



LEMUR NEWS

The Newsletter of the Madagascar Section
of the IUCN SSC Primate Specialist Group
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Front cover: Sambirano mouse lemur (*Microcebus sambiranensis*) in the Anobohazo Forest, Sahamalaza – Iles Radama National Park, northwest Madagascar. This species is classified as Endangered on the IUCN Red List. © Dan Hending

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Editorial

Another year has passed since *Lemur News* 20, and much has happened in Madagascar lemur-wise. The most exciting development by far is the ongoing implementation of the IUCN Lemur Conservation Strategy 2013–2016 through the IUCN SOS Lemurs special initiative. After the second call for proposals in February 2017 we were able to fund another 19 lemur conservation projects through this mechanism, thus increasing the total number of SOS-funded projects to 28. Combined, these projects target 41 (44%) of the 93 threatened species of lemurs (17 Critically Endangered, 15 Endangered, 9 Vulnerable). A good number of the projects are run by Malagasy civil society organisations, which is exactly what we want to see.

In terms of new lemur discoveries, McLain *et al.* (2017) description of Groves' dwarf lemur, *Cheirogaleus grovesi*, brings the total number of extant lemur species to 108, with 112 taxa. Groves' dwarf lemur is the largest species in the *C. crossleyi* group and is distributed across the Haute Matsiatra region, between Andringitra and Ranomafana national parks. It is named after Prof. Colin Groves, probably the most influential primate taxonomist of our time, who sadly passed away in late 2017.

Last year saw the fourth iteration of the ever more popular World Lemur Festival. Despite the unfortunately hefty epidemic of bubonic and pneumonic plague that struck Madagascar in the latter half of 2017, the festival nevertheless went ahead undiminished, and numerous events were held in Madagascar and around the world.

Contrary to the World Lemur Festival (WLF), the plague epidemic meant that we decided to postpone the IUCN lemur Red List assessment workshop that was planned for November 2017. Scaremongering in the Malagasy and international press led to a number of organisations not letting their staff travel to Madagascar, so that, had we gone ahead, we would have wound up with only half the participants. There was also the lingering threat of a regional lockdown, with the Seychelles having already had flights to and from Madagascar suspended. The workshop will now take place in early May 2018.

For me personally, 2017 ended on a high. Her Royal Highness Princess Anne, the British Princess Royal, visited the AEECL field site in Sahamalaza – Iles Radama National Park, northwest Madagascar, together with her husband, the Vice Admiral Sir Tim Laurence, as well as the President of Madagascar, Hery Rajaonarimampianina, and three of his cabinet ministers (Fig. 1). Guy Randriatahina (AEECL Programme Director), Sylviane Volampeno (PSG Madagascar Section Programme Officer), Gary Batters (AEECL President) and I met the

Princess, the President and their party at our ecotourist camp, led them into the Ankarafa Forest and showed them a habituated group of blue-eyed black lemurs, arguably the most charming of all lemur species! The royal visit presented a great opportunity to talk to the President about the importance of lemurs for Madagascar and the world, and in particular to emphasise the value of protected areas for ecotourism.

Speaking of lemurs and tourism, it was saddening to learn that criminals had killed nine indri and a diademed sifaka in a forest connected to the Andasibe-Mantadia National Park in February 2018. Allegedly, the Vice President of the very VOI Federation (a group of grass roots organisations) that is tasked with helping to protect the natural resources that constitute the livelihoods of this community was one of the culprits. Let's be clear here: this is not poaching for subsistence by some rural poor – these people were organised criminals and had a whole arsenal of guns at their hands, and the lemurs were allegedly destined for a Chinese restaurant in Toamasina. Indri and diademed sifaka are the two lemur species that attract most tourists to Andasibe-Mantadia. Killing them will eventually also kill the economy of this region. The immediate action by the Malagasy and international primatological community, including many members of the PSG Madagascar Section, was heartening to see, and at the time of writing I am hopeful that the incident has led to greater awareness and, hopefully, more decisive law enforcement by the Malagasy authorities in the future.

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Christoph Schwitzer

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Fig 1: Her Royal Highness Princess Anne, Christoph Schwitzer, Gary Batters and His Excellency President Rajaonarimampianina during a visit to the Sahamalaza – Iles Radama National Park in October 2017. Photo: Tsilavo Hasina Rafelarisoa

News and Announcements

Of Conservation, Conflict and Conscience

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Keywords: COMATSA, biodiversity, category VI, community-managed forest

Our research expedition to COMATSA turned out to be, at times, a journalistic rather than a scientific endeavour. Our team comprised experienced Malagasy researchers and young students, most of whom have worked in other research sites in Madagascar. This is to say that we were, in principle, prepared to cope with the logistical challenges of surveying remote areas.

From earlier experiences, I have witnessed how research teams arriving to relatively isolated areas are received with welcoming words and enthusiasm, partly because expeditions are a source of curious inquiry, but partly because it is an opportunity, for all sides, to tell stories and create new ones. Although research teams bring a level of academic knowledge to the field, they always need the support and expertise of local partners to bring about the scientific operation. Without the guides who know how to navigate the trails, who tell stories about the forest and everything within, who communicate anecdotes and valuable experiences, the expedition cannot be a successful one. Many times, local participants help via finding and identifying plants and animals, and can provide critical ecological information by virtue of their careful observations. It is a sort of symbiotic enterprise that makes research missions so much more than the sum of the parts, i.e., the sum of data points or samples.

We had planned to conduct biological surveys at two sites in the forest of Antsahafito (Anjiabe), about 25 km west of the Doany commune in Madagascar's SAVA region. We were following on the steps of a research team who had already surveyed the sites in 2011. The forest of Anjiabe falls within the boundaries of COMATSA (forest corridor between Marojejy-Anjanaharibe Sud-Tsaratanana), an impressive area comprising more than 300,000 ha. The establishment of COMATSA as a protected area was a joint collaborative effort between the Ministry of Environment, Ecology and Forests of Madagascar, World Wildlife Fund (WWF), and Global Environment Facility/United Nations Development Program (GEF/UNDP) and additional funding sources such as the Symphysis Foundation and Zurich Canton. WWF still has the critical managing role, taking the responsibility both to bridge the gap between the needs and requirements of the government and local communities, and to help reinforce contractual agreements.

During the mission that I will describe below, we experienced situations that challenged my preconceived ideas about forest conservation. As I continue to reflect on some of the actions (or lack thereof) in response to specific problems we encountered, I find inspiration in the large number of people who seek collective wellbeing, despite injustice.

A new era of protection

Since my first trip to Madagascar over a decade ago, I became familiar with a few National parks in Madagascar. For

most of those years, I didn't know about the great number of protected areas that fell into different categories, allowing controlled management of natural resources by local communities. This relatively new system of protection (named SAPM: *Système des Aires Protégées de Madagascar*) began to be implemented in 2005, after the 2003 World's Park Congress held in Durban (South Africa), where the then President of Madagascar voiced his commitment to triple the amount of national protected area coverage (Virah-Sawmy *et al.*, 2014). This ambitious plan had to rely, to a great extent, on the willingness by the government and local communities to create a plan for controlled extraction of natural resources in previously unregulated forests. Most of the newly protected areas, like COMATSA, belong to categories V and VI under the IUCN system, which means that local communities play a key role in protecting, managing, and utilizing those forests (Virah-Sawmy *et al.*, 2014).

I later learned that a community-based forest management (CFM) system, relying on the GELOSE (*gestion locale sécurisée*) law had been put in place in Madagascar since 1996 and was later updated in 2001 (World Bank Group, 2015). This strategy aimed to transfer the management of natural resources to local communities or COBAs/VOLs (*Communauté de Base*/"grassroots communities") which are comprised of members with a variety of backgrounds but seeking common interests: e.g., participating in a variety of activities including reforestation, use of efficient agricultural techniques, alternative sustainable practices, among others. Discussions about resource management between government, local authorities, and community at large, are generally organized and assisted by members of environmental NGOs or other organizations (e.g., WWF) which help raise awareness about environmental crises, their sources and potential mitigation practices.

Community-managed protected areas are generally designed with a "hard core" of forest that is off limits to human use and that is surrounded by a series of "controlled use zones." Each part of the protected area is administered by a different COBA, each with its own management committee, that all work together through federations or unions (Gerety, 2017). The transfer of management of natural resources (TGRN), with all the rules and guidelines, is crystalized in a comprehensive document, which local associations use and obey when exerting their managing power. It is quite clear that the involvement of village communities, who remain the first beneficiaries of these natural habitats, is crucial for the protection of these forests, as the forest service cannot cover the management of these resources on their own (World Bank Group, 2015).

Although, in theory, it makes sense that local communities become stewards and managers of the land they live in and know, challenges to success are not unexpected. In protected areas across the world, deficiencies in program monitoring and evaluation have been identified as critical weaknesses when it comes to assessing the success of protected areas (Dudley *et al.*, 2004). Moreover to be effective, the local enforcement effort needs to be backed by a broader environment of good and appropriate governance that ensures that penalties are enforced (Dudley *et al.*, 2004). In other words, if a deviation or fault is detected, how is it ensured that appropriate measures will be taken? What are appropriate measures?

Although the spirit of the agreement is consensual, it is not unreasonable to come up with multiple scenarios in which challenges may occur: e.g., authorities for any given association may not equally represent the interests of all individuals in a particular area and this may cause frictions within

communities; even if association members agree to honor the contracts and stipulations, some may change their mind, and others may take advantage of a position of authority to carry out illegal activities.

Sadly, a recent analysis of community forest management and its impact on conservation in Madagascar indicates that, when deforestation and “wellbeing” measurements are considered, no significant effect is detected in those areas under CFM compared to non-CFM (World Bank Group, 2015). Unequal power relationships between participants and problems in enforcing contracts are listed as possible contributors undermining the program’s success.

COMATSA mission, an example

My inclination to share this experience is to promote the dialogue and listen to other perspectives. Given the heterogeneity in habitat and ethnic composition that is characteristic of Madagascar, successful practices, and means to reinforce policies may vary across regions. It is even possible to speculate that successful stories may depend on the charisma, commitment, and honor of the local authorities (e.g., COBAs) in charge of enforcing forest management.

Our mission started in Sambava, on the northeast coast of Madagascar where the Duke Lemur Center/SAVA Conservation office is located. From there, we drove ~4 h to Ambavala (Andapa district) and hiked for ~7 h to Doany, where we spent the night. We continued on foot early the following morning, and arrived a few hours later to the small village of Andranomilolo II (Mahasoia), our suggested final destination. There, we only encountered a few people in town, because most of the villagers had left for seasonal festivities. The porters who had come all the way from Ambavala gathered together, and dropped the 600 kg+ of food and equipment on the ground and went home. We unsuccessfully tried to find assistance in Andranomilolo II, so some of us went back to the closest town, Andranomilolo I, only 20 min backtracking the trail in search of new porters and guides. We met with a few people, including local authorities, to whom we showed our research documents. We were promised help and assistance the following day, so we returned to Andranomilolo II, where we were going to camp for the night.

The following morning our team decided to separate. Three of us would proceed ahead, leaving first thing in the morning to reach Anjiabe, where we would conduct a brief prospective search and wait for guides and porters, by the main road between Andranomilolo and Antsohihy to the west. The rest of the team would wait for help coming from Andranomilolo I and join us later the same day. That help never came and, after waiting a respectable amount of time, the team members that stayed behind returned to Andranomilolo I to find out what had happened. The person in charge of arranging the assistants was nowhere to be found. Eventually the team had to walk back to Doany (~4 h hike) to find porters to take our belongings from Andranomilolo all the way to Anjiabe.

At first, we were all surprised by the overall hesitation from the local villagers when we attempted to recruit local volunteers for our expedition in Andranomilolo I. Some of us, waiting in an improvised rest area close to Anjiabe, were not aware of the struggles the rest of the team was facing trying to recruit enough personnel. We were stranded for a couple of days without communication. When we all finally met, and managed to find enough people to move forward into the forest (several of the porters had to work multiple shifts), we were able to ob-

serve, first hand, the damage that has been recently done in the protected area.

I should straight away confess my naïveté with regards to all causes of deforestation. I have witnessed many times the challenges faced by people in space-constrained land, growing crops in the valleys and lower slopes while maintaining forest fragments in the top hills, as a potential reservoir; but also a buffer from erosion and desiccation. I came to embrace the idea shared by so many conservation organizations, of providing alternative subsistence practices to replace/minimize tavy (slash and burn) as it creates unsustainable conditions in areas with limited exploitable land; the dilemma of cutting the forest to grow food. Tavy is rooted in Malagasy culture, as it is across traditional agricultural systems in many areas of the world. It can prove sustainable under controlled conditions, depending on several factors, such as soil quality, fertilization techniques, and human reproductive rates, to name a few. The point I want to make here is that the idea that we are contrasting deforestation with subsistence agriculture, can be, in some cases, misleading.

At Anjiabe, a large-scale deforestation operation, at different and strategic places within the protected area, had taken place. Some of the deforested land was embedded inside larger forest blocks, hidden from passersby, far away from villagers (Fig. 1). In fact, little huts had been built to provide temporary shelters for the personnel in charge of the operation. Other deforested areas, however, were in proximity to the main road used by porters, for everybody to see. There was no denying it (Fig. 2). As we tried to make our way to the camping sites, GPS device in hand and climbing fallen trees, we realized that lots of these areas had been prepared for vanilla cultivation. Sporadic plantations were detected on our way as we navigated the narrow trail, areas that were more difficult to spot from a distance, because part of the tall canopy had been maintained to provide shelter to the vanilla orchids. Illegal vanilla plantations are an especially critical issue in the SAVA region. The dramatic increase in the international price of vanilla has changed the socioeconomic dynamics of villages in northern Madagascar. Although prices may drop and cultivations may fail, many people are prompted to clear land and plant vanilla with the hopes of enormous rewards in the near future. Incidentally, land clearing is facilitated by the flooding of efficient wood-cutting materials in the local markets (Andriatahiana, pers.comm.)

As we arrived to Camp I we stumbled upon piles of hardwood, neatly arranged in pre-cut planks, ready for shipment (Fig. 3). A leftover bucket, charcoal ashes, plastic bits scattered around. Nobody seemed very surprised about it. One of our guides, who had reluctantly joined our team, told some of the team members that he had been verbally threatened by one of the alleged responsible parties to not



Fig. 1: Selective logging around Camp I, at Anjiabe.



Fig. 2: Evidence of deforestation near Anjiabe.

come with us. That's why he had disappeared the morning following his promise to join us. People we informally talked to on the road, during rest breaks, alerted us that people wouldn't want to go to this forest because they knew of the operation. Nobody wanted to be associated with us, so they didn't have to see, they didn't have to explain. The apparent lack of enthusiasm by the porters and guides, was rooted in fear of retaliation. Credible rumors grew and got substantiated from many fronts: The illegal logging and large-scale cutting to grow vanilla were operations allegedly conducted by a few people tied to local authorities, who corrupted their power for personal economic benefits.

As we started our biological surveys around Camp 1, we realized the scale of the damage was larger than we had anticipated. The locations of pitfall traps had to be moved because the original sites had been replaced by savoka (secondary vegetation grown after clearing or burning forest) and were severely degraded. Trapping had to be displaced to areas with more forest protection, and transects had to be diverted because we could not find enough canopy cover. On several occasions lemurs were heard but not seen. We all wondered about the fate of *Propithecus candidus* (silky sifaka), one of the most endangered animals on Earth, who were heard and quickly seen on a few spots, rapidly leaping between forest fragments surrounded by savoka and open areas. Some areas showed fresh charcoal signatures, logs with green foliage, others had been cleared for a while.

Ironically, after we returned from the mission and briefly compared our results with those of the former expedition more than 5 years ago, we found out that biodiversity levels, as measured strictly by species numbers, were not decreased; in fact we identified more species in certain groups (e.g., herps). Why? Although many factors may be contributory (e.g., sampling effort or just luck), the take home message shouldn't be one of healthy populations inhabiting new savoka-rich environments. I can only think of the fate of those silkies leaping away.

