*NA*	-	wood		protection from thunder	3.33	-
-	manfabody	*NA*	-	leaves,	tea	stomach problems	3.33	-

				roots				
-	mangarato	*NA*	-	leaves	tea	cough	3.33	-
-	manidabody	*NA*	-	leaves	tea	stomach problems	3.33	-
-	masokoaky	*NA*	-	leaves	tea	low appetite (children)	-	4.16
-	mimy	*NA*	-	leaves	tea	stomach ache	-	4.16
-	omamata	*NA*	-	whole plant	placed under pillow	against bad dreams and bad spirits	-	4.16
-	raobe	*NA*	-	wood	bath, tea; powder	to avoid premature birth	3.33	-
-	remenso	*NA*	-	bark		skin burns, *hevo*	-	4.16
-	retately	*NA*	-	leaves	tea	stomach pain, fever	-	8.32
-	sangonakoho	*NA*	-	leaves	sap placed on the wound	stop bleeding cuts	3.33	-
-	sarivoandro	*NA*	-	leaves	tea	*hevo*	3.33	-
-	savoagasy	*NA*	-	leaves	tea	vomiting	3.33	-
-	siosio	*NA*	-	leaves	tea	cough (children)	-	4.16
-	soazanahary	*NA*	-	wood	bath, tea; powder	to avoid premature birth	3.33	-
-	solofafa	*NA*	-	leaves	tea, leaf sap	cough	3.33	-
-	taboara		-	leaves	paste	pain after breastfeeding	-	4.16
-	taritariky	*NA*	-	leaves	tea	cough	3.33	-
-	tatamo	*NA*	-	leaves	tea	heart problems	3.33	-
-	tegny	*NA*	-	leaves	tea	excessive bleeding during the period;	6.66	-

						rheumatism		
-	teloravi	*NA*	-	leaves	tea	bloating	3.33	-
-	tenakarabo	*NA*	-	roots, seeds	mixed with water into paste	painful wounds	3.33	-
-	teto	*NA*	-	leaves, bark	leaf and bark eaten	injury, blood loss, dizziness	-	4.16
-	tishitafototsy	*NA*	-	stem	tea	tiredness, anaemia	3.33	-
-	tserize	*NA*	-	leaves	tea	stomach problems, diarrhoea	3.33	-
-	tsibordjano	*NA*	-	leaves	tea	low appetite (children)	-	4.16
-	tsilitafototsy	*NA*	-	vine	tea	prostate problems	3.33	-
-	tsimahavagno	*NA*	-	bark	powder	wound swelling	3.33	4.16
-	tsingirifiry	*NA*	-	leaves	tea	fever (children)	-	4.16
-	tsingirimitiky	*NA*	-	leaves	sap	eye infection	-	4.16
-	tsintirimitiky	*NA*	-	leaves, stem	tea	stomach problems; diarrhoea (children)	13.32	8.32
-	tsipanga	*NA*	-	leaves	tea	excessive bleeding during the period	3.33	-
-	tsipotiky	*NA*	-	leaves	tea	excessive bleeding during the period	3.33	-
-	tsiromotsi ambilahy	*NA*	-	grass	boiled, cooled off, used to massage	sprained ankle	3.33	-
-	tsivoandrofito	*NA*	-	wood	bath, tea; powder	to avoid premature birth	3.33	-
-	vahatry fotabe	*NA*	-	roots,	mixed with	painful wounds	3.33	-

				seeds	water into paste			
-	vahimasoandro	*NA*	-	leaves	crushed leaves, mixed with pepper	to close wounds	-	4.16
-	voajrokitra	*NA*	-	leaves	tea	excessive bleeding during the period	3.33	-
-	zira	*NA*	-	leaves	tea	diarrhoea	3.33	-
Ananas comosus	mananasy	Bromeliaceae	-	leaves	tea	rheumatism	3.33	-
Acacia bellula	betratra	Fabaceae	-	leaves	tea	constipation	3.33	-
Aloe vera	vaho	Asphodelaceae	-	leaves	sap - rubbed or drank, tea	cramps, stomach ache, internal bleeding, skin burns	6.66	24.96
Anisophyllea fallax	hazomasy	Anisophylleacea	LC (decreasing)	wood	bath, tea; powder	to avoid premature birth	3.33	-
Anno senegalensis	coeur du boeuf	Annonaceae	LC (stable)	leaves	inhalation	fever	-	4.16
Anthocleista madagascariensis	lehendehemy	Gentianales	LC (decreasing)	leaves	tea, bath	post-giving birth; to get the period	6.66	-
Aristolochia sp.	tontonga	Aristolochiaceae	-	leaves	tea	stomach problems (children)	3.33	4.16
Asteropeia sp.	fanola fotsy/ fanola mena	Theaceae	LC	bark; leaves	powder; sometimes mixed with water; tea or bath	against bad luck, bad spirit possession; against thunder; after giving birth	16.65	4.16
Beilschmiedia madagascariensis	resonjo	Lauraceae	LC (decreasing)	bark, roots	mixed with water	wound infection, toothache	3.33	4.16

Burasaia madagascariensis	farisaty	Menispermaceae	LC (decreasing)	bark, roots	mixed with water, or drank as tea	wound infection, anaemia, stomach problems, diarrhoea	13.32	-
Cabucala madagascariensis	tandrokosy	Apocynaceae	LC (decreasing)	roots	tea	stomach ache	6.66	-
Campnosperma micranteia	roandria	Anacardiaceae	LC (decreasing)	leaves	sap, used to massage	breathing problems; eye problems	3.33	4.16
Carica papaya	papaya	Caricaceae	DD (decreasing)	leaves	tea	vomiting	3.33	-
Cassia sp.	sarongaza	Fabacaeae	-	roots	tea	stomach problems	3.33	-
Catharanthus roseus	tonga	Apocyaceae	-	roots; leaves	grated, mixed with water; tea	stomach problems	33.3	41.6
Cinnamosma madagascariensis	vahabahatry	Canellaceae	LC (decreasing)	leaves, roots, bark	tea	toothache, bad spirit; wound infection; liver problems	19.98	-
Citrus reticulata	tangerine	Rutaceae	-	leaves	tea	stomach problems	3.33	-
Citrus sp.	voasary	Rutaceae	-	leaves	inhalation	fever, headache	3.33	-
Cocos nucifera	coconut	Arecaceae	-	roots, milk, fruit	tea; fruit grated into paste	problems with urinating, alcohol poisoning; for energy; yellow fever, stomach problems; against pain after breastfeeding	16.65	4.16
Coffea canephora	coffee	Rubiaceae	LC (stable)	leaves	tea, bath	gout, high blood pressure	3.33	4.16
Dracae reflexa	falinandro	Liliaceae	LC (stable)	leaves	tea	anaemia	3.33	-

var.nervosa								
Dypsis nodifera	raotry	Areceae	LC (stable)	wood	bath, tea; powder	to avoid premature birth	3.33	-
Dypsis prestonia	boaka	Arecaceae	LC (stable)	leaves	bath, or placed on the wound	wound, nerve problems, nerve pain	3.33	4.16
Eliea articulata	hela	Hypericaceae	LC (stable)	leaves, bark	tea	heart problems; wound infection	3.33	12.48
Embelia incumbens	taratasy	Myrsinaceae	-	leaves, bark	leaf and bark eaten	injury, blood loss, dizziness	-	4.16
Eragrostis cilianensis	akatafotsy	Poaceae	-	leaves	tea	*hevo*	3.33	-
Erica densa	anjavidy	Ericaceae	-	roots, leaves	tea	stop excessive bleeding after the period; diarrhoea, *hevo*	6.66	-
Erythroxylum sp.	fangora	Erythroxylaceae	-	leaves	tea	diarrhoea with blood	3.33	-
Eucalyptus sp.	eucalyptus	Myrtaceae	-	leaves	tea, inhalation	fever; headache	6.66	-
Ficus megapoda	aviavy	Moraceae	-	leaves	tea	anaemia	3.33	-
Ficus pyrifolia	nonoka	Moraceae	-	bark	tea, bath	after giving birth	-	4.16
Ficus sp.	fihamy	Moraceae	-	leaves	powdered and drank as tea	anaemia, circulation	6.66	4.16
Intsia bijuga	harandrato	Fabaceae	NT (decreasing)	bark	powder	pain, infection of skin, burns	3.33	8.32
Jatropa curcas	savoa	Euphorbiaceae	-	dry leaves	tea, wash	tetanus	3.33	-

Lanta camara	radriaky	Verbenaceae	-	leaves; sap	tea, inhalation; leaves placed under the nose	fever; dizziness, high blood pressure; breathing problems	13.32	-
Lygodium sp.	tsylitolito	Lygodiaceae	-	leaves	tea	dizziness	3.33	-
Mangifera indica	mango	Anacardiaceae	DD (unspecified)	bark	boiled and used to wash the burnt skin or powdered placed on the burnt skin	skin burns	-	4.16
Monathotaxus sp.	fagnota	Anonaceae	-	leaves, roots	tea, bath; powdered roots	bad spirit possession; heart problems; stomach problems	33.3	-
Morella spathulata	tsilaka	Myricaceae	LC (unknown)	bark	boiled and placed in mouth	toothache	3.33	-
Musa paradisiaca	banana	Musaceae	-	fruit	tea	diarrhoea	3.33	-
Neotina isoneura	sagnira	Sapindaceae	LC (decreasing)	leaves	tea	*hevo*	-	12.48
Litchi chinensis	lychee	Sapindaceae	-	dry leaves	tea	toothache	-	4.16
Ocimum canum	romba	Lamiaceae	-	leaves	tea; leaves placed under the nose	asthma, cough, post-giving birth pain; unconsciousness	9.99	4.16
Ocimum	romba be	Lamiaceae	-	leaves	tea	post-giving birth pain, brings appetite	3.33	-

gratissimum								
Olax dissitiflora	ambiotsy	Olacaceae	LC (stable)	leaves	leaves crushed and put on the wound	stop the swelling	-	4.16
Phaseolus vulgaris	tsaramaso	Fabaceae	LC (stable)	beans	cooking water	anaemia	3.33	-
Phylloxylon xylophylloides	sotro	Fabaceae	NT (decreasing)	leaves; bark	tea; bark powder mixed with water	de-worming; headache; diarrhoea; anaemia	9.99	-
Priva humberti	mamiaho	Verbenaceae	-	leaves	tea	*hevo*	3.33	4.16
Psidium guayave	goavy	Myrtaceae	-	leaves	tea	stomach problems, diarrhoea	3.33	4.16
Psorospermum brachypodium	haronga	Clusiaceae	VU (decreasing)	leaves, leaf buds	tea	heart problems, cough	3.33	4.16
Ricinus communis	kinagna	Euphorbiaceae	-	leaves	inhalation	fever, headache	3.33	-
Suregada baronii	kalavelo	Euphorbiaceae	-	leaves	tea; bath	fever, stomach problems, *hevo*, constipation; diarrhoea; spirit possession	23.31	-
Syzygium emirnense	rotry	Myrtaceae	LC (stable)	leaves	tea	*hevo*; bad spirit possession	6.66	-
Termilia fatraea	katrafa	Combretaceae	LC (decreasing)	bark, leaves	powder, tea	*hevo*; diarrhoea; diarrhoea with blood	9.99	8.32
Tetracera madagascariensis	vahimara	Dilleniaceae	-	leaves	crushed leaves put on the injury	injury	-	4.16

Trema orientalis	anjarezo	Cannabaceae	LC (unknown)	leaves	tea	to get period	3.33	-
Vepris eliotii	ampoly	Rutaceae	LC (decreasing)	wood; leaves	bath, tea; powder	to avoid premature birth; stomach problems	9.99	-
Vernonia pectoralis	famoty	Asteraceae	-	leaves	tea	stomach problems	16.65	-

Appendix IV

Table A2. Plants used as construction materials in Sainte Luce (N=29, n=38) and Mandena (N=29, n=36), and the percentage of participants who reported using particular species.

Scientific name	Vernacular name	Family	Conservation status and population trend	SL (%)	MND (%)	Most important (SL) (%)	Most important (MND) (%)
-	halapo	*NA*	-	-	3.44	-	-
-	hela	*NA*	-	3.44	-	-	-
-	mantsa	*NA*	-	13.76	-	-	-
-	taimbarika	*NA*	-	-	10.32	-	-
-	tendrokazo	*NA*	-	-	24.08	-	13.76
-	valotsy	*NA*	-	-	3.44	-	-
-	vintano	*NA*	-	-	6.88	-	-
Anthostema madagascariensis	bamby	Euphorbiaceae	LC (decreasing)	3.44	-	-	-
Aphloia theiformis	fangiamana	Aphloiaceae	LC (stable)	-	3.44	-	-
Asteropeia micraster	fanola mena	Asteropeiaceae	VU (decreasing)	37.84	20.64	6.88	10.32
Asteropeia multiflora	fanola fotsy	Asteropeiaceae	LC (decreasing)	37.84	20.64	6.88	10.32
Brochoneura acuminata	mafotra	Myristicaceae	LC (decreasing)	-	6.88	-	-
Buxus madagascariensis	haramboanjo	Buxaceae	LC (decreasing)	10.32	-	3.44	-
Scolopia erythrocarpa	lampivahatry	Canellaceae	EN (decreasing)	34.40	6.88	6.88	-
Cinnamosma madagascariensis	vahabahatry	Canellaceae	LC (decreasing)	34.40	-	3.44	-
Clerodendrum sp.	fasinakoho	Lamiaceae	-	-	6.88	-	3.44
Dillenia triquetra	varikanda	Dilleniaceae	LC (decreasing)	6.88	-	-	-
Diospyros myriophylla	hazomainty	Ebenaceae	LC (decreasing)	6.88	3.44	-	-
Dypsis nodifera	raotry	Araceae	LC (stable)	6.88	3.44	-	-
Erythroxylon sp.	menahy	Erythroxylaceae	-	6.88	-	-	-

*Eucalyptus citriodora**	kinini bonaky	Myrtaceae	LC (stable)	-	72.24	-	10.32
*Eucalyptus globulus**	kinini boasary	Myrtaceae	LC (stable)	-	27.52	-	-
*Eucalyptus maculata**	kinini fotsy	Myrtaceae	LC (decreasing)	-	10.32	-	-
*Eucalyptus robusta**	kinini mena	Myrtaceae	NT (decreasing)	-	34.40	-	3.44
Homalium albiflorum	voakazoala	Salicaceae	LC (decreasing)	6.88	-	-	-
Homalium albiflorum var. leucophleum	tapinandro	Salicaceae	LC (decreasing)	24.08	-	3.44	-
Homalium planiflorum	hazofotsy	Salicaceae	LC (decreasing)	-	3.44	-	-
Homalium louvelianum	ramirisa	Salicaceae	VU (decreasing)	6.88	-	-	-
Humbertia madagascariensis	endrangendra	Humbertiaceae	LC (decreasing)	-	34.40	-	24.08
Intsia bijuga	harandrato	Fabaceae	NT (decreasing)	75.68	10.32	68.8	-
Leptolaena pauciflora	fonto	Sarcolaenaceae	LC (decreasing)	6.88	13.76	-	3.44
Mimusops voalela	nato	Sapotaceae	DD (unspecified)	10.32	3.44	-	-
Monathotaxus sp.	mahimety	Annonaceae	-	-	3.44	-	-
Neotina isoneura	sagnira	Sapidaceae	LC (decreasing)	-	3.44	-	-
Noronhia cf. lanceolata	hazondraotry	Oleaceae	LC (decreasing)	3.44	-	-	-
Noronhia emarginata	belavenoky	Oleaceae	LC (decreasing)	10.32	-	3.44	-
Noronhia ovalifolia	zora fotsy	Oleaceae	EN (decreasing)	10.32	-	-	-
Ocotea racemosa	varongy	Lauraceae	LC (unknown)	-	3.44	-	3.44