During the mission, as a primatologist, I was rewarded with sightings of my favorite lemurs. As an anthropologist, I was fascinated and concerned about the social dynamics we witnessed among the local assistants, villagers, and others who came across our path during our expedition. In a few days, in this fairly isolated location, we have witnessed the behavior of unsupportive authority figures, officials who voiced their intention to help, but looked the other way when faced with evidence of corruption, forest rangers who had promised to come, but never made it to the forest, assistants who didn't want to participate in our expedition for fear of retaliation, and assistants who were aware of the situation but came, though asking insistently that we didn't say anything that



Fig. 3: Evidence of logging near Camp 1, at Anjiabe.

could jeopardize their safety or that of their families. We encountered many people willing to talk about this informally, anonymously, but unwilling to do anything to bring this issue up in the open, having an institutionalized discussion. We were left with this -oversimplified- image of local people willing to follow the rules with no benefits, and a few alleged authority figures, openly breaking the rules and showing off greed and impunity.

What to do when things do not work

Why would anyone care to make a deal in the first place? Why would anyone want to have restrictions on their natural resources (e.g., planks to build houses)? How can we dream of, and share in, a long-term vision of forest conservation if many people are just fulfilling basic subsistence needs? It is difficult to inspire someone who cannot imagine a future for himself/herself or his/her immediate family. What can be done, when people posting signs to discourage hunting and deforestation are generally responsible and trying to honor their agreement, whereas people carrying out illegal activity know exactly what they are doing and fully understand the illegality of it all?

Empowering local communities in forest management is a crucial step for the effective and efficient protection of biodiversity sites. Conservation organizations have been instrumental in funding alternatives for more sustainable practices, helping to facilitate discussions about issues that matter today and will affect the next generations. Sometimes, trying to find syncretism in environmental practices to provide a balance between traditional and innovative activities that are worth keeping in the long run. But to think of traditional communities as one body, with homogeneous interests, behaviors, and morals may be romantic and unrealistic. The correlation between corruption levels and money is undeniable, and fighting the cycle may be especially challenging for people fighting poverty in the first place. The rationale that forest protection may be inconsistent with the needs of local communities warrants reevaluation in some areas, where the complexities of social inequality, corruption and personal greed may challenge well intentioned conservation programs. As it was mentioned in a recent report, although the areas managed for conservation have increased significantly over the past years in Madagascar, the threats faced by those very areas have not been consequently reduced (Waeber *et al.*, 2016).

And yet, there are people who care. Across Madagascar there are environmental education programmes in place targeting curious and interested youth, bringing awareness of the problems and challenges of the present and future; workshops and training for adults interested in improved

techniques, sustainable practices; capacity building, family planning, and subsidized programs to increase productivity. These are necessary, indispensable, for bringing opportunities. Across Madagascar there are public signs and other forms of advertisement discussing the importance of biodiversity and forest protection, condemning destructive and illegal practices. I wonder if it would be also possible to generate programmes that can deal with the corruption and illegal behavior threatening the implementation and success of environmental sustainability. It's not about sending people to prison, but holding the responsible parties accountable, many times parties with ties to the wealthy and powerful. We all are accustomed to tolerating a background level of corruption, but how much is too much? And how much should we, the biologists, anthropologists, researchers and volunteers involved in conservation research, tolerate before acting?

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Short Communications

Mouse lemurs with “eyes bigger than their belly”: A case of primates being out-muscled by hawk-moths

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Dietary knowledge is paramount in the study of nocturnal cheirogaleid lemurs, because they must both satisfy their energy requirements and build up enough white adipose tissue during hyperphagic, pre-hibernation periods to endure phases of unfavourable food availability (Fietz and Ganzhorn, 1999; Schmid, 2000). Therefore, the diets of many cheirogaleids, such as the mouse lemurs (genus *Microcebus*) are well studied and a substantial literature of their feeding ecology exists. Mouse lemurs are known to have highly varied, omnivorous diets that comprise fruits, leaves, flowers, nectar, gum and small invertebrates (Atsalis, 1999; Lahann, 2007; Thorén *et al.*, 2016). However, due to profound fluctuations in the availability of different food resources throughout the year, the feeding patterns of mouse lemurs are highly seasonal (Radespiel *et al.*, 2006; Thorén *et al.*, 2011). A high proportion of insect material is known to constitute the diet of many mouse lemur species throughout the year due to its constant availability, in addition to its high energy, protein and carbohydrate content (Atsalis, 1999; Atsalis, 2008). Here we describe observations of the Sambirano mouse lemur (*Microcebus sambiranensis*) (Fig. 1A) actively pursuing moths and other invertebrates for consumption, and how on one occasion the targeted moths proved physically too strong for one *M. sambiranensis* individual to catch.

During March – May of 2015, we tracked and followed a study-population of radio-collared *Microcebus sambiranensis* in the Anabohazo forest of the Sahamalaza peninsula, North West Madagascar. During the study, it became evident to us that some of our individuals frequently revisited a few regular feeding sites, as has previously been observed in the closely related species *M. murinus* (Joly and Zimmermann, 2007), within the central areas of their home ranges (Hending *et al.*, 2017). These feeding sites were large mango trees (*Mangifera indica*) around which an abundance of invertebrate species were drawn by the odour of rotting mango fruit. Whilst observing *M. sambiranensis* at these sites, we did not observe the lemurs consuming the mango fruit. However, *M. sambiranensis* appeared to use these trees to forage for moths and cockroaches that were attracted by the fruit, whilst occasionally feeding on the berries that grew in the shrub layer beneath. Many of the moths observed to be consumed were very small and required minimal effort for the mouse lemurs to catch. However, on one night we observed one of the adult males persistently attempt to catch large hawk-moths (*Hippotion cf. celerio*) (Fig. 1B) that were abundant at the mango tree. We watched as the hawk-moths flew within such close proximity to the male that the lemur was able to reach out and grab the moths repeatedly



Fig. 1. (A) The radio-collared Sambirano mouse lemur (*Microcebus sambiranensis*). (B) The hawk-moths (*Hippotion cf celerio*) observed in the Anabohazo forest of the Sahamalaza Peninsula, north west Madagascar (Photos: Dan Hending).

in a “bear hug” hold. However, despite the lemur’s best efforts to control the hawk-moths, the moths were always able to out-muscle the lemur and break free from its hold, only to be captured again soon after. This cycle repeated over a period of 10-15 minutes, until the lemur eventually lost interest and chose a smaller more-manageable meal, much to our amusement.

The struggle that the mouse lemur had with the hawk-moth is in profound contrast to the high pull-strength (i.e., ability to hang onto an object) recently proposed for mouse lemurs (Toussaint *et al.*, 2013; Thomas *et al.*, 2016). Our observation is also surprising considering that the observed individual appeared to be in good overall health; we witnessed typical foraging and locomotion behaviour in this individual in multiple subsequent nights following after this observation took place. However, at ~40-50 g, *M. sambiranensis* are small, even for mouse lemurs, whilst with a wingspan of 60-80 mm and a weight of 3-4 g, *Hippotion* hawk-moths are relatively large Lepidoptera (Miller, 1991; Scoble, 1992); perhaps in this scenario, the mouse lemur literally attempted to ‘bite off more than it could chew’. Furthermore, another mouse lemur species (*M. lehilahytsara*) was previously documented to have been unable to break its way out of a spider’s web in which it had become entangled (Crane and Goodman, 2013) suggesting a limitation of the strength of these small primates, particularly when it comes to large invertebrates. The observation that we describe here provides insight into the feeding ecology of *M. sambiranensis* and highlights the importance of insects in the mouse lemur diet. Additionally, our observations suggest that some invertebrates, such as hawk-moths, are simply too large and too strong for mouse lemurs to successfully catch and consume, despite their best efforts.

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Buteo brachypterus: Aerial predator of *Hapalemur g. griseus* in Maromizaha rain-forest

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Habitat can be defined as the set of resources (shelter, food) and environmental conditions (abiotic and biotic factors) that determine the presence, survival and reproduction of a species (Hall *et al.*, 1997; Gaillard *et al.*, 2010). Various authors have shown lemurs experience predation all across Madagascar (Goodman and Rakotozafy, 1997; Rakotondravony *et al.*, 1998; Wright, 1998; Mandl *et al.*, 2017). However, there is no information for the Maromizaha rainforest thus far. *Hapalemur griseus griseus*, classified as Vulnerable (Mittermeier *et al.*, 2010; IUCN, 2014) living in this forest has to deal with ecological issues including predators. Wet and dry season ecological surveys were conducted using focal sampling method (Altman, 1974) for groups of *Hapalemur g. griseus* in 2016.

Our results showed that *Hapalemur g. griseus* resides in low forest strata between 0.1-3 m in height during its behavioural activities. Major food sources were plants: *Panicum* sp. (Poaceae), *Cephalostachyum* sp., (Poaceae) and *Hypoestes* sp.



Fig. 1: Baby *Hapalemur g. griseus* protected by the adult male. Photo: Andrianandrasana Z.A. (2016).

(Acanthaceae). These plants appeared to be spread from the valley to the versant of its habitat at the same strata level, explaining why *Hapalemur g. griseus* may prefer this level. On the other hand, vigilance behaviours were detected during surveys; the lower strata may provide good places to hide from predators such as *Buteo brachypterus*, an endemic raptor in Madagascar (Woog, 2006; GERP, 2008). When this aerial predator whistled, *Hapalemur g. griseus* was observed to disperse, flee and hide in a very tight place of the low stratum. Similarly, during the passage of human trackers or their dogs, the lemur was observed to remain motionless or flee.

As far as social organization, *Hapalemur g. griseus* stayed together and sometimes it dispersed. The minimum and the maximum mean distance (\pm standard error) between the focal animal and its nearest neighbour were: minimum 1.272 ± 0.039 m, $n = 756$; maximum 3.217 ± 0.054 m, $n = 1039$. The spatial occupation by *Hapalemur g. griseus* in the face of habitat disturbance and predators has a social implication that plays a key role in the dynamics of its population. *Hapalemur g. griseus* is certainly vigilant (Fig. 1). We found that the adult male took the main role of protector of the group, especially protector of infants.

In summary, for the exploitation and control of space in the face of ecological challenges, *Hapalemur g. griseus* uses an appropriate strategy in its social structure, including the vigilance system. In terms of conservation of this species in its natural habitat, given its plasticity against predators, a study on the latter would be encouraged.

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Unsuccessful predation event of an aye-aye (*Daubentonia madagascariensis*) by a fosa (*Cryptoprocta ferox*)

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Fosa (*Cryptoprocta ferox*) are one of the few non-human predators of lemurs, and the only one that will remove large bodied lemurs (Wright *et al.*, 1997; Patel, 2005; Dollar *et al.*, 2007). Fosa are cathemeral and occur in a variety of forests across the island of Madagascar; thus the list of lemur species preyed upon is varied (Tab. 1). Since fosa occur in such low population densities and observational studies are rare (Hawkins 1998; Gerber *et al.*, 2010; Goodman 2012), all prey species to this point have been identified either by their corpses or by examining fosa scat (Wright *et al.*, 1997; Dollar *et al.*, 2007; Karpanty and Wright, 2007; Hawkins and Racey, 2008).

Tab. 1: List of primate species, including temporality and regional location, known to be preyed upon by fosa.

Prey Lemu Species	Temporality	Region	Reference
<i>Haplemur griseus</i>	Diurnal	SE	Karpanty and Wright, 2007
<i>Prolemur simus</i>	Diurnal	SE	Wright <i>et al.</i> , 1997
<i>Propithecus candidus</i>	Diurnal	NE	Patel, 2005
<i>Propithecus edwardsi</i>	Diurnal	SE	Wright <i>et al.</i> , 1997
<i>Propithecus tattersalli</i>	Diurnal	NE	Goodman, 2004
<i>Propithecus verreauxi</i>	Diurnal	W	Dollar <i>et al.</i> , 2007; Hawkins and Racey, 2008
<i>Varecia variegata</i>	Diurnal	SE	Karpanty and Wright, 2007
<i>Eulemur fulvus</i>	Cathemeral	SE, W	Wright <i>et al.</i> , 1997; Dollar <i>et al.</i> , 2007
<i>Eulemur mongoz</i>	Cathemeral	W	Dollar <i>et al.</i> , 2007
<i>Eulemur rubriventer</i>	Cathemeral	SE	Wright <i>et al.</i> , 1997
<i>Avahi laniger</i>	Nocturnal	SE	Karpanty and Wright, 2007
<i>Avahi occidentalis</i>	Nocturnal	W	Dollar <i>et al.</i> , 2007
<i>Cheirogaleus major</i>	Nocturnal	SE	Goodman <i>et al.</i> , 1997; Karpanty and Wright, 2007
<i>Cheirogaleus medius</i>	Nocturnal	W	Dollar <i>et al.</i> , 2007; Hawkins and Racey, 2008
<i>Lepilemur edwardsi</i>	Nocturnal	W	Dollar <i>et al.</i> , 2007
<i>Lepilemur mustelinus</i>	Nocturnal	E	Goodman <i>et al.</i> , 1997
<i>Lepilemur ruficaudatus</i>	Nocturnal	W	Hawkins and Racey, 2008
<i>Microcebus berthae</i>	Nocturnal	W	Dollar <i>et al.</i> , 2007; Hawkins and Racey, 2008
<i>Microcebus murinus</i>	Nocturnal	W	Dollar <i>et al.</i> , 2007; Hawkins and Racey, 2008
<i>Microcebus rufus</i>	Nocturnal	SE	Goodman, 2004
<i>Mirza coquereli</i>	Nocturnal	W	Hawkins and Racey, 2008
<i>Phaner furcifer</i>	Nocturnal	W	Hawkins and Racey, 2008

A Malagasy primate that has proven difficult to obtain observational data on is the aye-aye (*Daubentonia madagascariensis*). There have been some short term studies (e.g. Iwano and Iwakawa 1988; Ancrenaz *et al.*, 1994) and a few longer studies (e.g. Sterling, 1993, 1994; Randimbiharirina *et al.*, in review; Sefczek *et al.*, in press) conducted on aye-ayes to this point. Of those studies, several were conducted on Nosy Mangabe (Iwano and Iwakawa, 1988; Iwano, 1991; Sterling, 1993, 1994) where fosa are absent, and two were conducted in disturbed forests (Ancrenaz *et al.*, 1994; Randimbiharirina *et al.*, in review), which support fewer fosa than continuous forests (Gerber *et al.*, 2012). Despite the lack of supporting evidence, aye-aye are believed to be a viable prey species for fosa (Petter, 1977; Garbutt, 1999).

During the course of a behavioural study on aye-ayes (unpublished data), we witnessed a fosa attack a juvenile aye-aye. The interaction took place in Torotorofotsy (18° 46'S and 48° 25' E, Fig. 1), a 1,100 ha eastern wetland rainforest adjacent to Mantadia National Park, Madagascar (Dolch *et al.*, 2004). There were three radio-collared aye-ayes at Torotorofotsy: a male aye-aye approximately one-year old named Cobalt, an adult female and mother to Cobalt named Tsinjo, and an adult male named Masy. On February 24, 2017 between 1:30 am – 4:15 am, we were collecting behavioural observations on Tsinjo and Cobalt concurrently. Wild aye-aye are known to practice infant parking (Sterling and Feistner, 2000); in this instance, Cobalt was circling the canopy of the nesting tree while Tsinjo was foraging several hundred metres away. The team following Tsinjo was not aware of the events that transpired until the behavioural follows ended. That we could determine, no vocalizations were made or received by Tsinjo and no indication was made that Cobalt was in danger.