Oncostenum dauphinensis	lalona	Myrsinaceae	-	3.44	-	-	-
Phyllarthron ilicifolium	zahambe	Bignoiaceae	EN (decreasing)	6.88	-	-	-
Phylloxylon xylophylloides	sotro	Fabaceae	NT (decreasing)	44.72	37.84	44.22	24.08
Plectronia densiflorum	fantsikahitry	Rubiaceae	LC (decreasing)	72.24	-	6.88	-
Poupartia chapelieri	sisikandrongo	Anacardiaceae	LC (decreasing)	3.44	-	-	-
Psidium guayave	goavy	Myrtaceae	-	-	3.44	-	-
Raphia sp.	rafia	Arecaceae	-	-	3.44	-	-
Ravenala madagascariensis	ravenala	Strelitziaceae	LC (decreasing)	79.12	3.44	3.44	-
Saldinia littoralis	mangavoa	Rubiaceae	-	3.44	-	3.44	-
Sarcoleana sp.	vondroza	Sarcoleaceae	-	41.28	3.44	3.44	-
Schizolaena elongata	fotondahy	Sarcolaenaceae	LC (decreasing)	27.52	-	6.88	-
Scolopia orientalis	zora mena	Salicaceae	VU (decreasing)	24.08	-	-	-
Streblus sp.	dipaty	Moraceae	-	-	6.88	-	3.44
Symphonia verrucosa	hazingy	Clusiaceae	LC (decreasing)	3.44	3.44	-	-
Syzygium emirnense	rotry	Myrtaceae	LC (stable)	24.08	6.88	-	3.44
Tambourissa purpurea	ambora	Monimiaceae	LC (stable)	6.88	-	-	-
Terminalia fatraea	katrafa	Combretaceae	LC (decreasing)	24.08	-	13.76	-
Trema orientalis	anjarezo	Cannabaceae	LC (unknown)	-	6.88	-	-
Uapaca sp.	voapaky	Phyllanthaceae	-	30.96	24.08	-	3.44
Vepris eliotii	ampoly	Rutaceae	LC (decreasing)	3.44	3.44	-	-
Vitex tristis	nofotrakoho	Lamiaceae	EN (decreasing)	3.44	-	-	-

Table A3. Plants used as firewood in Sainte Luce (N=26, n=48) and Mandena (N=18, n=30), and the percentage of participants who reported using particular species.

Scientific name	Vernacular name	Family	Conservation status and population trend	SL (%)	MND (%)
-	anjavidy	*NA*	-	7.70	11.10
-	fitagiano/fotandrano	*NA*	-	-	5.55
-	halampo	*NA*	-	-	5.55
-	hela	*NA*	-	7.70	-
-	lamoty	*NA*	-	7.70	-
-	lokasa	*NA*	-	3.85	-
-	mantsa	*NA*	-	19.25	-
-	sariakata	*NA*	-	3.85	-
-	tendrokazo	*NA*	-	-	5.55
-	tokambakasy	*NA*	-	-	5.55
-	tsirahay	*NA*	-	7.70	-
-	valotsy	*NA*	-	3.85	-
-	voandelaky	*NA*	-	-	5.55
-	votaky	*NA*	-	15.40	5.55
Acacia sp.*	acacia	Fabaceae	-	-	11.10
Aphloia theiformis	fangiamana	Aphloiaceae	LC (stable)	-	5.55
Asteropeia micraster	fanola mena	Asteropeiaceae	VU (decreasing)	65.45	-
Asteropeia multiflora	fanola fotsy	Asteropeiaceae	LC (decreasing)	65.45	-
Beilschmiedia madagascariensis	resonjo	Lauraceae	LC (decreasing)	3.85	-
Bembicia uniflora	bemalemy	Flacourticeae	LC (decreasing)	3.85	-
Buxus madagascariensis	haramboanjo	Buxaceae	LC (decreasing)	3.85	-
Campylospermum obtusifolium	hazombato	Ochnaceae	DD (unspecified)	-	5.55
*Casuarina equisetifolia**	filao	Casuarinaceae	LC (stable)	3.85	-
Scolopia erythrocarpa	lampivahatry	Canellaceae	EN (decreasing)	11.55	-
Cinnamosma madagascariensis	vahabahatry	Canellaceae	LC (decreasing)	23.10	-

Cynometra cloiselii	mampay	Fabaceae	-	3.85	-
Diospyros myriophylla	hazomainty	Ebenaceae	LC (decreasing)	7.70	-
Enterospermum aff. berieranium	maranirtatoraka	Euphorbiaceae	LC (decreasing)	3.85	-
Erythroxylon sp.	menahy	Erythroxylaceae	-	3.85	-
*Eucalyptus citriodora**	kinini bonaky	Myrtaceae	LC (decreasing)	3.85	38.85
*Eucalyptus globulus**	kinini boasary	Myrtaceae	LC (decreasing)	-	27.75
*Eucalyptus maculata**	kinini fotsy	Myrtaceae	LC (decreasing)	-	5.55
*Eucalyptus robusta**	kinini mena	Myrtaceae	NT (decreasing)	-	11.10
*Grevillea banksii**	grevilia	Proteaceae	LC (stable)	-	27.75
Grisollea sp.	zambo	Stemonuraceae	-	3.85	-
Homalium albiflorum	voakazoala	Salicaceae	LC (decreasing)	3.85	-
Homalium albiflorum var. leuchophleum	tapinandro	Salicaceae	LC (decreasing)	46.20	-
Homalium louvelianum	ramirisa	Salicaceae	VU (decreasing)	23.10	-
Humbertia madagascariensis	endrangendra	Humbertiaceae	LC (decreasing)	-	16.65
Intsia bijuga	harandrato	Fabaceae	NT (decreasing)	11.55	-
Lantana aculeata	radriaky	Verbenaceae	-	3.85	-
Litchi chinensis	lychee	Sapindaceae	-	-	5.55
Macaranga sp.	makaranga	Euphorbiaceae	-	-	11.10
Magnistipula tamenaka	tamenaky	Chrysobalanaceae	LC (decreasing)	-	11.10
Mimosa latispinosa	rakaraka	Fabaceae	-	-	5.55
Mimusops voalela	nato	Sapotaceae	DD (unspecified)	3.85	-
Monathotaxis sp.	mahimety	Annonaceae	-	-	5.55
Morella spathulata	tsilaka	Myricaceae	LC (unknown)	3.85	-
Noronhia emarginata	belavenoky	Oleaceae	LC (decreasing)	7.70	-
Noronhia ovalifolia	zora fotsy	Oleaceae	EN (decreasing)	11.55	-
Oncostenum dauphinensis	lalona	Myrsiaceae	-	3.85	-
Phyllarthron ilicifolium	zahambe	Bignoniaceae	EN (decreasing)	19.25	-
Phylloxylon xylophylloides	sotro	Fabaceae	NT (decreasing)	7.70	5.55
*Plectronia densiflorum**	fantsikahitry	Rubiaceae	LC (decreasing)	50.05	-
Polyalthia	fotsyvavo	Annonaceae	EN (decreasing)	-	5.55

madagascariensis					
Psidium guayave	guavy	Myrtaceae	-	-	22.20
Psorospermum brachypodium	haronga	Hypericaceae	VU (decreasing)	-	11.10
Ravenala madagascariensis	ravenala	Strelitziaceae	LC (decreasing)	3.85	-
Sarcoleana sp.	vondroza	Sarcoleaceae	-	38.50	-
Neocussonia rainaliana	vonsilana	Araliaceae	EN (decreasing)	-	5.55
Schizolaena elongata	fotondahy	Sarcolaenaceae	LC (decreasing)	15.40	-
Scolopia madagascariensis	zora (be)	Salicaceae	VU (decreasing)	3.85	-
Scolopia orientalis	zora mena	Salicaceae	VU (decreasing)	15.40	-
Syzygium emirnense	rotry	Myrtaceae	LC (stable)	15.40	5.55
Tambourissa purpurea	ambora	Monimiaceae	LC (stable)	19.25	11.10
Terminalia fatraea	katrafa	Combretaceae	LC (decreasing)	7.70	-
Trema orientalis	anjrezo	Cannabaceae	LC (unknown)	-	5.55
Uapaca sp.	voapaky	Phyllanthaceae	-	34.65	11.10
Vepris elliotii	ampoly	Rutaceae	LC (decreasing)	11.55	-
Vernonia pectoralis	famoty	Asteraceae	-	3.85	-
Vitex tristis	nofotrakoho	Lamiaceae	EN (decreasing)	3.85	-

Appendix V

Table A1. Crops grown by the participants from Sainte Luce (N=29) and Mandena (N=29).

	Sainte Luce	**Mandena**
Avocado	0	3
Bambara nut	0	1
Banana	9	11
Beans	1	1
Cassava	29	26
Coconut	25	6
Greens (unspecified)	3	2
Jackfruit	0	1
Jive (locally grown fruit)	0	6
Lychee	1	12
Mandarin	0	1
Maize	3	2
Mango	4	3
Moringa	3	0
Orange	3	6
Papaya	8	1
Pigeon pea	1	0
Pineapple	14	4
Pumpkin	4	0
Red pepper	4	4
Rice	3	22
Soursop	0	2
Sugarcane	1	8
Sweet potato	9	12
Taro	5	2
Turnip	0	1
Vanilla	6	0
Vegetables	0	3
Wild apricot	1	0
Wild custard apple	3	3

Table A2. Animal species hunted in Sainte Luce and Mandena, and the number of participants who hunted them before and since the establishment of the protected areas.

Common name	Scientific name	Sainte Luce		Mandena	
		past	present	past	present
bushpig	*Potamochoerus larvatus*	2	0	1	0
common jery	*Neomixis tenella*	1	0	0	0
Ganzhorn's mouse lemur*	*Microcebus ganzhorni*	-	-	1	0
green pigeon	*Treron australis*	1	1	0	0
helmeted guineafowl	*Umida meleagris*	2	1	0	2
Madagascan blue pigeon	*Alectroenas madagascariensis*	1	0	0	0
Madagascan crowned ibis	*Lophotibis cristata*	2	0	1	0
Madagascar buttonquail	*Turnnix nigricollis*	1	0	0	1
Madagascar flying fox	*Pteropus rufus*	0	0	1	0
Madagascar fody	*Foudia madagascariensis*	0	0	0	2
Madagascar partridge	*Margaroperdix madagarensis*	1	0	0	0
Malagasy bulbul	*Hypsipetes madagascariensis*	1	0	0	0
Malagasy kestrel	*Falco newtoni*	0	0	1	0
Malagasy turtle dove	*Nesoenas picturatus*	3	1	0	0
red-collared brown lemur	*Eulemur collaris*	4	0	1	1
ring-tailed mongoose	*Galidia elegans*	0	0	0	1
Souimanga sunbird	*Cinnyris sovimanga*	2	0	0	0
southern woolly lemur	*Avahi meridionalis*	2	0	1	0
tenrec	Tenrecinae	5	0	4	1
Thomas's dwarf lemur	*Cheirogaleus thomasi*	1	0	1	0
Vasa parrot	*Coracopsis* sp.	1	0	0	0
whistling teal	*Dendrocygna javanica*	0	0	0	2

* Species only present in Mandena.

General appendix

1. **Ethogram**

ACTION	CODE	DESCRIPTION
Feeding	F	Bite, chew, and swallow food items
Moving	M	Get around on trees or on the ground
Sitting	S	Remain inactive and motionless, no contact with conspecifics, less than 10 mins
Resting	R	Remain inactive and motionless, no contact with conspecifics, at least 10 mins
Huddling	H	Remain inactive in close body contact with one or more conspecifics
Self-grooming	GR	Repeatedly licking or using tooth comb on own fur
Mutual grooming	MG	Sharing "grooming" simultaneously or interchanging in rapid succession with one or more conspecifics
Play	P	Chase, fight a conspecific, and vice versa, with no signs of aggression (vocalizations, displays of attack)
Defecating	DE	Expel the stool
Drinking	DK	Drink water from the leaves, in tree holes or in pools
FOOD ITEMS		
Fruits	RF	Fruit with the seed already developed
Flowers	FL	The bloom or blossom of a plant, usually of a different colour, shape, and texture from the foliage
Young leaves	YL	Newly formed leaves, tender, light green or reddish
Mature leaves	ML	Leaves of old formation, leathery, green or dark green
Invertebrates	I	Small animals, especially arthropods, like insects, millipedes, spiders, etc.

2. The Participant Information Sheet

Study title

"Lemurs as protectors of the forest: Lemur seed dispersal, forest regeneration and local livelihoods in the littoral forest fragments of Madagascar"

Invitation paragraph

You are being invited to take part in a research study. Before you decide whether or not to take part, it is important for you to understand why the research is being done and what it will involve. ***Please take time to read the following information carefully.***

What is the purpose of the study?

The purpose of this study is to understand and learn about the **interaction of the local population and their environment**. The first step towards this goal is to identify the plant species that are of importance to people living in villages in the areas of Mandena and Sainte Luce. We are interested in revealing the locally specific factors of human reliance on forest resources, such as which plants are used, what they are used for, and to what extent. We also want to know where they are obtained, and whether this has changed in recent years.

The data collection will take **approximately three months**. This study is a part of a larger project that will continue for **approximately three years**, aimed to improve the understanding of the role of collared lemurs' seed dispersal in forest regeneration, with special attention given to plant species used by these lemurs that are of importance to humans. We will use these results to better tailor the other parts of the project, so as to maximise the usefulness of our findings to the local population, as well as wildlife.

By examining potential differences, as well as similarities in specific ways in which people in different villages, as well as different areas obtain forest resources, we want to learn more about **the dynamic of people-forest interactions**. Our ultimate goal is to use this information to model potential consequences that forest overexploitation, combined with potential local extirpations of collared lemurs, could have on the local population's livelihoods. We will use our conclusions to promote a **sustainable use of forest resources**.

Why have I been invited to participate?

You have been chosen because **you live in the area that is of interest to us** due to the aims of our study. We will be recruiting about **60 other participants** from this area.

Do I have to take part?

Your participation in this study is **completely voluntary**, you can decide whether or not you would like to take part. If you decide to take part, you are still **free to withdraw at any time** and without giving a reason.

What will happen to me if I take part?

If you decide to take part, you will be interviewed about your use of forest resources. We will ask you questions about the plant species you use, locations from which you obtain them, and the purpose for which you use them. You will also be asked about the extent to which you perceive to be reliant on the forest for your livelihood.

If you are selected for the first part of the study, you will be a part of a **focus group**, in which you will discuss these topics with a group of your peers. This is likely to take place in a **communal area in your village**, and could take **up to two hours** of your time.

If you are selected for the second part of the study, you will be **interviewed individually**. During this interview, we will discuss the topics of your forest use in more detail. This could take place in **your home**, or in a **communal area of your village**, and is likely to last **about one hour**.

The levels of stress in this study are no higher than those you experience in everyday situations. The questions will not be intrusive, and we will only ask for **factual information**. You will not be put at any risk during or after the data collection.

What are the possible benefits of taking part?

Participating in this study will be an opportunity for you to think about your relationship with the environment to a new extent, and in ways you otherwise may not have. It will give you a chance to think about your **daily habits** in more detail, and look at the way in which you use the forest resources **from a different perspective**.