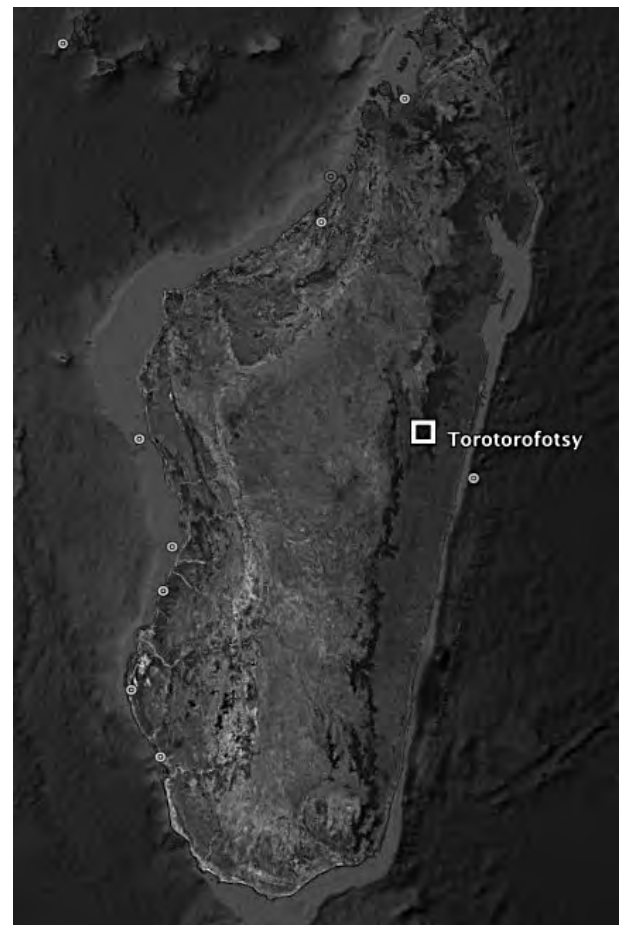


Fig. 1: Location of Torotorofotsy, Madagascar.



Fig. 2: Remains of aye-aye, Nickel, believed to be killed by a fosa.

Cobalt was in a Longotra tree (*Cryptocarya fulva*, Lauraceae) approximately 10 m high, circling the canopy. At 2:45 am a fosa approached from an adjacent tree. Cobalt noticed the fosa and immediately ran around the tree canopy, the fosa giving chase. They circled the tree top three or four times before Cobalt left the tree, running through the forest. The fosa was unaware that Cobalt had left the tree and made another circle in the canopy before leaving via the ground. The entire event lasted approximately ten minutes. At no point did Cobalt or the fosa make any vocalizations. It was an additional 50 min before our observational team could locate Cobalt. Once found, it was another 30 min until Cobalt and Tsinjo reconvened at their shared nest.

In addition to the aforementioned encounter, on January 16, 2017, we found the remains of another collared aye-aye, Nickel, an adult female. Though the kill was not fresh, we know Nickel was alive as late as December 13, 2016. Her body was missing with only her head, tail and collar remaining (Fig. 2). Previous reports (Wright *et al.*, 1997) have described fosa's penchant for removing the mid-section of lemurs. Remains of a *Varecia variegata* immediately following a successful fosa attack (Fig. 3a, b) further support that fosa remove organs from the thoracic and abdomen. Based on these findings, we believe this particular aye-aye was killed by a fosa.

This near-predation event and corpse represents the first known evidence of fosa hunting aye-aye. Even lemurs are cryptic as the aye-ayes are not exempt from fosa predation. Karpanty and Wright (2007) suggest that a lemur's ability to become 'scarce' could be an anti-predation strategy. Given the aye-aye's solitary nature and large home ranges, few lemurs are as scarce in the environment. As no aye-aye remains were found in fosa scat from previous studies (Wright *et al.*, 1997; Dollar *et al.*, 2007; Karpanty and Wright, 2007; Hawkins and Racey, 2008), it is possible that low population density is part of the aye-aye's anti-predation strategy, although we are more inclined to suggest feeding and mating as primary motivations. However, it would be interesting to see how success rates of fosas hunting aye-ayes relate to the lemur's cryptic nature. Unfortunately, basic information about feeding and ranging behaviours for aye-ayes and fosa in a contiguous forest, as well as the interactions between these two species, is severely lacking (Farris *et al.*, 2014; Sefczek *et al.*, 2017; Randimbiharirina *et al.*, in review). As predators may influence primate social behaviour and spatial distribution (Isbell, 1994), so too can prey diversity and composition influence predator populations (Petchey, 2000). Therefore, proper conservation for both



Fig. 3a: Puncture marks by a fosa on the back of a *Varecia* neck.



Fig. 3b: Opening in thoracic cavity and abdomen where organs were removed by a fosa.

species should consider the extent to which this dynamic influences their respective behaviours.

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A wild aye-aye (*Daubentonia madagascariensis*) raids chicken eggs in eastern Madagascar

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Aye-aye diets are adaptable to the environment they inhabit (Sterling, 1993; Ancrenaz *et al.*, 1994; Randimbiharirinirina *et al.*, in review). There have been reports of *Canarium* seeds, insect larvae, adult insects, *Ravenala* nectar, *Intsia* cankers, and a variety of plantation crops such as coconuts, mangos, and bananas being part of the aye-aye's diet (Petter, 1977; Iwano and Iwakawa, 1988; Sterling, 1993, 1994; Ancrenaz *et al.*, 1994; Andriamasimanana, 1994; Randimbiharirinirina *et al.*, in review). In captivity, aye-aye diets include honey, sugar cane, meal worm, various fruits and vegetables, and eggs (Petter, 1977; Simons, 1995). While they may consume eggs in captivity, this behaviour has never previously been recorded in wild aye-eyes. Marcelin witnessed an aye-aye consuming multiple chicken eggs from his property on three separate occasions.

The feeding events took place in the eastern rural commune of Ambosary, located approximately 27km northwest of Andasibe, Madagascar (18° 46'S and 48° 23' E, Fig. 1). This commune is approximately 80 ha in size and is only 50 m from the Vohitsara base camp in Torotorofotsy (18° 46'S and 48° 25' E), a continuous, wetland rainforest adjacent to Mantadia National Park (Dolch *et al.*, 2004).

The first two feeding events occurred in the week between December 25, 2016 and January 1, 2017. For the first two nights chickens were heard making noise and Marcelin assumed a fossa was attacking. When he went to check, none of the chickens were missing but eggs were missing. On January 4, 2017, the chickens again became restless. This time Marcelin was alert and quickly checked the cause of the commotion. Instead of the anticipated fossa, he witnessed an aye-aye eating chicken eggs, approximately five meters away from the chickens. The aye-aye quickly left and returned to the forest. In total, 37 eggs were consumed over the three events.

While previous reports have identified aye-eyes as crop raiders (Ancrenaz *et al.*, 1994; Andriamasimanana, 1994), no one has previously reported them as egg thieves. Although this resource is not available to aye-eyes whose home range does not include human dwellings, it is possible that an opportunistic aye-aye may consume bird eggs they encounter in the forest. This should be considered in future dietary studies, not as a primary resource, but as a potential resource of which to remain aware. Additionally, if this egg stealing behaviour is more common than previously realized, it could represent another complication in alleviating aye-aye-human relations from a conservation perspective.

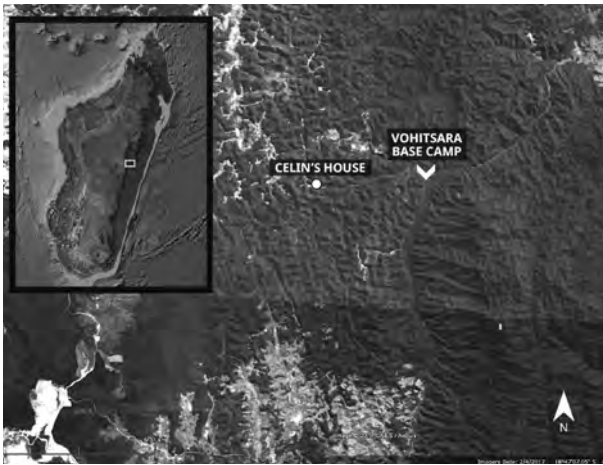


Fig. 1: Location of Marcelin's (abbreviated to Celin) house where egg feeding events by an aye-aye occurred in Ambo-sary, Madagascar.

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Non-forest matrix crossing in the blue-eyed black lemur *Eulemur flavifrons* (Gray, 1867)

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The population of the Critically Endangered blue-eyed black lemur *Eulemur flavifrons* found in the Ankarafa Forest in northwestern Madagascar is well-characterised (Volampeno *et al.*, 2011). The area consists of primary and secondary forest fragments and supports the largest remaining connected population of *E. flavifrons* (Schwitzer *et al.*, 2005, Schwitzer *et al.*, 2007). In the current study, lemur groups within two neighbouring, unconnected forest fragments (72 m apart at their closest point) were being studied: Forest Nora (a highly degraded fragment) and Forest Guy (a less degraded fragment).

On one study day during the 2012-13 wet season, a group of lemurs were observed crossing a large stretch of non-forest matrix on the ground, showing terrestrial quadrupedalism as opposed to their usual arboreal movement. The group was identified as the Green group described by Volampeno *et al.* (2011), and was known at the time to consist of 12 individuals occupying a territory in the northeastern part of Forest Guy. The route taken by the group was tracked, GPS coordinates were plotted and further information was collected on vegetation cover and the distance that the group travelled.

The group was first located whilst feeding in a large mango tree at the very edge of Forest Nora and was tracked across the savannah right to the edge of Forest Guy, where they rested and fed again in a mango tree on the very eastern point of the fragment (Fig. 1). The route they travelled spanned a large open area between the two forests with sparse tree cover; the ground was covered mostly in long grass and small shrubs or young trees and there were very few substantially sized trees along the route. Further to this, the group crossed the main path leading into camp – a 10 m wide, well-established trail frequented by humans and zebu, which has been cleared of all vegetation. The route that the group took was re-enacted and it was found that the lemurs covered a total distance of 226 m between the two forests. Of this, 137 m was covered only on the ground where the group was led by the *Chef du groupe* (dominant female) and moved quadrupedally, where over 30 m at a time crossed scrubland and dirt paths. The remaining 89 m were crossed in the sparse areas of tree cover (Fig. 1).

The crossing of non-forest matrix over open savannah has not been previously documented in this species (C. Schwitzer, *pers. comm*). This behaviour is likely an adaptation to two things: changing resource availability/the depletion of resources within the usual home range, and between-group competition. As the observed group's home range was based in the mostly intact forest, in this instance the movement is more likely to have been driven by intense resource competition amongst neighbouring groups in Forest Guy and large group size. However, it could also be suggested that groups in highly degraded forest are also capable of travelling significant distances between fragments to exploit

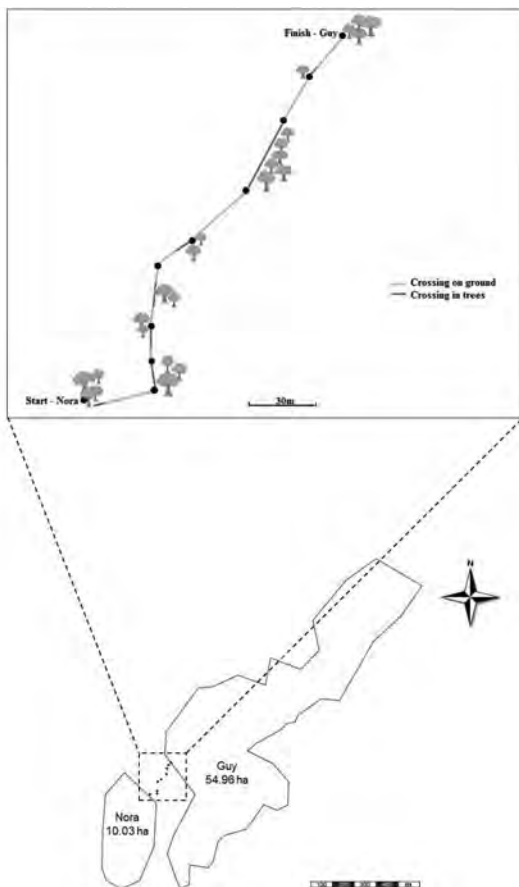


Fig. 1: The pathway of non-forest matrix crossed between two forest fragments (Forest Nora and Forest Guy) by a group of *Eulemur flavifrons*, and the proportion of the journey spent on the ground and in the trees.

more favourable conditions in nearby lesser-degraded forest. This expansion of the home range is another example of the species demonstrating a degree of habitat and behavioural flexibility.

The ability of the species to cross non-forest matrix between fragments has conservation implications. Navigating the patchy, mosaic fragments of the Ankarafa Forest is one of the toughest challenges the remaining population faces. The removal of all continuous forest has left a series of connected and unconnected forest fragments, and the ability of *E. flavifrons* groups to move between patches in search of food when resources have been depleted in one area is crucial to their survival. Habitat alteration often removes the understory so it is promising to see that the lemurs are adapting to movement on the ground (Moresco *et al.*, 2012). It has been found in numerous studies on primates that the survivability of a fragment-living species is positively correlated with their ability to cross non-forest matrix, utilise all areas of a fragment and move between patches (Onderdonk and Chapman, 2000; Ramanamanjato and Ganzhorn, 2001). This gives us hope that the viability of the *E. flavifrons* population in the Ankarafa Forest is higher than previously thought.

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Articles

Diet and behaviour of adult *Propithecus verreauxi* (Verreaux's sifaka) in southern Madagascar during the birth season

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Key words: *Propithecus verreauxi*, reproductive females, diet, behaviour, dry season, lactation

Abstract

The environment in which *Propithecus verreauxi* (common name: Verreaux's sifaka) is found is highly seasonal, arid, and frequently undergoes periods of drought. *P. verreauxi* compounds these challenges by giving birth during the dry season. Considering that lactation is the most energetically expensive reproductive stage, understanding how *P. verreauxi* females meet energetic requirements during the dry season is important. We examine the behaviour and diet of adult male and lactating female *P. verreauxi* to identify if sex differences exist. Continuous-time focal observations were conducted at Berenty Private Reserve, southern Madagascar, over six weeks early in the birth season. The number of bites of food an individual consumed of an item was recorded along with plant part and species. Males and females did not differ significantly in intake rate, the total amount of food consumed, or food types consumed. However, females did spend significantly more time feeding from one plant species (*Rhinorea greveana*). Females devoted a greater

portion of time to feeding than did males, but both sexes allocated similar amounts of time to resting.

Introduction

Propithecus verreauxi live in an environment with large seasonal fluctuations (Richard *et al.*, 2002); In the dry season (July and August) female *P. verreauxi* have to cope with reduced nutrient value (Irwin *et al.*, 2013; Koch *et al.*, 2016), but also with higher energetic expenditure due to lactation (Hanwell and Peaker, 1977; Robbins, 1983; Gittleman and Thompson 1988; Clutton-Brock *et al.*, 1989). The timing of mid and late-lactation, the period of greatest energetic cost (Altmann, 1980; Tardif *et al.*, 2001), occurs when resources are increasing; giving birth and weaning offspring are timed when resources are very low (Jolly, 1984; Lewis and Kappeler, 2005). Female lemurs face notably high physiological stress during reproduction (Young *et al.*, 1990; Sautner, 1994; Gould *et al.*, 2011) with female *P. verreauxi* at Beza Mahafaly losing more mass than do males during gestation and lactation periods (Richard *et al.*, 2000). Thus, it is possible these first weeks following birth, corresponding with the end of the dry season and low resource availability, are a difficult time. *P. verreauxi* may exhibit strategies to cope with giving birth during a period of low food availability.

Propithecus species employ several strategies to cope with the seasonality of Madagascar, such as reductions in home range, core area, and daily path length during the dry season (Richard, 1978) and balancing active behaviours with periods of inactivity, which is likely to conserve energy (Norscia *et al.*, 2006). *P. verreauxi* focus on consuming mature leaves during the dry season (Simmen *et al.*, 2003; Norscia *et al.*, 2006; Yamashita, 2008). *P. verreauxi* at Kirindy consume the highest amount of protein during the late dry season, and higher amounts of carbohydrates when fruit production is at its peak (March). Mature leaves are always available at Kirindy (Norscia *et al.*, 2006), but fruit, flowers, and young leaves, with their greater nutrition due to higher sugar and protein content, are not (Waterman, 1984), and *P. verreauxi* preferentially feed on these items when available (Norscia *et al.*, 2006). During the dry season, *Propithecus diadema* in Tsinjoarivo Forest in central-eastern Madagascar rely on non-fruit foods that are high in protein but low in macronutrients and energy, suggesting this species is nutritionally compromised at this time (Irwin *et al.*, 2013).

We studied the diet and behaviour of *P. verreauxi* during the early lactation period to determine if there are any sex differences in 1) food intake rate, 2) time spent feeding and resting, and 3) food type and plant species consumed.