Will what I say in this study be kept confidential?

Confidentiality is guaranteed. Your answers will be **anonymous** and no one other than the investigators will have access to data. Data will be retained in accordance with the University's policy on Academic Integrity, and kept securely for a period of ten years after the completion of a research project.

What should I do if I want to take part?

If you decide to take part in this study, you will indicate this by making a **verbal agreement** with the principal investigator (i.e. the interviewer). This information sheet will be given to you to keep and refer to, should you have any questions about the study. Contact information you may find useful is included here, and you are welcome to contact the investigators during or after the study, for inquiries or clarifications.

What will happen to the results of the research study?

The results of this study will be used in principal investigator's **PhD dissertation**. In any **publications and conference papers** that result from this research, we will only mention the **overall results**. All publications will be available for free download from investigators' online profiles.

Who is organising and funding the research?

This research is organised and conducted by a student and staff at **Department of Social Sciences, Faculty of Humanities and Social Sciences, Oxford Brookes University**, Oxford, UK.

Who has reviewed the study?

The research has been approved by the **University Research Ethics Committee, Oxford Brookes University**.

Contact for Further Information

If you have any questions or concerns, please **do not hesitate to contact** the following:

Elena Račevska, MA, MSc, MPhil/PhD Candidate (principal investigator)
e mail: elena.racevska-2016@brookes.ac.uk

Dr Giuseppe Donati, PhD (supervisor)
e mail: gdonati@brookes.ac.uk

University Research Ethics Committee
e mail: ethics@brookes.ac.uk

Thank you

Thank you very much for taking time to read the information sheet.

Date

July 2017

3. Interview questions

Village name:	
Date:	
Team:	
Notes:	

Participant information

Age:	
Gender:	
Main source of income:	
Number of children:	

Use of Plants

1. Which tree species do you and your family collect from the forest?
2. For what purpose do you use each of the trees listed?

3. Do you or your family use any medicinal plants?
   a. Which species? What is the most important?
   b. Where do you find them? (i.e. which forest or fragment)
   c. What do you use them for? Please explain how you use them to prepare the medicine.
   d. Do you use western medicines? Do you prefer to use them or the medicinal plants? Which do you use more often? What does it depend on?

4. Do you or your family use any trees to build houses?
   a. Which species? What are the most important?
   b. Where do you find them? (i.e. which forest or fragment)
   c. How often do you collect them? How many each time?
   d. Do you sell any wood trunks? Which species? How much?
   e. Do you need a permit to collect this? From who? How much does it cost?

5. Do you or your family collect firewood?
   a. Which plant species?
   b. Where from? (i.e. which forest or fragment)
   c. How often do you collect them?
   d. Do you use charcoal? If YES, how do you make it and where?
   e. Do you prefer to use charcoal or firewood? Why?

6. Do you make any products to sell? Which ones? How many? Where do you collect the wood/leaves you use to make these product?

Use of Animals

1. Do you or your family hunt any animals?
   Which species?
   Has this changed since the formation of the protected area? How?

2. Where do you hunt these animals (which forest fragments)?
   How often? How much do you catch (each week or each moth)?
   Has this changed since the formation of the protected area? How?
3. Do you fish?

Where? Which species? How often? Has this changed since the formation of the protected area? How?

4. Do you collect any other water animals (e.g. lobster)?
   Where from? Which species? How often?

5. Do you keep any animals for food (e.g. chicken, zebu, pig, etc.)?
   Which ones? How many do you keep?
   How often do you eat these animals?
   Do you sell them?

6. LEK about lemurs:
   a. Species recognition + name
   b. Where do you see them?
   c. What do you know about them? What do they eat?
   d. Do you or your family hunt it? What do you use to catch them? How often? Where from?
   e. Did you used to hunt it before the establishment of the protected area?

<u>Growing Crops</u>

1. Do you or your family grow any crops or fruit?
   Which ones? When (are they seasonal)? Where do you plant them (near the house, in the forest, somewhere else?)
2. Do you sell any of the crops or fruits? Which ones?
3. Which farming system do you use? (e.g. tavy)

<u>Forest Protection</u>

1. What do you think about the establishment of the protected area? Has forming the protected area impacted you and your family? How?
2. What do you think about the mining in the region?
3. What do you think about foreigners in your area?

CURRICULUM VITAE

ELENA RAČEVSKA

EDUCATION

PhD in Anthropology and Geography Oxford Brookes University Oxford, UK	2020	**"Lemurs as protectors of the forest: Lemur seed dispersal, forest regeneration and local livelihoods in the littoral forest fragments of SE Madagascar"** Supervisors: Dr Giuseppe Donati, Prof Catherine M. Hill
MPhil in Anthropology and Geography Oxford Brookes University Oxford, UK	2019	-
MSc in Primate Conservation (Distinction) Oxford Brookes University Oxford, UK	2015	**"Investigating human-animal relationship between zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*) and their keepers"** (Paignton Zoo Environmental Park, Paignton, UK) Supervisor: Prof Catherine M. Hill
MA in Psychology University of Zagreb Zagreb, Croatia	2012	**"Predictors of Musical Preferences (Testing the Savannah-IQ Interaction Hypothesis)"** (Zagreb, Croatia) Supervisor: Prof Meri Tadinac
BA in Psychology University of Zagreb Zagreb, Croatia	2009	-

PUBLICATIONS

In preparation:

- **Račevska, E.**, Hill, C. M., Longosoa, T. H., & Donati, G. (in review). People, lemurs, and plants of Southeast Madagascar. *International Journal of Primatology.*
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- **Račevska, E.**, & Tadinac, M. (2019). Intelligence, music preferences, and uses of music from the perspective of evolutionary psychology. *Evolutionary Behavioral Sciences, 13*(2), 101-110. doi: 10.1037/ebs0000124
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- **Račevska, E**., Catherine M. Hill & Donati, G. (2020). *Impact of forest protection on the ecology of red-collared brown lemur (Eulemur collaris) in the littoral forests of southeast Madagascar.* PSGB Winter Meeting. 1-2 December 2020, online meeting. (oral presentation)
- **Račevska, E**., Longosoa, T. H., Hill, C. M. & Donati, G. (2019). *The importance of local ecological knowledge for species conservation: a case study of the lemur community in southeast Madagascar*. EFP/PSGB International Conference. 8-11 September 2019, Oxford, UK (short talk)

- Donati, G., Baldi, N., Balestri, M., Barresi, K., Kesch, K., Morelli, V., Ndremifidy, K., **Račevska, E.**, Rowe, F., Ravoahangy, A., Roma, M., Serra, V., Ramannamajato, J., Campera, M. (2018). *Life in fragments: 18 years of research on collared brown lemurs, Eulemur collaris, in the littoral forests of south-eastern Madagascar.* XXVII IPS Congress, Nairobi, Kenya, 19-25 August 2018.

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- **Račevska, E.** (2017). *University students' knowledge and perception of, and attitudes towards local wildlife in West Java, Indonesia*. Student Conference on Conservation Science, 28-30 March 2017, Cambridge, UK. (poster presentation).

- **Račevska, E.** (2016). *Human-animal relationships between zoo housed western lowland gorillas (Gorilla gorilla gorilla) and their keepers.* Adventures with Primates: Reports from tropical field research, 12 October 2016, Oxford Brookes University, Oxford, UK (oral presentation).

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- **Račevska, E.** (2014) *Kids and Pets.* 1st Pets Fair, West Gate Shopping City, Jablanovec, 4-6 April 2014 (oral presentation).

- **Račevska, E.**, Tomić, I., & Huić, A. (2014) *Authoritarianism and attitudes toward homosexuals: mediating role of sexist beliefs about women and men.* 19th Psychology Days in Zadar, 29-31 May 2014, Department of Psychology, University of Zadar, Zadar, Croatia (oral presentation).

- **Račevska, E.** (2013) *Intelligence and musical preferences – the evolutionary perspective*. 21st Ramiro and Zoran Bujas' Days, 11th-13th April 2013, Faculty of Humanities and Social Sciences, University, of Zagreb, Zagreb, Croatia (oral presentation).

- Davidović, N., **Račevska, E.**, Bastijanić, T., & Tumbas, M. (2011) *Personality and Musical Preferences*. 20th Ramiro and Zoran Bujas' Days, 7-9 April 2011, Faculty of Humanities and Social Sciences, University, of Zagreb, Zagreb, Croatia (oral presentation).

PUBLIC TALKS AND INVITED SEMINARS

- **Račevska, E.** (2021). *From psychology to lemur ecology*. Oxford Brookes University Primate Conservation Seminar Series. 15 February 2021. Online talk.

- **Račevska, E.** (2020). *How to Find Lemurs and Expose Their Seed Dispersal Secrets*. Lemur Day 2020. 30 October 2020. Oxford Brookes University. Online talk.

- **Račevska, E.** (2020). *O lemurima i ljudima – suživot uz zaštićene šume na jugoistoku Madagaskara.* {Of people and lemurs – the coexistence next to the protected forests in the southeast of Madagascar.} 20 February 2020. BIOM (Environmental NGO). Department of Biology, Faculty of Science, University of Zagreb.

- **Račevska, E.** (2020). *Od Prve do Oxforda i Madagaskara*. {From the First Gymnasium to Oxford and Madagascar.}. 18 February 2020, First Gymnasium, Zagreb, Croatia. Invited talk for high school students and teachers.

- **Račevska, E.** (2020). *Of Locals and Lemurs: Local Ecological Knowledge of and Attitudes towards Red-Collared Brown Lemur (Eulemur Collaris) among the Rural Communities of Southeast Madagascar.* Oxfordshire Mammal Group. 12 February 2020. Oxford University Museum of Natural History. Oxford, UK. Invited talk.

- **Račevska, E.** (2020) *Od Prve do Madagaskara*. {From the First Gymnasium to Madagascar.}. 4 February 2020, First Gymnasium, Zagreb, Croatia. Invited talk for high school students in elective psychology/members of the volunteers' club.

- **Račevska, E.** (2020). *Lemuri, ljudi i šume: život uz zaštićena područja na jugoistoku Madagaskara*. Priroda Uživo, Hrvatsko prirodoslovno društvo. {*Lemurs, people and the forest: living with the protected areas in the southeast of Madagascar*. Nature Live, Croatian Society for Natural History.} 23 January 2020. Bogdan Ogrizović Library, Zagreb, Croatia. Invited talk for the general public.

- **Račevska, E.** (2019). *Lemurs of Madagascar.* Biodiversity Café at the Natural History Museum's Late Night (Bio)Diversity event, organised by Oxford Biodiversity Network. 7th November 2020, Oxford University's Museum of Natural History, Oxford, UK. Publi outreach through short interactive talks.

- **Račevska, E.** (2019). *Lemurs, People and the Forest: Life After the Forest Protection in Southeast Madagascar.* Oxford University Nature Conservation Society. Invited seminar. 5 November 2019, St John's College, Oxford, UK.

- **Račevska, E.** (2011). *Personality and Music Preferences*. Seminar for MA Psychology students, as a part of their "Psychology of music" module. Department of Psychology, Faculty of Humanities and Social Sciences, University of Zagreb.

- **Račevska, E.** (2012). *Intelligence and music preferences – the evolutionary perspective.* Seminar for BA Psychology students, as a part of their "Evolutionary psychology" module. Department of Psychology, Faculty of Humanities and Social Sciences, University of Zagreb.

BOOK CHAPTERS, SPECIAL ARTICLES and MONOGRAPHS

- **Račevska, E.** (2020). *Moj život s lemurima na Madagaskaru* (*My life with lemurs in Madagascar*). Lemur Day 2020. Zagreb Zoo. Online article. *Event organised by me.

- **Račevska, E.** (2018). *Evolutionary Psychology*. In: Encyclopedia of Animal Cognition and Behavior. Vonk, J. & Shackelford, T.K. (Eds.). Springer. doi: 10.1007/978-3-319-47829-6_561-1

- **Račevska, E.** (2018). *Natural Selection*. In: Encyclopedia of Animal Cognition and Behavior. Vonk, J. & Shackelford, T.K. (Eds.). Springer. doi:10.1007/978-3-319-47829-6_542-1

- **Račevska, E.** & Hyde Roberts, S. (2018). *Sexual Selection*. In: Encyclopedia of Animal Cognition and Behavior. Vonk, J. & Shackelford, T.K. (Eds.). Springer. doi: 10.1007/978-3-319-47829-6_565-1
- **Račevska, E.** (2017). *Richard Dawkins*. In: Encyclopedia of Animal Cognition and Behavior. Vonk, J. & Shackelford, T.K. (Eds.). Springer. doi:10.1007/978-3-319-47829-6_452-1
- Nekaris, K.A.I. & **Račevska, E.** (2017). *Folia Primatologica*. In: The International Encyclopedia of Primatology. Fuentes, A. (Ed.). Wiley-Blackwell.
- **Račevska, E.** (2013). *Just friends - cross-gender friendships*. "Istraži me" Psychological Portal. Article.
- **Račevska, E.** (2013). *Mate choice - what do men want*." Istraži me" Psychological Portal. Article.
- **Račevska, E.** (2013). *Mate choice - what do women want, and why*. "Istraži me" Psychological Portal. Article.
- **Račevska, E.** (2013). *Evolution of music*. "Istraži me" Psychological Portal. Article.
- **Račevska, E.** (2013). *Intelligence from an evolutionary psychology perspective*. "Istraži me" Psychological Portal. Article.
- Butković, A., Vukasović, T., & Bratko, D. (Eds) (2011). *Personality and music preferences: XXth Psychology Summer School).* FF Press. ISBN 978-953-175-390-6. Monography. (A contributor)

MEDIA OUTREACH

- Dublin's FM104 radio – an interview about my research of musical preferences and intelligence. (15 March 2021)
- World Lemur Day 2020 Croatia – *Nacional Independent News Magazine, Glas Istre, Index.hr, Net.hr, Živim.hr, Cronika.hr, Beli Zagreb Grad, Zg-kult, HRT Magazin, Dobro jutro Hrvatska* (morning TV program), *Moj Zagreb Info, Lice grada, Politika plus* (30-31 October 2020). A press release with a statement on lemur conservation.
- *Večernji list* Croatian national newspaper – an article about primate conservation, with special focus on why primates should not be pets or photo props. (In print 31 July 2020, online 9/10 August 2020)
- *Zašto?(Why?)* Croatian educational online program – an interview about human evolution (recorded: May 2020; published: October 2020))
- Croatian National Radio, 1st programme – an interview about my research in Madagascar (18 March 2020)
- First Gymnasium Zagreb 2020 Yearbook – an alumna interview about my work and research (February 2020)
- *Canopy* journal – an alumna interview about my master's project, current projects, and expectations for the future of primate conservation (March 2020, Oxford Brookes University)
- *24 sata* Croatian national newspaper – an interview about my research (June 2017)

- *Jutarnji list* Croatian national newspaper – an interview about my research (June 2017)
- *Jet set* Croatian national magazine – an interview about slow loris conservation and my work with the Little Fireface Project (May 2016)
- *Croatian Autoclub Magazine* – Interview about dogs and people (May 2015)
- *Jutarnj list* Croatian national newspapers – Interview about my studies (March 2015)