Methods

Study site and subjects

Data collection took place from August 8th to September 15th, 2014 at Berenty Private Reserve in southern Madagascar (S 25° 0.5' latitude, E 46° 18.5' longitude). Berenty Reserve is approximately 240 ha in size flanked by sisal plantation at the south and the Mandrare River at the north (Soma, 2006). The climate in this area fluctuates between a hot, wet season (November to April) and a cool, dry season (May to September) (Jolly, 1966; Jolly *et al.*, 2006). Rainfall is seasonal with 70% of the annual rainfall occurring between November and February (Jolly *et al.*, 2002). Temperatures at Berenty range from above 40° C in the daytime during the hot, wet season, to below 10° C at night in the cool dry season (Jolly *et al.*, 2006).

Data were collected by the primary investigator KM in the closed-canopy gallery forest section of Berenty (Malaza)

dominated by *Tamarindus indica* and *Acacia* (Jolly, 2004; Jolly *et al.*, 2006; Soma, 2006), and in Ankoba, a second-growth, open-canopy forest adjacent to Malaza (Fig. 1). Three study groups were chosen: two groups in Ankoba forest (A1 and A2) and one group in Malaza forest (M). Data were collected from five lactating females and five adult males (Tab. 1). No group with more than two lactating females was found out of approximately ten groups surveyed. Study troops and focal individuals were chosen in order to maximize data collection on lactating females. No non-lactating adult females were present in the study troops.

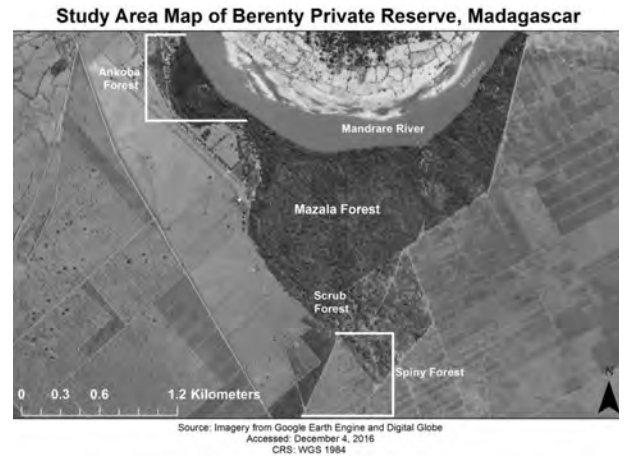


Fig. 1: Map of study area.

Tab. 1: Sex, maturity, and total observation time per focal animal. A1=Ankoba 1, A2=Ankoba 2, M=Malaza.

Individual	Sex	Maturity	Group	Total time observed (hh:mm:ss)
Blackspot	F	Adult	A1	21:38:18
Katrina	F	Adult		19:20:31
Bob	M	Adult		18:55:43
Fred	M	Adult		19:17:12
Unnamed 1	F	Sub-adult		
Unnamed 2	M	Subadult		
Blondie	F	Adult	A2	16:29:47
Jenny	F	Adult		16:10:48
Sofina	M	Adult		17:25:30
Ted	M	Adult		17:38:20
Unnamed 3	M	Sub-adult		
Unnamed 4	M	Sub-adult		
Sarah Louise	F	Adult	M	16:59:21
Dido	M	Adult		18:26:55
Unnamed 5	M	Adult		
Unnamed 6	F	Sub-adult		
Unnamed 7	M	Sub-adult		
Unnamed 8	M	Sub-adult		

Data collection

KM collected data over six weeks with the aid of a Malagasy student assistant, Saotra Rakotonomenjanahary. Data were collected six days per week, for seven hours per day. Continuous focal animal data (Altmann, 1974) were collected in fifteen-minute sessions to record activity: rest, self-groom, groom, feed, locomote, vigilance, and aggression. A focal session was disregarded if the total time the focal animal was in view was less than ten minutes. A feeding bout was defined as the amount of time a focal animal was observed continuously chewing and swallowing a food item. The food item (young leaf, mature leaf, flower bud, flower, ripe fruit, and

unripe fruit), the plant species, and the number of bites each individual consumed were recorded.

Data analysis

KM analyzed data using the statistical software RStudio, versions 97.332 and 98.501 (R Core Team, 2014). The Mann-Whitney *U* test was used to examine if there were sex differences in feeding intake rate, activity budget, most frequently consumed plant species, and total amount of food consumed. If an effect of sex was found, the Kruskal Wallis test was then used to determine if group had a significant effect. Because multiple tests were run on the same data set, *P*-values were Bonferroni corrected and significance level set to 0.02.

Results

Food intake and time spent feeding

Males and females did not differ in the total amount (bites) of food consumed ($U_{10} = 22$, $P = 0.55$). On average, males consumed 1197.28 (SD= 117.41) and females 1009.63 (SD= 112.17) total bites of food over the study. We found no significant sex difference in average food intake rate regardless of food type or plant species (Mann Whitney test, $U_{10} = 3$, $P = 0.06$; male intake rate= 1130.15 bites/hour, SD= 145.74; female intake rate= 935.07 bites/hour, SD= 139.51). Specifically, males and females did not differ in the average intake rate of flowers ($U_{10} = 3$, $P = 0.06$), mature leaves ($U_{10} = 3$, $P = 0.6$), or young leaves ($U_{10} = 3$, $P = 0.06$). Animals consumed very limited amounts of fruit during this study and did not consume seeds. Males and females did not differ in the average proportion of feeding time devoted to any of the three food types (flowers: $U_{10} = 13$, $P = 1.0$, mature leaves: $U_{10} = 17$, $P = 0.42$, young leaves: $U_{10} = 8$, $P = 0.42$). We found no significant sex differences in the five most frequently consumed plant food: *Pithecellobium dulce* ($U_{10} = 5$, $P = 0.15$), *Acacia ro-vumae* ($U_{10} = 21$, $P = 0.10$), *Azadirachta indica* ($U_{10} = 12.5$, $P = 1.0$), and *Tamarindus indica* ($U_{10} = 19.5$, $P = 0.16$); however, females spent more time feeding on *Rinorea greveana* compared with males ($U_{10} = 25$, $P = 0.01$, Fig. 2) and no effect of group was found ($\chi^2 = 0.23$, $P = 0.90$).

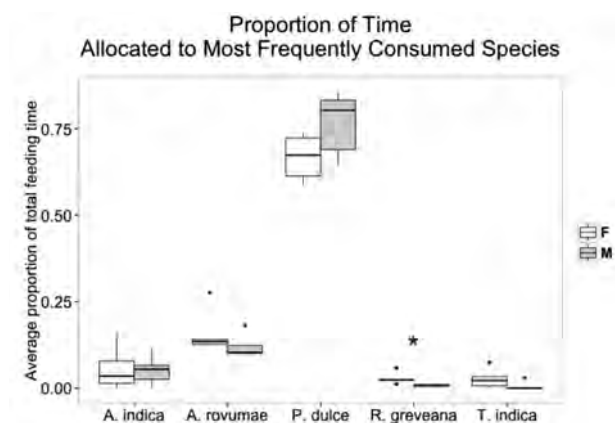


Fig. 2: Average proportion of total feeding time allocated to species. Whiskers are the first and fourth quartiles. Bars indicate median values. Outliers are plotted as individual points. Asterisk indicates significant difference between males and females. Note: *A. indica* and *P. dulce* are introduced species.

Sex differences in activity budget

Females allocated more observed time to feeding than males ($U_{10} = 25$, $P = 0.01$), whereas males spent a significantly

greater proportion of time scent-marking ($U_{10} = 1.5$, $P = 0.02$) compared with females (Fig. 3, 4). There was no significant effect of group on either time spent feeding ($\chi^2 = 0.41$, $P = 0.82$) or scent-marking ($\chi^2 = 0.02$, $P = 0.99$).

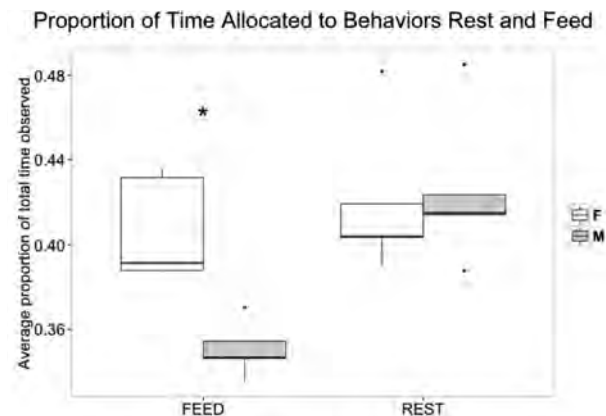


Fig. 3: Average proportion of total time observed allocated to behaviours feed and rest. Whiskers are the first and fourth quartiles. Bars indicate median values. Outliers plotted as individual points. Asterisk indicates significant difference between males and females.

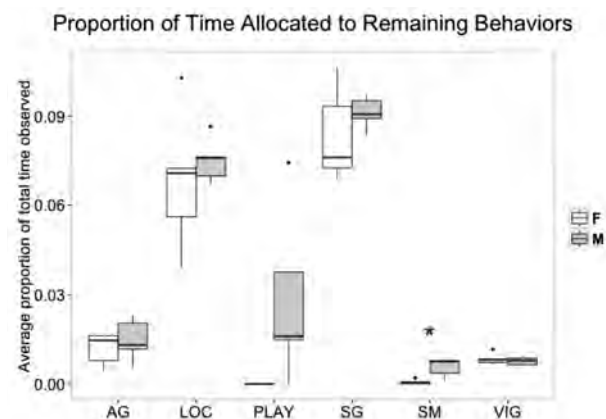


Fig. 4: Average proportion of total time observed allocated to remaining behaviours. Whiskers are the first and fourth quartiles. Bars indicate median values. Outliers plotted as individual points. Asterisk indicates significant difference between males and females. (AG= Allo-groom, F= Feed, LOC= Locomote, SG= Self-groom, SM= Scent-mark, VIG= Vigilance.)

Post-Hoc Power Analysis

Because sample sizes were small, post-hoc power analyses were run. Using the Bonferroni corrected significance level of $P = 0.02$, an effect size over 2.4 is needed to achieve a significant power of 0.8, an effect size which was reached for the behaviours feed and scent-mark (effect size= 4.5 and 3.3 respectively).

Discussion

Our study focussed on the differences between males and lactating females and concurs with the limited previous research on sex differences, or lack thereof, in other *Propithecus* species. Hemingway (1999) found no differences between males and females in food intake rate, percentage or duration of feeding time, percentage of time allocated to social behaviours, or time allocated to resting for *Propithecus edwardsi*. Charrier and colleagues (2007) studying *P. verreauxi* at Berenty in March and April (the gestation period) found

no sex differences in activity budget and food preferences but females consumed 30-40% more food. Pichon and Simmen (2015) report no significant differences between the sexes in food intake or energy budget for *Propithecus coronatus* inhabiting the dry, semi-deciduous forests in north-western Madagascar. We found no significant differences in the amount of time allocated to resting, the overall feeding intake rate, the proportion allocated to or the feeding rate, or the total amount of food consumed (measured in bites) during the early lactation period between *P. verreauxi* females with infants and males at this site.

Contrary to our results, Richard (1978) found no sex differences in the amount of time devoted to feeding in *P. verreauxi* at Berenty. Richard's (1978) results span multiple reproductive stages and compare lactating and non-lactating females to males. Richard (1978) did not quantify the amount of food consumed. Recent results on *P. verreauxi* from Kirindy show that females have a higher intake of macronutrients during the late lactation (Koch et al., 2016).

Across *Propithecus* species and habitat types, leaves compromise a large portion of the diet (Sato et al., 2015). Previous studies have shown that *P. verreauxi* feed mainly on mature leaves in the birth season (Carrai et al., 2003; Lewis and Kappeler, 2005; Norscia et al., 2006). *P. diadema* consume a large proportion of young leaves during the dry seasons in the mid-altitude Tsinjoarivo Forest (Irwin et al., 2013). At Berenty, the majority of time spent feeding was on flowers (~59 % of feeding time) for both sexes, and mature leaves made up less than 20% and 24% of female and male feeding time respectively. The hourly intake rate for flowers was also high for both sexes at Berenty. A diet composed mainly of flowers has been reported in other studies. Yamashita (2008) found that *P. verreauxi* at Beza spend a large portion of feeding time on flowers for the last two months of the dry season, comparable with our findings. Flowers are a preferred food for *P. diadema* in Mantadia National Park (Powzyk and Mowry, 2003), and flowers and buds are majority components of *P. diadema*'s diet in the mid/late dry season in Tsinjoarivo Forest (Irwin, 2006).

Despite taking place during a time of limited resource availability, rates of agonism were low (< 0.07 % of observation time), suggesting there is little competition over food between the sexes during the early period of lactation. Previous research on male *P. verreauxi* has shown higher levels of fecal glucocorticoids and aggression rates during the reproductive season compared to the birth season (Fitchel et al., 2007). Increased male agonism during the mating season has been observed for *P. verreauxi* at Kirindy Forest as well (Kappeler et al., 2009). Differences in measurements of agonism prevent direct comparisons with our results.

The environment at Berenty is modified and contains introduced plant species. Females spent 66% and males 76% of feeding time on *P. dulce*, an introduced tree species. That this species was relied on so heavily is of particular interest for the group found in the Malaza portion of Berenty, as it is not an abundant species in terms of number of individuals or basal area (Simmen et al., 2012). Individuals allocated over 72% of feeding time on average to non-native plant species. Multiple species of lemurs found at Berenty have been reported to consume introduced species previously and, depending on the season, these species can make up a substantial portion of the diet (Simmen et al., 2003). That *P. verreauxi* is able to rely so highly on introduced plant species during the early lactation period at Berenty potentially makes this site unique from other study sites that contain fewer or no introduced plant food species.

To better understand the diet of lactating female *P. verreauxi* during the dry season, future research should study non-lactating females as well to determine how data for males and lactating females compare. Nutritional analyses on food items consumed could potentially illuminate differences in energy or specific nutrient consumption and this analysis is lacking for all reproductive seasons.

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Etude préliminaire des comportements de *Haplemur griseus griseus* dans la forêt tropicale humide de Maromizaha (Andasibe)

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Résumé

Cette étude a été effectuée dans la forêt humide de Maromizaha (Andasibe) pendant la saison de pluie des mois de Février-Mars 2010, dans le but d'étudier les préférences écologiques et le comportement de *Haplemur g. griseus*. L'approche écologique par la méthode «groupe-scan» concernant l'étude comportementale de cette espèce permet de dire que ses activités sont différentes selon les strates, le diamètre des supports. Nos résultats montrent que *Haplemur g. griseus* préfèrent la strate basse (57.8%) comprise entre 0.1-3 m de hauteur, les petits et moyens supports (respectivement 51 et 46.5%). Par ailleurs, leurs activités semblent être influencées par les facteurs écologiques (climats, habitats). *Haplemur g. griseus* semble être plus actif durant les jours ensoleillés (64.2%) et fréquentait principalement la vallée (82.3%). L'alimentation des individus observés était composée principalement de bambou appartenant à la famille de Poaceae (92.1%) avec une préférence pour les jeunes pousses, les bases des feuilles et les jeunes feuilles.

Introduction

La majeure partie de la couverture végétale malgache se situe dans la partie orientale de l'île de Madagascar (Zimmermann, 1899; Rakotomalala et al., 2015). La dégradation anthropique des habitats naturels menace et érode d'une façon alarmante ces écosystèmes forestiers (Harrison et al., 2004; Rasolofson et al., 2007; Roger, 2008; Spiral, 2012). Le présent travail concerne l'écologie de *Haplemur griseus griseus*, un taxon inféodé à l'Est de Madagascar (Rabarivola et al., 2007; Mittermeier et al., 2010). *Haplemur g. griseus*, qui est le plus petit des lémuriens mangeurs de bambou, est classé Vulnérable par la liste rouge de l'UICN (2014). Il vit en groupe de 2 à 7 individus (Mittermeier et al., 2008) et n'a pas de dimorphisme sexuel (Peter, 1990; Garbutt, 2007; Mittermeier et al., 2010). Un inventaire rapide des lémuriens de Maromizaha, qui a été effectué par l'équipe du Groupe d'Etude et de Recherche sur les Primates de Madagascar (Raison et al., 2015) montre que sa densité est de 74 ind/km². Plusieurs auteurs (Petter et al., 1977; Wright, 1990; Tan, 1999; Tan, 2000; Grassi, 2001-2002; Rabarivola et al., 2007) ont déjà fait des études sur le comportement de cette sous-espèce surtout dans la partie Sud-est de Madagascar (Parc National de Ranomafana). Cependant, aucune étude

comportementale n'a encore été effectuée sur ce taxon dans la forêt de Maromizaha. C'est pourquoi nous avons décidé d'y effectuer notre recherche sur l'éco-éthologie de *Haplemur g. griseus*. Cette étude nous permettra d'acquérir des données suffisantes sur les activités de l'espèce, afin de mettre en place des activités de conservation adéquates à la préservation de la population de *Haplemur g. griseus* et de leur habitat.