FIELDWORK AND RESEARCH EXPERIENCE

▪ **Independent research** Zagreb, Croatia	05/2020	- **online survey** of Croatian **youth participation** in wildlife conservation, **knowledge** of national and international endangered wildlife, **attitudes** towards conservation - ***Activism Orientation Scale*** (AOS) - collaborators: Marko Kovačić, dr.sc. (Institute of Social Research, Zagreb, Croatia); 300 participants (15-30 old)
▪ **Sainte Luce & Mandena Conservation Zone** Southeast Madagascar	07/2017 - 11/2018 **PhD fieldwork**	**- collaborators:** SEED Madagascar (*Sustainable Environment, Education & Development*), TBSE (*Tropical Biodiversity and Social Enterprise*) - 12-hour **behavioural observations** of collared brown lemur (*Eulemur collaris*), **diurnal** and **nocturnal** - **telemetry (radio tracking)** and **GPS mapping** - **camera trapping** for my seed predation study **- focus groups** and **interviews** with local communities (N=80) - **spatial ecology**, **nest ecology, measurements**, and **collaring** of mouse lemurs (*Microcebus sp.nov.*), **phenology sampling, invertebrate surveys** (helping another PhD student)
▪ **Little Fireface Project** West Java, Indonesia	02/2016 - 05/2016	- 6-hour nocturnal **behavioural observations** of Javan slow loris (*Nycticebus javanicus*) **- camera trapping, agricultural mapping, phenology monitoring, presence surveys** (*N. javanicus*)
▪ **Little Fireface Project** West Java, Indonesia	04-05/2016	- study of **university students' knowledge, perception of and attitudes towards the Javan slow loris** (*Nycticebus javanicus*), **common palm civet** *(Paradoxurus hermaphroditus)*, **leopard cat** *(Prionailurus bengalensis)*, and **flying fox** (*Pteroptus vampyrus*); 140 participants

▪ **Little Fireface Project** West Java, Indonesia	04-05/2016	- study of **human-animal bonds among animal sanctuaries' staff and the animals in their care** - wildlife sanctuaries in West Java (Cikananga, Aspinall Foundation, Javan Eagle Project); 30 participants
▪ **Paignton Zoo** Paignton, Devon, UK	05/2015 **MSc thesis research**	**- behavioural observations** of western lowland gorillas in a **zoo** (n=5); **semi-structured interviews** with zookeepers (N=5) **-** gorilla **personality questionnaire** administration with zookeepers, gorilla social dynamics (**social network analysis**)
▪ **Oxford Brookes University** Oxford, UK	10/2014	**- online survey** of attitudes towards keeping **primates as pets**, use primates as **photo props**, use of primates in the **pharmaceutical industry**, and willingness to consume **primate meat** - also examined people's **knowledge of primates** using a ten-item questionnaire; 99 participants
▪ **Oxford Brookes University** Oxford, UK	11/2014	**- online survey** of **attitudes towards using primates in research** **-** instruments: ***Multi-Dimensional Emotional Empathy Scale*** (30 item questionnaire), five-item questionnaire measuring attitudes towards using primates in research (**biomedical, cosmetics testing, military experiments, mental disorders research, and neurological studies**), five-item scale of **belief in a "primate mind";** 150 participants
▪ **University of Zagreb** Zagreb, Croatia	05-06/2012 **MA thesis research**	**-** investigating the relationship between **intelligence**, **music preferences** and **uses of music** **-** instruments: ***Nonverbal Sequence Test*** (general intelligence), ***Uses of Music*** questionnaire, ***Scale of Music Preferences*** - 480 participants (high school students)
▪ **University of Zagreb** Zagreb, Croatia	02/2010-04/2011	- **XX. Psychology Summer School** research project - psychology of music, personality psychology - instruments: ***Big Five Inventory*** (personality), ***Scale of Music Preferences,*** a measure of **conformity**, **the importance of nationality, religion**, and **music** in participant's life - 219 high school students, 197 university students, 182 adults

TEACHING EXPERIENCE

▪ **Associate Lecturer** 01/2020 - 08/2020	*Primate Societies/ Advanced Study of Primate Societies* Oxford Brookes University	- **lecture preparation and teaching (remote emergency teaching** (COVID-19 pandemic)) - **third year undergraduate students, MSc students** (~ 50 students) 1. *Primate communication* 2. *Primate cognition and tool use* 3. *Conservation (+ Ethnoprimatology)* - **marking:** quiz, annotated bibliography, essay, executive summary
▪ **Associate Lecturer** 09/2019 - 12/2019	*People and Other Animals* Oxford Brookes University	- **lecture preparation and teaching** - **second year undergraduate students** (~ 25 students) 1. *Animals on display* 2. *Pets and pet keeping* 3. *Animal intelligence and animal emotions* - **excellent feedback** from students and module leader
▪ **Associate Lecturer** 01/2019 - 06/2019	*Primate Societies; Advanced Study of Primate Societies* Oxford Brookes University	- **lecture preparation and teaching** - **third year undergraduate students, MSc students** (~ 50 students) 1. *Primate communication* 2. *Ethnoprimatology* - **marking**: student notes, annotated bibliography, essay - **excellent feedback** from students and module leader

OTHER WORK EXPERIENCE

▪ **Associate statistician** 01/2020	*Institute for Social Research Zagreb, Croatia*	- data analysis, reports and summaries - projects: Youth study Southeast Europe 2018/2019 (more than 10,000 respondents from 10 countries)
▪ **Research Coordinator** 02/2016 - 05/2016	*Little Fireface Project, Garut, Java, Indonesia*	- training incoming team members on data collection and entry, advice on ongoing research projects, ensuring all data is correctly entered, organised and backed up - data collection (continuous and instantaneous behaviour sampling), and data analysis (SPSS, MS Excel, Basecamp) - writing blogs, newsletter pieces, reports, new protocols - ensuring all equipment is cared for, stored correctly and working

▪ **Student Editor of *Canopy* Journal** (ISSN: 2054-2070) 02/2015 - 09/2015	*MSc Primate Conservation, Oxford Brookes University*	- selecting articles to be published in the journal - reviewing and editing the articles - distributing the journal copies at conferences
▪ **School psychologist** 10/2013 - 09/2014	*First Gymnasium* Zagreb, Croatia	- individual student counselling - organising students' study schedules - co-managing school's Volunteer Club (~ 20 people) - conducting analyses of students' academic performance - organising and delivering professional guidance activities - preparing and delivering workshops on various topics (e.g., communication, addiction prevention, bullying, sexuality), for groups of ~ 30 people
▪ **Zoo volunteer** (primate sector) 07/2013 - 09/2014	*Zoological Garden of Zagreb* Zagreb, Croatia	- husbandry of primates (*Pan troglodytes, Semnopithecus entellus, Cercopithecus diana, Colobus guereza, Lemur catta, Eulemur albifrons, Hylobates lar, Alouatta caraya, Cebus albifrons)* and other species (*Zalophus californianus*, *Nasua nasua*, *Panthera pardus japonensis*, *Canis lupus*, *Leptailurus serval*) - husbandry of the petting zoo (rabbits, goats, sheep) - conducting various educational activities for the public (mostly designed for, but not limited to preschool and school children) - food preparation and distribution, cleaning and maintaining visitor areas, preparing and delivering enrichment, collecting behavioural data (various primate and bird species)
▪ **Psychology tutor** 02/2012 - 06/2012	Private tutoring Zagreb, Croatia	- tutoring an art high school senior on the Croatian national psychology program for gymnasium students, as preparation for her national graduation exam
▪ **Horseback riding therapy volunteer** 04/2011 - 09/2013	*Jedni za druge* Zagreb, Croatia	- working with children of different ages with various types of disabilities (physical and mental), and their parents - helping with re-socialisation of recovered drug addicts - horse grooming and preparation
▪ **Psychology intern** 03/2011	*University Psychiatric Hospital "Vrapče"*	- helping with small group therapy activities for patients with diagnosed alcohol addiction, helping with resocialisation of former hospital patients in horseback

		Institute for the Treatment of Addictions Zagreb, Croatia	riding therapy *Jedni za druge*
▪	**Psychology intern** 05/2011	*"Croatia Airlines" Department for Human Resources* Zagreb, Croatia	- data management (e.g., entering and updating information, informing employees of the upcoming educational activities) - entering structural organisation changes into the internal software

PEER REVIEW

- *Society & Animals*
- *Behavioral Evolutionary Sciences*
- *International Journal of Primatology*

PRPROFESSIONAL MEMBERSHIPS

- Primate Society of Great Britain (2014-)
- British Ecological Society (2016-)

OTHER TRAINING AND CERTIFICATIONS

Introduction to Teaching in Higher Education	Oxford Brookes University	03/ 2017
Coursera certifications:		
Teaching science at university	University of Zurich	06/ 2020
University teaching	Hong Kong University	06/ 2020
Chimpanzee behaviour and conservation	Duke University	06/ 2020
Understanding plants - Part 2: Fundamentals of Plant	Tel Aviv University	12/ 2016
Biology	Tel Aviv University	11/ 2016
Understanding plants - Part 1: What a Plant Knows	Duke University	06/ 2015
Dog Emotion and Cognition	University of Edinburgh	08/ 2014
Animal Behaviour and Welfare	University of Edinburgh	06/ 2014
EDIVET: Do You Have What It Takes To Be a Vet?	University of Wisconsin -	03/ 2014
Human Evolution: Past and Future	Madison	10/ 2013
Animal Behaviour	University of Melbourne	07/ 2013
Synapses, Neurons and Brains	Hebrew University of Jerusalem	
Volunteer Coordinator Certificate	Volunteers' Centre Zagreb	09/ 2014

OTHER: conference attendance

- Unifying Tropical Ecology - BES/gtö meeting (8 – 12 April 2019, Edinburgh, UK)
- Malagasy Primatological Society Inaugural Congress (13 – 16 December 2017, Toamasina, Madagascar)
- British Ecological Society Meeting (12-14 December 2016, Liverpool, UK)
- XXIX International Congress of Psychology (20-25 July 2008, Berlin, Germany)

RELEVANT AND TRANSFERABLE SKILLS

Languages

Croatian	Native
English	Full professional proficiency
German	Work proficiency
French	Elementary proficiency
Portuguese	Basic
Spanish	Beginner
Indonesian	Beginner
Sundanese	Beginner
Malagasy	Beginner

IT Competences

SPSS	Full professional proficiency
NVivo	Full professional proficiency
MS Office	Full professional proficiency
R	Work proficiency
Basecamp	Full professional proficiency
GroupDynamics	Work proficiency
ArcGIS	Work proficiency
UCINET	Work proficiency

Extensive experience in:

- **Writing research articles and reports**
- **Preparing and delivering scientific talks, lectures and seminars**
- **Writing for expert audience** (peer-reviewed journal manuscripts), and **general public** (blogging, and social media), **in two languages** (Croatian, English)
- **Developing questionnaire surveys** for high school and university students. as well as adults, in **four countries** (Croatia, UK, Indonesia, Madagascar)
- Administering **personality inventories** and **intelligence tests**
- Delivering **presentations** in **formal and informal settings**, to small (~ 10), medium-sized (~30), and big groups (100+ people) in two languages (English, Croatian)
- **Working independently**, as well as a part of a **team**
- **Managing** small (~ 15) and medium-sized (~30) **groups of people**
- **Photography (**Pentax K-50, GoPro; ADOBE Photoshop)

AWARDS

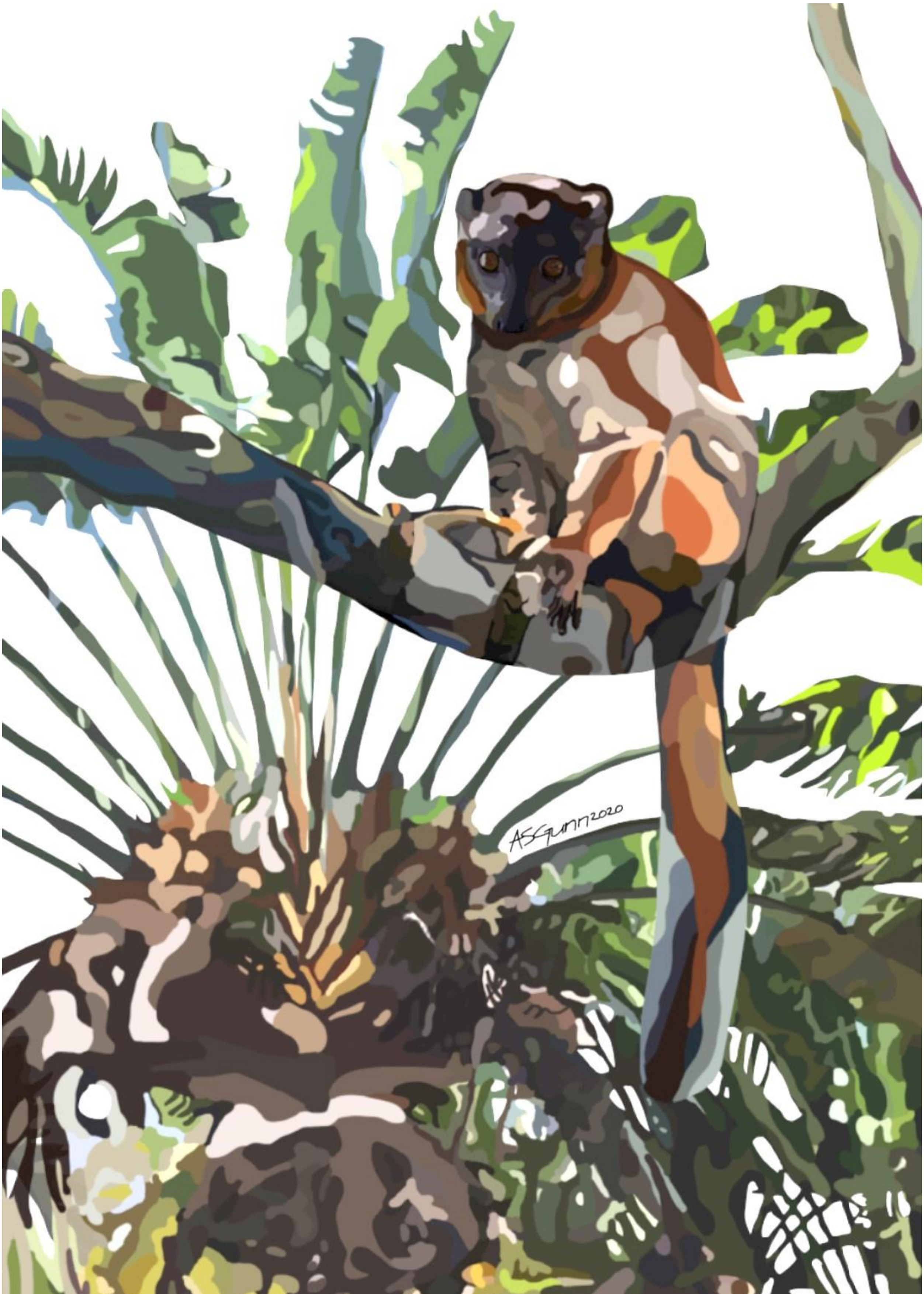
"Capturing Ecology" Photo Competition — 11/2020
British Ecological Society
Student winner of categories "Individuals and populations" and "People and nature"

Department of Social Sciences Research Studentship — 09/2016 - 09/2019
Faculty of Humanities and Social Sciences
Oxford Brookes University

The Alison Jolly Prize for Primate Conservation — 12/2015
Faculty of Humanities and Social Sciences
Oxford Brookes University

Special Rector's Award — 04/2014
University of Zagreb
(*Awarded to the Academic choir of University of Zagreb "Concordia Discors" for* W. A. Mozart's "*Great Mass in c minor*")

Best volunteer — 10/2013
Zoological Garden of Zagreb
Awarded to the volunteers with the most volunteering hours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