Méthodes

Site d'étude

La forêt de Maromizaha se trouve dans la partie Est de Madagascar, au Sud-est du Parc National d'Andasibe, au PK 142 du village d'Anevoka. Le site d'étude (Fig. 1) est situé aux coordonnées géographiques suivantes: 18.9760 S° et 48.4648 E°. Les habitats fréquentés par les groupes étudiés sont situés entre 826 et 1099 m d'altitude.

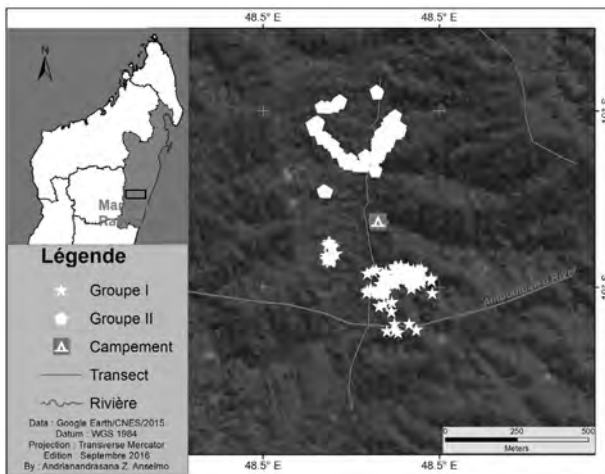


Fig. 1: Localisation du site d'étude et répartition des groupes étudiés.

La forêt de Maromizaha servait d'abris aux populations fuyant l'autorité coloniale (1896-1960), c'est pourquoi le site a pris une importante valeur socio-culturelle (Gerp, 2008). L'ensemble du massif surplombant la forêt a une indéniable valeur culturelle et spirituelle pour la population locale. Le sommet de la chaîne montagneuse de Maromizaha (Fig. 2), possède un couvert forestier. Cette forêt est un lieu sacré destiné au culte des ancêtres selon la population environnante. En conséquence, cette réserve forestière bénéficie d'une certaine protection locale.



Fig. 2: Rocher de Maromizaha (Photo:Andrianandrasana, Z.A.).

Suivi écologique des groupes étudiés

Nous avons choisi la méthode de «groupe-scan» qui permet d'étudier l'activité de *Haplemur g. griseus* toutes les trois minutes (Altmann, 1974). Deux groupes de *Haplemur g. griseus* ont été choisis pour la facilité de leur observation. Les groupes sont constitués d'individus mâles et femelles adultes, subadultes et juvéniles dont le groupe I et le groupe II sont respectivement composés de 5 et de 4 individus. Les observations ont été collectées, de 5h30 à 17h30. L'utilisation des strates, le diamètre et l'orientation des supports et l'utilisation de l'habitat ont été relevés. Le test de chi-deux a été utilisé pour analyser les données prélevées. Le tableau 1 présente l'ensemble des comportements observés au cours de cette étude et le tableau 2 rassemble les caractéristiques des supports utilisés par les individus étudiés.

Tab. 1: Descriptif des comportements observés

Terminologie	Descriptif
Déplacement	L'individu change de place le long d'une branche ou bien d'un support à un autre
Alimentation	Comportement incluant la recherche de nourriture et sa consommation
Repos	L'individu cesse toute activité
Activités sociales	Activités qui concernent les rapports entre un individu et les autres membres du groupe (toilettes, jeux)

Tab. 2: Caractéristiques des supports

Caractéristique	Descriptif
Strate	Basse: 0.1-3m Moyenne: 3.1-6m Supérieure: >6m
Diamètre des supports	Petit: 0.1-5cm Moyen: 5.1-10cm Large: >10cm
Orientation des supports	Horizontale: 0.1°-30° Oblique: 30.1°-60° Verticale: 60.1-90°

Résultats

Aperçu général sur l'observation de Haplemur g. griseus

Au total, le temps d'observation a duré 3720 minutes. Les individus observés étaient principalement actifs de 7h00 à 10h00.

Budget-temps des activités

Selon nos résultats (Fig. 3), *Haplemur g. griseus* passe la majorité de son temps à se reposer (48.1%), à s'alimenter (29%) et à se déplacer (18%). A l'opposé, le toilettage et les jeux ne représentent respectivement que 2% et 2.8%.

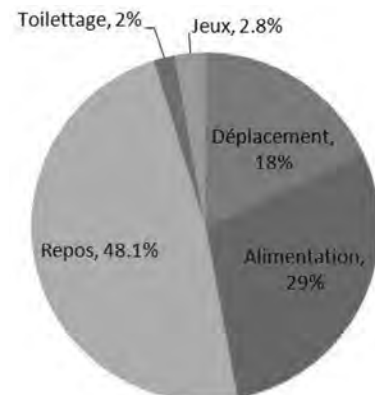


Fig. 3: Budget-temps des activités de *Haplemur g. griseus*.

Fréquentation des strates

Lors de nos observations, les individus fréquentaient majoritairement la strate basse (57.8%), alors que les strates moyennes et supérieures étant moins utilisées (respectivement 36% et 6.1%). Ils étaient plus actifs durant les jours ensoleillés (64.2%) que pendant les temps couverts et pluvieux. Pour le temps nuageux, le test de chi-deux de fréquence au seuil de signification $\alpha = 0.05$ ($\chi^2 = 18.02$; $ddl = 4$; $p < 0.05$) montre que la fréquentation des strates par classe d'âge est différente.

Utilisation des supports selon leur diamètre

Les petites et moyennes branches sont les supports les plus utilisés (respectivement 51% et 46.5%). Le choix de ces supports est différent selon la classe d'âge ($\chi^2 = 38.78$; $ddl = 4$; $p < 0.05$). Les juvéniles et adultes utilisent des branches à petit diamètre (respectivement 40.5% et 46.8%) et des branches à moyen diamètre (54.6% et 50.8%). Chez les subadultes, les branches à diamètre petit sont les plus utilisées (61.9%).

Utilisation des supports selon leur orientation

En général, les individus observés utilisaient principalement des branches horizontales: respectivement 71.8%; 61.5% et 59.3% pour les juvéniles, les subadultes et les adultes. En revanche, les branches verticales étaient rarement utilisées (15.7%).

Activités par classe d'âge et par habitat

En comparant le pourcentage des activités effectuées par classe d'âge dans chaque type d'habitat (Fig. 4), la vallée est l'habitat le plus visité par *Hapalemur g. griseus* (82.3%). Le versant n'est que faiblement fréquenté (16.7%) et la crête ne l'est pratiquement pas (1%). Dans la vallée, le pourcentage de temps dédié aux jeux diminue avec l'âge de 8.1% chez les juvéniles à 0.7% chez les adultes. Les individus de tout âge pratiquent aussi le toilettage, mais avec une faible fréquence de l'ordre de 2%. Il est à remarquer que les subadultes et adultes s'alimentent avec des fréquences quasiment égales (34.8%; 35%). Les juvéniles se déplacent à raison de 32.8%. Au niveau des versants, ce sont toujours les juvéniles et les subadultes qui pratiquent les jeux (11.4%; 4.6%). Le toilettage ne s'observe que chez les subadultes (4.6%) et chez les adultes (1.9%). Contrairement aux juvéniles, les subadultes et adultes mangent beaucoup (27.7%; 40.2%) puis se déplacent moins (27.7%; 17.8%).

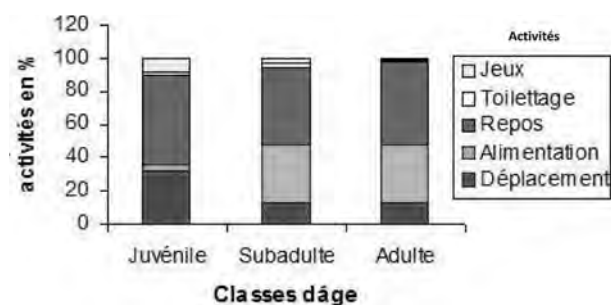


Fig. 4: Pourcentage des activités par classe d'âge par type d'habitat.

Espèces de plantes consommées par *Hapalemur g. griseus*

Hapalemur g. griseus consommait principalement du bambou appartenant à la famille de Poaceae avec un taux (92.1%). Le Tab. 4 présente les préférences de chaque groupe d'âge pour les différentes parties de la plante: subadultes et adultes préfèrent les pousses de bambou dont les taux sont

respectivement 55.1% et 76.8%). Par contre, les juvéniles semblent préférer la base des feuilles de ces plantes (71.4%). Les jeunes feuilles d'autres plantes constituent des aliments complémentaires chez les subadultes (9.5%) et les adultes (7.2%).

Tab. 3: Pourcentage des parties consommées par classe d'âge parmi les individus étudiés

Classes d'âge	Fréquence des parties consommées en %		
	Poussede bambou	Base des feuilles de bambou	Jeunes feuille-sautres que bambou
Juvénile	28.6	71.4	0
Subadulte	55.1	35.4	9.5
Adulte	76.8	15.9	7.2

Discussions

Activités comportementales

Les données collectées sur le comportement de *Hapalemur g. griseus* dans la forêt tropicale humide de Maromizaha ne sont pas exhaustives à cause de la mobilité de l'animal dans son habitat. A cet effet, le présent travail n'est qu'une étude préliminaire sur l'*Hapalemur g. griseus* dans cette forêt et mérite d'être approfondie. Au cours de notre recherche, *Hapalemur g. griseus* de la forêt de Maromizaha était moins actif lors des heures les plus chaudes de la journée (après 10h).

Pendant le suivi écologique de *Hapalemur g. griseus*, le comportement alimentaire et le «déplacement» présentent une interdépendance. En effet, si les aliments sont de qualités insuffisantes dans leur habitat, l'animal est obligé de les chercher ailleurs. Grassi (2002) dans son ouvrage l'a été constaté: elle a décrit que les activités «déplacement et alimentation» comme dépendantes de la distribution des ressources de nourritures et des caractéristiques de l'habitat. Le fait que les juvéniles et les subadultes font les activités «déplacements et jeux», il est considéré comme un début d'apprentissage de la vie et un moyen pour le développement et l'épanouissement physique du corps. Lors de leurs activités, ces individus se trouvaient généralement autour de la femelle et du mâle adulte qui assurent leur protection. Nous avons également observé un juvénile toujours allaité par sa mère: en effet, due à l'insuffisance de nourriture, il ne consommait que très peu d'aliments complémentaires. Concernant les activités sociales (jeux et toilettage), ce sont les juvéniles et subadultes qui les préfèrent souvent lorsqu'ils se trouvent dans un endroit en sécurité.

Fréquentation des strates

D'après nos recherches, *Hapalemur g. griseus* de Maromizaha fréquente toutes les strates de son habitat, mais reste la plupart du temps dans la partie inférieure de la forêt (57.8%). Cela pourrait s'expliquer par le régime alimentaire de cet animal du fait que constituant leur aliment de prédilection, les bambous (notamment leurs pousses et jeunes feuilles) se trouvent dans cette strate (Fig. 5). L'abondance de jeunes pousses de bambou durant la saison des pluies oblige l'animal à descendre près du sol pour s'alimenter; par ailleurs, chez les adultes, le fait d'occuper ce niveau est considéré comme un moyen de surveiller et de protéger le groupe surtout les juvéniles.

Les canopées des arbres visités par *Hapalemur g. griseus* sont fermées ou semi-ouvertes. Les individus observés fréquentaient la strate moyenne pour se reposer. Il est à noter



Fig. 5: *Hapalemur g. griseus* lors du comportement alimentaire (Photo: Andrianandrasana, Z.A.).

que d'après nos observations dans certaines circonstances douteuses comme la vue des hommes, les cris d'oiseaux prédateurs ou d'autres lémuriens, *Hapalemur g. griseus* reste immobile. En effet, le mâle du groupe lance un signal pour avertir les autres individus. Cela veut dire que l'animal est une espèce considérablement vigilante. Nous pouvons donc avancer que la fréquentation des strates par *Hapalemur g. griseus* dépend de l'abondance des aliments et de la caractéristique de l'habitat.

Diamètre des supports utilisés

Nos observations ont démontré que les branches de petit et à moyen diamètre sont les plus utilisées par *Hapalemur g. griseus*, notamment au cours du déplacement et de l'alimentation, car les jeunes feuilles sont abondantes à l'extrémité des branches. De plus, le faible poids des adultes 700-850 g (Mittermeier et al., 2010) permet à *Hapalemur g. griseus* d'utiliser des branches de petite dimension.

Pendant les activités de jeux et de toilettage, les juvéniles restent toujours près de la femelle et du mâle adulte sur les branches horizontales à diamètres moyens (Fig. 6). Ceci nous informe que le fait de bien se grouper est importante dans la structure sociale de *Hapalemur g. griseus*.



Fig. 6: Mâle de *Hapalemur g. griseus* avec juvénile (Photo: Andrianandrasana, Z.A.).

Choix de l'orientation des supports

En tant que petit lémurien quadrupède-arboricole, *Hapalemur g. griseus* utilise souvent les branches horizontales et obliques lors des jeux, du déplacement et de l'alimentation; les branches verticales sont adoptées pour les sauts. L'utilisation de ces deux types de support permet à l'animal de

passer d'une branche à l'autre, de façon stable. Durant le déplacement, les coussinets palmaires et plantaires ainsi que la queue jouent un rôle important dans le maintien d'équilibre (Andriaholinirina, 2003). D'après Stevens et al. (2011), concernant la locomotion d'*Eulemur cinereiceps*, l'utilisation des branches horizontales et obliques lors du déplacement est en relation avec le centre de gravité de l'animal et avec le point de contact du support. Ceci est renforcé par le fait que les coussinets palmaires et plantaires jouent le rôle d'antidérapage (Andriaholinirina, 2003).

Au cours de cette étude, il a été constaté que *Hapalemur g. griseus* ne saute que rarement. En cas d'alerte ou de perturbation, l'animal s'enfuit alors en sautant de branche verticale à une autre en favorisant les supports à petit ou moyen diamètre. Par conséquent, s'il rencontre un support trop large, l'individu est contraint de le contourner. Grassi (2002) a montré que ce choix est propre au mode de locomotion, et à la morphologie des membres antérieurs et postérieurs de ce taxon.



Fig.7: *Hapalemur g. griseus* sur une branche oblique (Photo: Andrianandrasana, Z.A.).

Influence des climats sur les activités

L'animal fait l'auto-toilettage ou le toilettage mutuel (lèche ou peignage) et parfois les individus se débarrassent mutuellement des insectes parasites. Lorsque le temps est orageux, *Hapalemur g. griseus* cesse toute activité et reste grouper au-dessous du feuillage dense, ce qui corrobore les résultats de Petter et al. (1977). Grassi (2001) a également souligné que pendant la saison de pluie, cette espèce diminue l'activité «déplacement».

Comportement alimentaire

Hapalemur g. griseus est folivore (Grassi, 2002), il préfère consommer le bambou dans la forêt de Maromizaha. Deux types de bambou ont été identifiés: *Cephalostachyum* sp et *Panicum* sp, toutes deux de la famille des Poaceae. Les plantes complémentaires appartiennent aux familles de Moraceae (*Ficus sorocoides*) et Acanthaceae (*Hypoestes* sp). L'animal utilise ses organes de sens pour sélectionner les plantes et leurs parties à consommer en utilisant la vision et l'odorat. Selon nos observations, la femelle et le mâle adultes apportent souvent des pousses de bambou pour les juvéniles. Pour les individus immatures, c'est un exercice d'apprentissage.

Retombées scientifiques

Par rapport aux résultats obtenus, il serait nécessaire de: (a) faire un suivi écologique permanent pour la population de *Hapalemur g. griseus* et les autres espèces de lémuriens afin de mettre à jour les informations scientifiques et pour

approfondir les recherches (éthoécologie; plantes sources de nourriture) face aux problèmes liés à leur environnement, (b) faire l'inventaire des espèces de bambou ainsi que leur usage local.

Conclusion

L'étude du comportement de *Haplemur g. griseus* pendant la saison de pluie, du mois de Février au mois de Mars 2010 dans la forêt tropicale humide de Maromizaha par la méthode de «groupe-scan» permet de dire que: (i) le repos, l'alimentation et le déplacement constituent les principales activités de *Haplemur g. griseus*; (ii) les individus fréquentent majoritairement les strates basses et moyennes de la forêt; (iii) ils préfèrent les branches horizontales à diamètres petits et moyens; (iv) la vallée et le versant sont les deux lieux les plus fréquentés par *Haplemur g. griseus*; (v) leur régime alimentaire est constitué principalement de bambous dont il consomme principalement les pousses, la base des feuilles et les jeunes feuilles.

Cette étude apporte de nouvelles connaissances écologiques sur *Haplemur g. griseus* classée Vulnérable selon la liste rouge de l'UICN (2014). Elle contribue à la mise à jour des informations scientifiques sur une espèce de lémurien encore peu étudiée dans la forêt de Maromizaha. Cette forêt se trouve actuellement dans un état de dégradation primaire et si des mesures de conservation appropriées seront mises en place pour renforcer les efforts déjà effectués, nous espérons que les menaces qui pèsent sur cette population n'aient pas d'impact négatif sur la pérennité de ce taxon.

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Mouse lemurs' use of degraded habitat: a review of the literature

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Abstract

Madagascar is known for its unique biodiversity including its endemic primates, the lemurs. This biodiversity is threatened by deforestation, forest degradation and anthropogenic disturbances. Several mouse lemurs (genus *Microce-*

bus) have been shown to cope with habitat disturbances and degradation, although it is not clear whether all 24 currently recognized mouse lemur species respond similarly to forest degradation. Here, we review the literature on mouse lemur use of degraded habitat and highlight the conditions under which populations may survive in degraded forest (DF). Further, we question whether mouse lemurs show variation in degraded habitat use, with respect to forest type, species conservation status and distribution range. We show that data on DF use are available for 14 species of *Microcebus* and data are limited to a few geographical locations. Our results confirm that most mouse lemur species are apparently able to cope with a certain level of degradation. The long-term survival in DF, however, depends mainly on food resource availability, understory structure, availability of tree holes for torpor and hibernation, and predation pressure. The relative frequency of these four factors vary among forest types suggesting that differences may exist but still require research efforts for ecological and environmental differences among regions to be fully understood. We found no variation in degraded habitat use, with respect to conservation status and distribution range. To better understand what drives mouse lemurs ability to survive in degraded habitat, further research should focus little known microendemic species, and should concentrate on estimating densities, characterizing diet and parasite load, and understanding habitat and shelter use across seasons.

Introduction

Madagascar is considered one of the world's "hottest" biodiversity hotspots due to its exceptional biodiversity and the high level of threats this diversity faces (Myers *et al.*, 2000, Goodman and Benstead, 2005). Home to 101 currently recognized lemur taxa (Louis Jr. and Lei, 2016; Mittermeier *et al.*, 2014; Setash *et al.*, 2017), Madagascar harbours the second-highest primate diversity of all countries and the highest proportion of primate endemism (Mittermeier *et al.*, 2010).

Mouse lemur habitats and population sizes are decreasing, while their level of threat is rising, mainly from deforestation, forest degradation, and poaching (Schwitzer *et al.*, 2013; Schwitzer, Mittermeier, *et al.*, 2014). Since 2014, 18 out of 24 recognized mouse lemur species are considered threatened (Schwitzer *et al.*, 2013). This high proportion of threatened species is not surprising if we consider the high rate (>50%) of forest loss in Madagascar between 1950's and 2000 (Schwitzer *et al.*, 2014). Besides most lemur species being threatened, many authors found mouse lemurs to be able to use degraded habitat (Ganzhorn, 1995; Mittermeier *et al.*, 2010).

Mouse lemurs are commonly observed in degraded forest (we use the term broadly, to include partially logged, partially deforested, partially cultivated, regenerating forest, but not completely denuded landscape (Herrera *et al.*, 2011; Miller *et al.*, submitted; Randrianambinina *et al.*, 2010). They are also commonly observed in rural areas (Deppe *et al.*, 2007; Ganzhorn, 1987), and in suburban areas (Irwin *et al.*, 2010). Aside these evidences, mouse lemurs are forest-dwelling species, and depend on forest for survival (Ganzhorn and Schmid, 1998; Karanewsky and Wright, 2015). Thus, DF might only harbour sink populations of *Microcebus*. Understanding the use of DF by mouse lemurs may therefore be crucial to their conservation (Schwitzer *et al.*, 2013). Dry and humid forest mouse lemur species typically have a different diet (Kappeler and Rasoloarison, 2003; Radespiel, 2007), and dry forests generally harbour higher mouse lemur population densities than humid forests (Randrianam-

binina *et al.*, 2010; Setash *et al.*, 2017). In addition, western dry and eastern humid regions harbour contrasting climatic conditions and climatic extremes and, hence, mouse lemurs from different regions have developed independent unique resource use strategies (Génin, 2008, 2010; Kobbe and Dausmann, 2009). We therefore ask the following question (Q1): "Do mouse lemurs vary in their responses to DF in humid and dry forests?"

Mouse lemur species show a large diversity of distribution range size. Species with large distribution (e.g. *M. murinus*) show high seasonal variability in feeding behaviour and high colonization ability (Radespiel, 2016). Contrastingly, other species occupy only small areas reasons that are not yet clear. We therefore ask the following question (Q2) "Do mouse lemur species with different distribution ranges vary in their responses to DF?"

Finally, conservation status is primarily based on population and distribution trends as well as on threats faced by the species (IUCN, 2012). In other words, it summarizes a large panel of factors that may be involved in the ability of mouse lemur species to use DF. We therefore question (Q3) "Do species with different conservation status vary in their responses to DF?"

Methods

To perform the literature review, we searched JSTOR, Science Direct, Wiley, Springer Link, and Google Scholar databases as well as all issues of the journals Lemur News and Primate Conservation that contain precious information about lemurs but are not always well referenced by the above mentioned databases. We searched the following key words: *Microcebus*, adaptation, habitat use; habitat/forest degradation, secondary forest, and anthropogenic environment to capture most of the relevant literature concerning mouse lemur habitat use. From identified papers we subsequently extracted information about species, sex, forest type (e.g. dry, humid), degradation level (cf. classification below), type of degraded habitat use: positive, neutral and negative responses to DF, diet, habitat characteristics, sleeping sites, seasonal variation in habitat use, daily torpor/hibernation, territoriality, home range size, competition/coexistence). We considered all studies reporting the presence or absence of mouse lemurs in DF and/or assessing mouse lemur habitat or diet preferences. Review papers reporting information from case studies were not considered.

To compare degradation levels and mouse lemur responses to DF described in different manners in the considered studies, we categorized them, based on the terminology used by the authors. The following terms were considered to characterize primary forest: primary, pristine or natural forest, unexploited forest, undisturbed forest, intact forest, continuous canopy, high density of large trees, high tree species diversity, and absence of human activities. For DF, we considered: secondary forest, lightly, moderately, severely degraded or disturbed habitat, forest edges, "savoka" (i.e. transitional secondary vegetation after abandonment of agriculture, Radespiel *et al.*, 2012), forest harbouring human activities such as logging, mining, charcoal production, cattle grazing, and fire or traces of fire. For cultivated areas, we considered plantations or areas of slash-and-burn agriculture i.e. "tavy". We categorized open sites, grassland or savanna as "grassland".

A factor putatively influencing DF use was considered when specifically investigated in a particular study. We pooled studies conducted by the same researchers, on the same species, in the same study area and presenting similar re-

sults in study clusters. We treated each study cluster as one study in the evaluation. We considered results on more than one species reported in a single study independently for each species. From hereon, all single studies and study clusters are called “studies” without distinction.

The taxonomy of mouse lemurs has been subject to regular changes within the last decades (Rasoloarison *et al.*, 2013; Schwitzer *et al.*, 2013; Thiele *et al.*, 2013; Hotaling *et al.*, 2016; Lei *et al.*, 2015). Hence, we provide current and previously given species names in the analysis, where relevant.

We retrieved the size of each species’ distribution (extent of occurrence, EOO) from the IUCN red list database (IUCN, 2013). Since there is a large uncertainty in the way EOOs are drawn, we assigned each EOO to one of three categories to distinguish small and large distribution range species: small (for microendemic species with very few localities or an area of less than 2100 km²), large (for species with large distributions of more than 8350 km², i.e. *M. murinus*, *M. griseorufus* and *M. myoxinus*), and medium. This category comprises the remaining species that do not fall in any of the other two categories (with distributions between 2100 and 8350 km²). This simplification allows little known but restricted species to fall in the “small” category even though their EOO was sometime originally extrapolated from a single location. We geographically represented studies using ArcGIS (ESRI®).

To compare mouse lemurs’ use of DF, we categorized the reported responses and/or use of DF into three categories: positive effect of forest degradation (mentions of preferential use of DF, higher abundance and greater fitness in DF), neutral responses (tolerance to DF, similar abundance at degraded and non-degraded sites, and foraging on cultivated plant species, or no detected differences), negative

responses (exclusive use or higher abundance in primary forest, reduced fitness, reduced long-term population viability in DF, poaching, increased predation by domestic or wild animals in DF, and increased parasite spillover from humans or domestic animals). We did not consider single reports for observations of mouse lemurs in DF, since they do not indicate clear quantitative DF use trend.

To test for variation in degraded habitat use, with respect to forest type (dry, humid), conservation status and distribution range, we used a two sided Fisher’s exact independence test using R (R Core Team, 2015). This research adhered to the American Society of Primatologists’ principles for the ethical treatment of primates.

Results

We found a total of 84 studies (see the definition of “studies” in the method section) reporting effects of forest degradation on mouse lemurs. In 75 studies, the species names were specified (Tab. 1, 2). In the other nine studies, the species name was not specified and could not be identified based on current taxonomy or geographic data (Tab. 2). Of these 75 studies, only 24 primarily focused on differential habitat quality use (i.e. 32%), but a larger proportion (n= 65, i.e. 87%) evaluated responses of mouse lemurs towards DF (Tab. 2). Of these 65 studies, 27 (42%) reported negative, 23 (35%) neutral and 15 (23%) positive responses towards DF (Fig. 1a, Tab. 1, 2). While at the genus level a larger proportion of studies suggests that DF has a negative effect, our results also confirm that most of the studied mouse lemur species (12 out of 14) are able to use DF (Fig. 1a, Tab. 2). Reports of DF use, however, are scarce for the majority of mouse lemur species, and unequally distributed across Madagascar (Fig. 1).

Tab. 1: Summary of mouse lemurs’ degraded habitat use bibliography. Number of studies reporting use of degraded forest and factors invoked or demonstrated to influence degraded forest use per species.

Species	IUCN status	Distribution range	# DF studies	# DF response studies	# Positive responses	# Neutral responses	# Negative responses	Positive factors	Negative factors
<i>M. murinus</i>	LC	L	24	18	3	8	7	Diet ^a , predator release ^b	Diet ^c , poaching ^{be} , predation ^c , tree holes ^{cd} , temperature ^{cd} , understory structure ^{bc}
<i>M. rufus</i>	VU	M	14	12	2	2	8	Diet ^{hik} , understory structure ^l	Diet ^k , parasites ^l , poaching ^{im} , predation ⁿ , tree holes ^o , temperature ^k
<i>M. ganzhorni</i>	ns	ns	7	5	0	3	2	ns	Understory structure ^g , parasites ^d
<i>M. ravelobensis</i>	EN	M	7	4	1	3	0	Diet (insects) ^o	ns
<i>M. griseorufus</i>	LC	L	8	3	1	0	2	Parasites ^p	Poaching ^q
<i>M. berthae</i>	EN	S	4	3	0	0	3	na	Competition ^{bs} , understory structure ^{bs}
<i>M. lehilahytsara</i>	VU	M	4	3	1	1	1	Diet (fruit) ^t	Diet (fruit) ^u , understory structure ^u
<i>M. sambiranensis</i>	EN	S	2	2	1	1	0	ns	ns
<i>M. arnholdi</i>	EN	S	1	1	0	1	0	ns	ns
<i>M. danfossi</i>	EN	M	1	1	1	0	0	ns	ns
<i>M. gerpi</i>	CR	S	1	1	0	1	0	ns	ns
<i>M. mittermeieri</i>	EN	S	1	1	0	0	1	ns	ns
<i>M. myoxinus</i>	VU	L	1	1	1	0	0	Diet (fruit) ^v	ns
<i>M. tavaratra</i>	VU	S	1	1	1	0	0	Understory structure ^y	ns

Key: ns= not specified; IUCN status: LC= Least Concern, VU= Vulnerable, EN= Endangered, CR= Critically Endangered; Distribution range: L= large, M= medium, S= small; # DF studies: number of studies reporting DF use; # DF response studies= Number of studies assessing responses to DF; # Positive/neutral/negative= number of studies reporting positive/neutral/negative responses. Positive/negative factors: main positive or negative factors cited as influencing DF use.

Literature shown as superscript letters: ^aCorbin and Schmid, 1995; Smith *et al.*, 1997. ^bSchäffler, 2011; Schäffler *et al.*, 2015. ^cGanzhorn and Schmid, 1998. ^dRaharivololona, 2009; Raharivololona and Ganzhorn, 2009. ^eGardner and Davies, 2014. ^fSchmid, 1998. ^gAndriamandimbarisoa *et al.*, 2015; Rakotondravony and Radespiel, 2009. ^hAtsalis, 1999. ⁱLehman, 2006; Lehman *et al.*, 2006a,b; Rajaonson *et al.*, 2010. ^jHerrera *et al.*, 2011. ^kWright *et al.*, 2005; Karanewsky and Wright, 2015. ^lRasambainarivo *et al.*, 2013; Bublitz *et al.*, 2014; Zohdy *et al.*, 2015. ^mLehman and Ratsimbazafy, 2001; Ravoahangy *et al.*, 2008. ⁿRatsirarson and Ranaivonasy, 2002; Goodman, 2003. ^oBurke and Lehman, 2014. ^pRodriguez *et al.*, 2015. ^qDammhahn and Kappeler, 2008a, b; 2009; 2010. ^rSchwab and Ganzhorn, 2004. ^sGanzhorn, 1988. ^tGanzhorn, 1987. ^uGanzhorn, 1995. ^vMeyler *et al.*, 2012.

Tab. 2: Overview on reviewed studies

Literature source/s	Species according to current taxonomy	Species according to literature source/s	IUCN status	Distribution range	Site	Forest type	Degradation	Response to DF
Andriamandimbarisoa <i>et al.</i> 2015	<i>ganzhorni</i>	<i>murinus</i>	ns	ns	Tolagnaro	H	I, II	0
Atsalis 1999	<i>rufus</i>		VU	M	Ranomafana	H	II	+
Blow <i>et al.</i> 2014	<i>rufus</i>		VU	M	Tampolo	H	ns	-
Bohr <i>et al.</i> 2011	<i>griseorufus</i>		LC	L	Tsimanampetsotsa	D	ns	-
Burke and Lehman, 2014	<i>murinus</i>		LC	L	Ankarafantsika	D	I	-
Burke and Lehman, 2014	<i>ravelobensis</i>		EN	M	Ankarafantsika	D	I	+
Corbin and Schmid, 1995	<i>murinus</i>		LC	L	Morondava	D	II	+
Dammhahn and Kappeler 2008a, b; 2009; 2010	<i>berthae</i>		EN	S	Morondava	D	ns	-
Dammhahn and Kappeler, 2008a, b, 2009; 2010; Dammhahn <i>et al.</i> , 2009	<i>murinus</i>		LC	L	Morondava	D	ns	0
Deppe <i>et al.</i> , 2007	spp		ns	ns	Ranomafana	H	I, II, c	0
Evans <i>et al.</i> , 1995	<i>rufus</i>		VU	M	Ambatovaky	H	I, II	0
Ganzhorn and Schmid, 1998	<i>murinus</i>		LC	L	Morondava	D	I, II	-
Ganzhorn, 1987	<i>lehilahytsara</i>	<i>rufus</i>	VU	M	Andasibe- Mantadia	H	I, c	-
Ganzhorn, 1988	<i>lehilahytsara</i>	<i>rufus</i>	VU	M	Andasibe- Mantadia	H	ns	+
Ganzhorn, 1988	<i>murinus</i>		LC	L	Ankarafantsika	D	ns	ns
Ganzhorn, 1989	<i>lehilahytsara</i>	<i>rufus</i>	VU	M	Andasibe- Mantadia	H	ns	ns
Ganzhorn, 1995	<i>myoxinus</i>		VU	L	Morondava	D	I, II	+
Ganzhorn, 1995	<i>murinus</i>		LC	L	Morondava	D	I, II	+
Ganzhorn, 2003	<i>murinus</i>		LC	L	Morondava	D	I, II, c, g	-
Ganzhorn <i>et al.</i> , 1997	<i>arnholdi</i>	<i>rufus</i>	EN	S	Montagne d'Ambre	H	I, II	0
Ganzhorn <i>et al.</i> , 2003	<i>rufus</i>		VU	M	ns	H	II	0
Ganzhorn <i>et al.</i> , 2007	<i>ganzhorni</i>	spp	ns	ns	Tolagnaro	H	II, c	0
Gardner and Davies, 2014	<i>griseorufus</i>		LC	L	Ranobe	D	II, c	-
Gardner and Davies, 2014	<i>murinus</i>		LC	L	Ranobe	D	II, c	ns
Génin, 2008	<i>griseorufus</i>		LC	L	Tolagnaro	D	ns	ns
Golden 2009; Golden <i>et al.</i> 2014; Golden and Comaroff, 2015	spp		ns	ns	Makira	H	ns	-
Goodman, 2003	<i>berthae</i>		EN	S	Morondava	D	ns	ns
Goodman, 2003	<i>griseorufus</i>		LC	L	ns	D	ns	ns
Goodman, 2003	<i>rufus</i>		VU	M	ns	H	ns	ns
Herrera <i>et al.</i> , 2011	<i>rufus</i>		VU	M	Ranomafana	H	I, II	+
Hladik <i>et al.</i> , 1980	<i>murinus</i>		LC	L	Morondava	D	ns	0
Jenkins <i>et al.</i> , 2011	spp		ns	ns	Moramanga-Anosibe -An'ala	H	I, c	-
Kobbe and Dausmann, 2009	<i>griseorufus</i>		LC	L	Tsimanampetsotsa	D	ns	ns
Lahann, 2006	<i>rufus</i>		VU	M	ns	H	ns	ns
Lahann, 2007	<i>ganzhorni</i>	<i>murinus</i>	ns	ns	Tolagnaro	H	I, II	ns
Lahann, 2008	<i>ganzhorni</i>	<i>murinus</i>	ns	ns	Tolagnaro	H	II	ns
Lehman and Ratsimbazafy, 2001	<i>rufus</i>		VU	M	Marolambo	H	ns	-
Lehman, 2006, Lehman <i>et al.</i> , 2006a, b; Rajaonson <i>et al.</i> , 2010	<i>rufus</i>		VU	M	Ranomafana	H	ns	-
Malone <i>et al.</i> , 2013	<i>murinus</i>		LC	L	Tolagnaro	H	II, c	0
Meyler <i>et al.</i> , 2012	<i>tavaratra</i>		VU	S	Daraina	D	I, II	+
Miller <i>et al.</i> , in prep.	spp		ns	ns	Manompana	H	I, II	+
Mittermeier <i>et al.</i> , 2010	<i>sambiranensis</i>		EN	S	ns	H	ns	0
Nash, 2000	<i>murinus</i>		LC	L	Beza Mahafaly	D	II, ns	+
Nguyen <i>et al.</i> , 2013	spp		ns	ns	Tolagnaro	H	II, c	0
Radespiel and Raveloson, 2001	<i>murinus</i>		LC	L	Ankarafantsika	D	I, II	0
Radespiel and Raveloson, 2001	<i>ravelobensis</i>		EN	M	Ankarafantsika	D	I, II	0
Radespiel <i>et al.</i> , 2012	<i>gerpi</i>		CR	S	Andasibe-Mantadia	H	c, ns	0
Radespiel <i>et al.</i> , 2012	<i>lehilahytsara</i>		VU	M	Andasibe-Mantadia	H	c, ns	0
Raharivololona 2009; Raharivolona and Ganzhorn, 2009	<i>ganzhorni</i>	<i>murinus</i>	ns	ns	Tolagnaro	H	ns	-
Rakotoarivony, 2007	<i>murinus</i>		LC	L	Ankarafantsika	D	II, ns	0

Literature source/s	Species according to current taxonomy	Species according to literature sources	IUCN status	Distribution range	Site	Forest type	Degradation	Response to DF
Rakotoarivony, 2007	<i>ravelobensis</i>		EN	M	Ankarafantsika	D	II, ns	0
Rakotondravony and Radespiel, 2009	<i>murinus</i>		LC	L	Ankarafantsika	D	ns	-
Rakotondravony and Radespiel, 2009	<i>ravelobensis</i>		EN	M	Ankarafantsika	D	ns	ns
Ralison, 2007	spp		ns	ns	Andranomanitsy	D	II	+
Ramanamanjato and Ganzhorn, 2001	<i>ganzhorni</i>	<i>murinus</i>	ns	ns	Tolagnaro	H	I, II, c	-
Ramarokoto, 2003	<i>ganzhorni</i>	<i>murinus</i>	ns	ns	Tolagnaro	H	II	0
Randriamanantsaina, 2010	<i>rufus</i>		VU	M	Ranomafana	H	II	-
Randrianambinina et al., 2003	spp		ns	ns	Antsohihy	H	II, c	+
Randrianambinina et al., 2010	<i>danfossi</i>		EN	M	Antsohihy	D	I, II	+
Randrianarisoa et al., 2001	<i>murinus</i>		LC	L	Kasijy	D	ns	0
Randriatahina et al., 2014	<i>sambira-nensis</i>		EN	S	S-Îles Radama	H	II, ns	+
Rasambainarivo et al., 2013; Bublitz et al., 2014; Zohdy et al., 2015	<i>rufus</i>		VU	M	Ranomafana	H	I, II, ns	-
Rasoazanabary, 2004	<i>murinus</i>		LC	L	Beza Mahafaly	D	I, II	-
Rasoazanabary, 2004	<i>griseorufus</i>		LC	L	Beza Mahafaly	D	I, II	ns
Rasolofoson et al., 2007; Rakotondratsimba et al., 2008	<i>mittermeieri</i>		EN	S	Makira	H	I, II	-
Rasolofoson et al., 2007; Rakotondratsimba et al. 2008	spp		ns	ns	Makira	H	I, II	-
Ratsirarson and Ranaivonasy, 2002	<i>rufus</i>		VU	M	Tampolo	H	II	-
Ravoahangy et al., 2008	<i>rufus</i>		VU	M	Anjombalava	H	c, ns	-
Ravoahangy et al., 2008	<i>griseorufus</i>		LC	L	Adabolava	D	II, ns	+
Rendigs et al., 2003, Radespiel et al., 2006	<i>murinus</i>		LC	L	Ankarafantsika	D	II, ns	ns
Rendigs et al., 2003, 2006	<i>ravelobensis</i>		EN	M	Ankarafantsika	D	II, ns	ns
Rodriguez et al., 2015	<i>griseorufus</i>		LC	L	Beza Mahafaly	D	I, II	ns
Schäffler, 2011; Schäffler et al., 2015	<i>murinus</i>		LC	L	Morondava	D	I, II	0
Schäffler, 2011; Schäffler and Kappeler, 2014; Schäffler et al., 2015	<i>berthae</i>		EN	S	Morondava	D	I, II	-
Schmid, 1998	<i>murinus</i>		LC	L	Morondava	D	I	-
Schwab and Ganzhorn, 2004	<i>murinus</i>		LC	L	Morondava	D	I, II, c	0
Schwab and Ganzhorn, 2004	<i>berthae</i>		EN	S	Morondava	D	I, II, c	-
Sehen et al., 2010	<i>ravelobensis</i>		EN	M	Ankarafantsika	D	II, ns	0
Sehen et al., 2010	<i>murinus</i>		LC	L	Ankarafantsika	D	II, ns	ns
Smith et al., 1997	<i>murinus</i>		LC	L	Morondava	D	I, II, g	-
Thorén et al., 2011	<i>murinus</i>		LC	L	Ankarafantsika	D	ns	ns
Thorén et al., 2011	<i>ravelobensis</i>		EN	M	Ankarafantsika	D	ns	ns
Wright et al., 2005, Karanewsky and Wright, 2015	<i>rufus</i>		VU	M	Ranomafana	H	I, II	-

Key to table: ns= not specified, IUCN: LC= Least Concern, VU= Vulnerable, EN= Endangered, CR= Critically Endangered. Range: L= large, M= medium, S= small. Forest type: D= dry, H= humid, DH= dry and humid. Degradation: I= primary forest, II= secondary forest, c= cultivated area, g= grassland. Response to DF: += positive, -= negative, 0= neutral.

Most studies are concentrated in a few parks and sites with research facilities and long term research programmes, such as Kirindy (9 studies), Ankarafantsika (8) and Ranomafana (13), resulting in a paucity of data for numerous species outside of these parks. Hence, seven species are represented by one or two studies (Fig. 2 main graph, Tab. 1, 2) and ten species are not represented (e.g. *M. bongolavensis*, *M. jollyae*). Most species with at least three studies showed variable responses to DF with at least one positive effect reported (Fig. 1 main graph, Tab. 1, 2). Similarly, the most frequently studied species, *M. murinus*, shows a high proportion of neutral responses (8 out of 18 studies) together with more negative than positive reports (7 vs. 3 studies). Likewise, *M. rufus* shows more negative than positive effects reports (8 vs. 2 studies). Of all species represented by more than two studies, *M. ravelobensis* (n= 4) is the only one with no report of negative responses to DF (Fig. 1., Tab. 1). In contrast, *M.*

berthae was the only species for which only negative effects were reported (n= 3, Fig. 1 main graph, Tab. 1).

Forest type

From the 65 studies evaluating responses towards DF, 31 were conducted in dry and 34 in humid forest (Fig. 1b, c, Tab. 2). We found no difference in response to DF between dry and humid forests (Fisher's exact test, $p= 0.63$) although, several reported or invoked factors influencing the response to DF showed contrasting frequency amongst forest types (Fig. 3a). For instance, increased food availability was the most frequently mentioned reason for the use of DF (n= 16) in both dry (n= 8) and humid (n= 8) forests, but the positive effects were associated to different causes. In dry forests, high insect abundance in degraded sites was invoked (n= 6), whereas high fruit abundance in DF was invoked in humid forests (n= 6); (Fig. 3a).

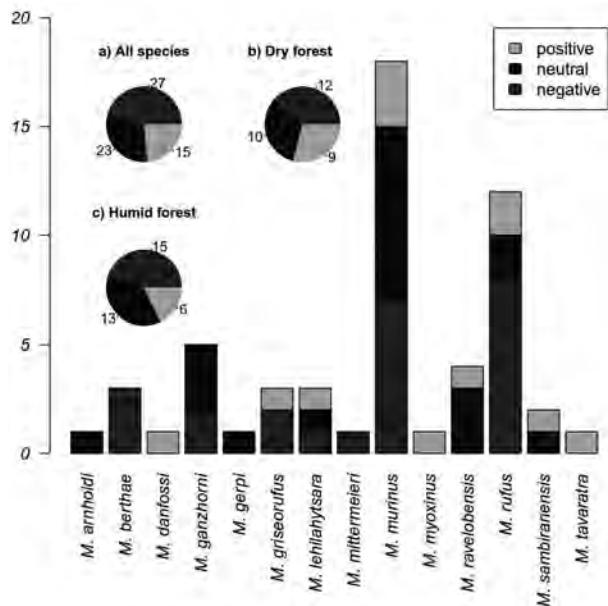


Fig. 1: Forest degradation effect on mouse lemurs. The main barplot represents the number of studies reporting negative, neutral or positive responses towards DF for each species. The pie charts represent the proportions (and numbers, beside the pie charts) of negative, neutral or positive responses obtained for a) all species, b) dry forest species and c) humid forest species.

Distribution range size

Of the 14 species represented in the literature, six have a small, four a medium-sized, three a large, and one an undescribed distribution range (Tab. 1, 2). We found a strong overrepresentation of species with large (n= 22), and medium-sized (n= 20) ranges and only a few studies (n= 9) focusing on species with small distribution ranges (Fig. 4a). In addition, we found no difference in responses to forest degradation amongst distribution range classes (Fisher’s exact test, $p= 0.99$, Fig. 4a).

IUCN status

The number of studies per species decreases with increasing IUCN (i.e. conservation) status (Fig. 4b). Although 18 out of 24 lemur species are threatened (i.e. categorized as Vulnerable, Endangered or Critically Endangered) (Schwitzer *et al.*, 2013), there are almost as many studies on Least Concern species (n= 32, most of them dealing with *M. murinus*) as on threatened species (n= 37). Only one study focused on a Critically Endangered species, *M. gerpi* (Radespiel *et al.*, 2012) (Fig. 2 main graph, Fig. 4b, Tab. 1, 2). We found no significant effect of IUCN status on DF use (Fisher’s exact test, $p= 0.58$), (Fig. 4b), what may be due to the bias towards species with lower conservation status. Almeida-Rocha *et al.* (2017) found a similar pattern in a general pantropical meta-analysis of primates’ responses to DF.

Key factors affecting the use of degraded forest habitats

Most of the 36 studies that cite or investigate putative causes of DF use reported food resource availability (44.4%; n= 16) and forest structure (30.6%; n= 11) as influencing mouse lemurs’ DF use. Poaching (22.2%; n= 8), predation (11.1%; n= 4), tree hole availability and pathogen transmission (8.3% each; n= 3) were also reported to potentially affect mouse lemur use of DF (Fig. 3b, c, Tab. 1).



Fig. 2: Geographic distribution of mouse lemur DF use studies. The diameters of the red dots are proportional to the number of studies (numbers beside dots) in the respective locations. Forest cover from the Madagascar Vegetation Mapping Project data (available online at www.kew.org/gis/projects/mad_veg/datasets.html); (Moat and Smith, 2007). Note that this figure represents numbers of single studies but the results description refers to “study” numbers as described in the method section.

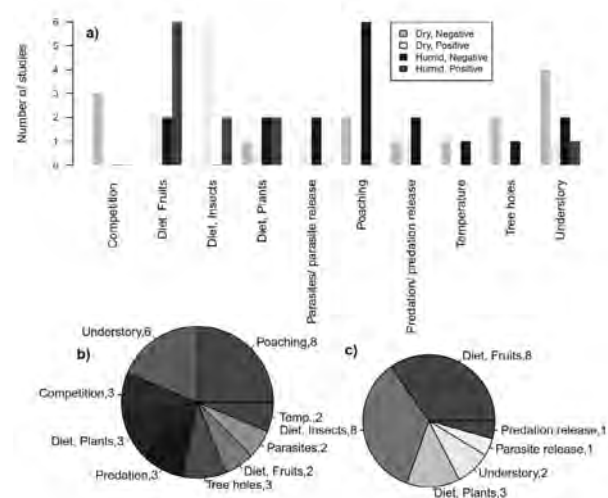


Fig. 3: Cited factors responsible for mouse lemur DF use. a) Numbers of studies suggesting positive or negative effects of factors on DF use in dry and humid forests; b) negative and c) positive effects reported to potentially influence mouse lemur DF use. Circle sizes are proportional to the number of studies.

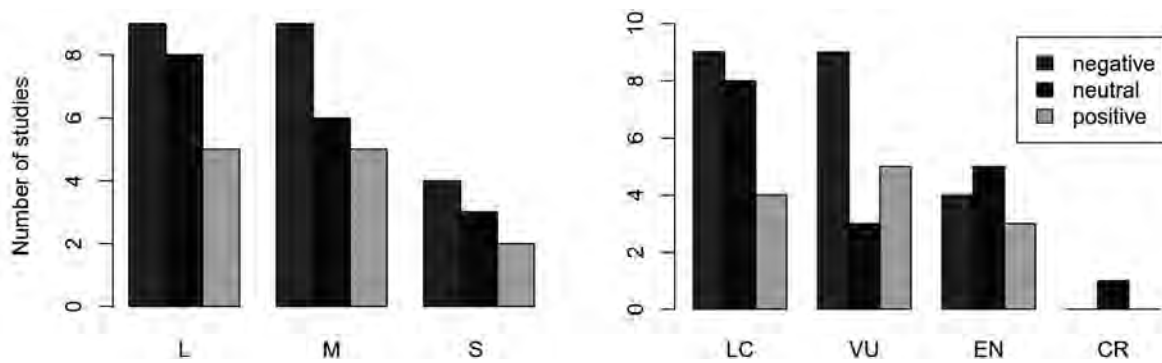


Fig. 4: Relation between species distribution range size, conservation status and DF use. Number of studies reporting negative, neutral or positive effect of habitat degradation on mouse lemur use of DF are represented as function of their a) distribution range size (L: large, M: medium, S: small) and b) IUCN status (LC: Least Concern, VU: Vulnerable, EN: Endangered, CR: Critically Endangered).

Discussion

Our literature analysis reveals that different mouse lemur species respond to forest degradation in different ways. Most species represented in the review (12 out of 14) are able to use DF. Our results confirm that the survival of most species in DF can be ensured in the presence of sufficient food resources and a suitable understory structure. Several studies found higher abundance and higher body mass of mouse lemurs at the edges of primary forests (Ganzhorn, 1995; Lehman, 2006; Burke and Lehman, 2014), emphasizing the preference of some species for degraded habitat. Depending on the degree of degradation, however, some species may not be able to survive in anthropogenic landscapes. Particularly diet specialists and hibernating species may not find sufficient resources to maintain stable populations on the long term. Since only 14 out of 24 species are represented in the literature and data on DF use are scarce for the majority of the represented species, our results do not allow for conclusions on the genus-level. In addition, it appears that most studies are concentrated in a few parks and sites with research facilities hosting long term research programs, as well as focused on a few overrepresented species (*M. murinus* and *M. rufus*). Also, these factors highlight the lack of data for the most endangered (micro-endemic) species and stress the need for a systematic and comprehensive investigation of species taxonomy, distribution, abundance and diet to accurately study mouse lemur use of DF (Lehman et al., 2016).

Despite dry and humid forest being substantially different and hosting mouse lemurs with distinct ecology (Kappeler & Rasoloarison, 2003; Radespiel, 2007) we found no clear variation of DF use between dry and humid forests (Q1). Nevertheless, the factors potentially influencing the use of DF varied (not statistically tested) between dry and humid forest. Food resources availability was reported or invoked by most studies investigating putative factors explaining the use of DF. While high insect abundance was positively associated with dry DF use, high fruit abundance was frequently reported from humid DF. This finding suggests that a systematic comprehensive investigation of diet in DF and non-DF is required to shed light on the differences between forests types as also suggested for the Cheirogaleidae family in general (Lehman et al., 2016).

Distribution range and conservation status (Q2 and Q3) are variables expected to be connected to habitat use flexibility. Our analyses of the literature, however, showed no evidence of relation between distribution range, conservation status and DF use. Most mouse lemur species have

been described in the last decades (Radespiel et al., 2012; Rasoloarison et al., 2013; Hotaling et al., 2016), and both their taxonomy and distribution range are not yet fully and definitively characterized (IUCN, 2013; Schwitzer et al., 2013; Hotaling et al., 2016; Lehman et al., 2016; Louis Jr. and Lei, 2016;). Therefore, relationship patterns between these variables and the use of DF might emerge in the near future from the completion of these data-sets. The conservation status is a complex and frequently evolving variable influenced not only by the distribution range and its variation but also by the species demographic trends and by the development of threats (IUCN, 2012). Hence, it is not necessarily surprising that we could not find a clear relation between DF use and the conservation status. In addition, our review highlights that food resources availability and habitat structure (e.g. understory structure) are the main factors invoked and/or reported to influence DF use. Below, we further discuss major putative factors in greater detail and finally propose a systematic and comprehensive framework to investigate DF use patterns.

Food resources availability

Food resources availability was the most frequently invoked factor to explain differential use of DF (Fig. 3) and is seen by many authors as a decisive factor determining the survival (Hladik et al., 1980; Ganzhorn and Schmid, 1998), the abundance (Ganzhorn, 1988; Lehman et al., 2006a; Sehen et al., 2010; Bohr et al., 2011), and the reproductive success (Wright et al., 2005) of mouse lemurs. Although mouse lemurs are omnivorous (Mittermeier et al., 2010), their diet varies amongst species and seasons (Dammhahn and Kappeler, 2008, 2009; Radespiel et al., 2006; Rakotondranary et al., 2011; Thorén et al., 2011). A large number of studies ($n=16$) invoked or reported higher abundance of particular food resources in degraded forests (Fig. 3, Tab. 1). One of the most frequently invoked or reported positive effect of forest degradation is the abundance of insects in DF and along forest edges (Fig. 3, Tab. 1), which constitute a considerable share of several mouse lemurs species' diet (Corbin and Schmid, 1995; Lehman et al., 2006a). Finally, mouse lemurs have been reported to feed on cultivated plant species (Deppe et al., 2007; Ganzhorn et al., 2003), further emphasizing the role of mouse lemur diet flexibility for its use of modified habitat. Negative effects, however, were also suggested, often by the same authors. For instance, Wright et al. (2005) pointed out that a large number of tree species selectively logged for wood are important components of *M. rufus*' diet.

Understory structure and tree hole availability

Mouse lemurs are mostly found in the shrub and understory layer of the forest (Hladik *et al.*, 1980; Kappeler and Rasoloarison, 2003). A dense understory seems to constitute the ideal substrate for feeding (Andriamandimbarisoa *et al.*, 2015; Radespiel *et al.*, 2006), sleeping (Rasoazanabary, 2004), movements and locomotion (Ganzhorn, 1987; Andriamandimbarisoa *et al.*, 2015). Although anthropogenic disturbances may have a negative effect on understory structure, several authors reported positive selective logging and degradation effects on understory plant production and density (Ganzhorn, 1995, 1999; Herrera *et al.*, 2011). For instance, Miller *et al.* (submitted) found higher population densities in the dense understory of mature secondary forest. Similarly, Ganzhorn (1987) reported the presence of mouse lemurs in old (but not young) *Eucalyptus* plantations with a developed shrub layer.

Tree holes constitute ideal shelters for daily torpor, sleeping, communal breeding and against predation for hollow dwelling species (Ganzhorn and Schmid, 1998; Karanewsky and Wright, 2015). Selectively logged or degraded forests may provide less suitable tree hole shelters (Fig. 3), a potentially limiting resource for hollow dwelling mouse lemurs' DF use, in times of resource scarcity and climatic extremes (Ganzhorn and Schmid, 1998; Schmid, 1998; Kobbe and Dausmann, 2009; Karanewsky and Wright, 2015).

Predation and poaching

Poaching pressure is often associated with DF and forest edges (Lehman *et al.*, 2006b; Lehman and Wright, 2000). Eight studies negatively associated mouse lemur poaching with differential use of DF (Fig. 3, Tab. 1). Although mouse lemurs suffer lower hunting pressure than larger-bodied lemur species (Lehman and Ratsimbazafy, 2001; Jenkins *et al.*, 2011), they are consumed by humans (Jenkins *et al.*, 2011; Gardner and Davies, 2014). In addition, domestic carnivores (*Canis familiaris*) (Goodman, 2003; Gerber *et al.*, 2012) and *Felis catus* (Ratsirarson and Ranaivonasy, 2002; Gerber *et al.*, 2012; are likely to forage more frequently along forest edges (Fig. 3, Tab. 1) and in forests used by humans (Farris *et al.*, 2015a, b). Contrastingly, mouse lemurs may reduce predation rates from wild predators (carnivores, snakes) (Ratsirarson and Ranaivonasy, 2002; Goodman, 2003), birds of prey (Goodman, 2003; Mittermeier *et al.*, 2010) by foraging in dense understory vegetation and by resting in tree holes (Schmid, 1998; Rasoazanabary, 2004). Indeed, higher predation pressure in DF was used to explain low DF use in three studies (Fig. 3, Tab. 1). Contrastingly, Schäffler *et al.* (2015) suggested a positive effect of predation on DF use (decreased predation of *M. murinus* by *Mirza* spp.), which in turn released *M. berthae* from competition in primary forest.

Conservation Implications

We highlight five key factors influencing DF use: (i) food resources availability, (ii) understory and forest structure, (iii) poaching and predation, (iv) tree hole availability and (v) pathogen transmission. Besides the work required to limit or stop deforestation, forest degradation and poaching, namely the most important threats to lemur populations (IUCN, 2013; Schwitzer *et al.*, 2013; Schwitzer *et al.*, 2014), conservation managers may need to consider these five factors (also highlighted in Lehman *et al.* (2016). For instance, reforestation projects may want to consider plant species belonging to the diet of mouse lemurs (and other species) such as *Bakerella* spp. (Atsalis, 1999), fruit trees (Ganzhorn, 1988; Atsalis, 1999;), trees favoring high insect abundance, as well as hollow-forming trees (e.g. *Strychnos*

madagascariensis (Salmona *et al.*, 2015), and fast growing shrubs to facilitate dispersal and provide shelter for mouse lemurs (Andriamandimbarisoa *et al.*, 2015). Mixed plantations and agroforestry incentives may be beneficial to rural communities and wild populations (Ganzhorn, 1987; Deppe *et al.*, 2007). Conservation projects including localized selective logging (e.g. "KoloAla Manompana", Rakotomavo, 2009) may not be detrimental to mouse lemur populations (Ganzhorn, 1995; Atsalis, 1999), if middle sized trees, the understory and the shrub layer are maintained. More long-term field studies focusing on mouse lemurs in rural landscapes may help to further deepen the understanding under which circumstances mouse lemurs and humans may coexist.

Although several studies reported mouse lemurs' poaching (Jenkins *et al.*, 2011; Gardner and Davies, 2014) and its negative effects on DF use (Fig. 3, Tab. 1), it seems not be as frequent as for larger-bodied lemur species (Lehman and Ratsimbazafy, 2001; Jenkins *et al.*, 2011). Mouse lemur populations are likely to be less susceptible to poaching than larger-bodied lemurs because of their shorter generation time and higher reproductive rate (Zimmermann and Radespiel, 2013; Hohenbrink *et al.*, 2015). Therefore, mouse lemur harvesting needs to be formally evaluated to determine under which conditions sustainability can be achieved (Golden, 2009; Gardner and Davies, 2014).

Conclusion

Our literature review highlighted that most studied mouse lemur species are able to use DF and some species may benefit from certain levels of degradation. Data on DF use, however, are geographically aggregated in a few locations, lacking for half of the described species and scarce for the majority of others. These findings highlight the need for a systematic and comprehensive investigation that will allow to accurately quantify the use of DF across species and regions.

Field efforts should aim at comparing multiple species, and focus on filling the existing data gap for most micro-endemic species. They should combine density estimates methods such as nocturnal distance sampling and capture mark recapture (e.g. Meyler *et al.*, 2012), with habitat characterization and opportunistic faecal material collection. In particular, habitat characterization may focus on describing forest structure (Lehman, 2016), flora and fauna diversity, but also on predator abundance using camera traps (e.g. Farris *et al.*, 2015 a, b) and tree hole availability. In addition, opportunistic faecal material sampling from capture studies combined with emergent meta-barcoding approaches will bring a better understanding of diet and parasite load (Quéméré *et al.*, 2013; De Barba *et al.*, 2014).

Finally, combined continuous field and genetic efforts (Hotaling *et al.*, 2016; Louis Jr. and Lei, 2016; Yoder *et al.*, 2016) will likely bring soon an accurate representation of species distribution and taxonomy necessary to study such ecological patterns at the genus scale. While our work focused on mouse lemurs, the second most speciose lemur genus, we stress that DF use should be studied across vertebrate species. In fact, similar studies will be required across all animals, plants and fungi as most habitats are likely to become increasingly fragmented and degraded in the future.

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The unique and isolated *Phaner* population of Analafiana (Vohémar, SAVA)

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Abstract

Despite the fact that lemurs are the most threatened group of mammals and live in one of the world's richest biodiversity hotspots, there are still lemur lineages and regions of Madagascar that suffer from a lack of naturalistic data. This is particularly striking for the genus *Phaner*

as well as for many unprotected forests of Northeastern Madagascar. We detected the presence of *Phaner* in the isolated lowland dry forest of Analafiana, located south of the Manambato River and close to the city of Vohémar. Little is known about the presence of *Phaner* in this region. The only record of *Phaner* in the area around Analafiana comes from museum specimens (Groves and Tattersall, 1991) geographically assigned to Vohémar and identified as belonging to a "doubtful subspecies". Here we provide morphological and genetic (mitochondrial DNA) data for a single juvenile individual captured in Analafiana. We compare our sequence data to the only four *Phaner* sequences publicly available: two *P. electromontis* individuals sampled in Montagne d'Ambre and Ankarana, and two other from *P. pallescens* and *P. parienti* species. We find that the new mtDNA sequence is divergent from the two *P. electromontis* sequences, but closer to these than other *Phaner* sequences. We also note that the Analafiana *Phaner* individual is morphologically more similar to *P. electromontis* than to the other species. Altogether, this data suggests this unique and isolated population of *Phaner* survives in the unprotected Analafiana forest in northeastern Madagascar. It is urgent to carry out more genetic, behavioral, acoustic, and demographic research in this region and on this population, whose exact taxonomic status should be urgently clarified. Our results strongly suggest that Analafiana's *Phaner* population likely holds the memory of a unique evolutionary history.

Introduction

In the last twenty years our understanding of Malagasy primates has profoundly changed (Mittermeier *et al.*, 2010; Schwitzer *et al.*, 2013). Genera such as *Microcebus* and *Lepilemur* have seen the number of recognized species increase tremendously (Hotelling *et al.*, 2016; Lei *et al.*, 2016; Louis and Lei, 2016), and regions rarely visited are now more thoroughly studied and sampled. These two changes are not independent and the identification of new species has been to some extent driven by the genetic analyses of samples obtained over large geographical areas. However, there are still regions of Madagascar that have been sparsely sampled and visited. This is true, for instance, for forests located in northeast Madagascar, south of the Manambato River (Fig. 1). These regions are mostly covered by humid forests but there are also a few isolated dry lowland forests, such as Analafiana, located ~20 km from Vohémar, and ~20 km south of the Manambato River.

The genus *Phaner*, commonly called fork-marked lemurs, belongs to the Cheirogaleidae family, which includes also the genus *Microcebus* (mouse lemurs), one of the most speciose lemur genera. Four subspecies of *Phaner* were described by Groves and Tattersall (1991), based on a limited number of morphological differences identified among *Phaner* museum specimens. Groves (2001) elevated all subspecies to the species rank, and this has been the consensus until now (Mittermeier *et al.*, 2010). Their distribution is discontinuous, and most southern and eastern regions of Madagascar do not host any *Phaner* species (Fig. 1; Mittermeier *et al.*, 2010). Three of the four species are distributed in the north of Madagascar: *P. parienti* in the north-west, *P. electromontis* in the north-northeast, and *P. furcifer*, in the east.

Mittermeier *et al.* (2010) noted that based on field observations (R.A. Mittermeier in 1995) the southernmost *P. electromontis* populations located between the Loky and the Manambato rivers could belong to a distinct species. This region is also known as Daraina, and is interestingly the only region where the golden-crowned sifaka (*Propithecus tatter-*

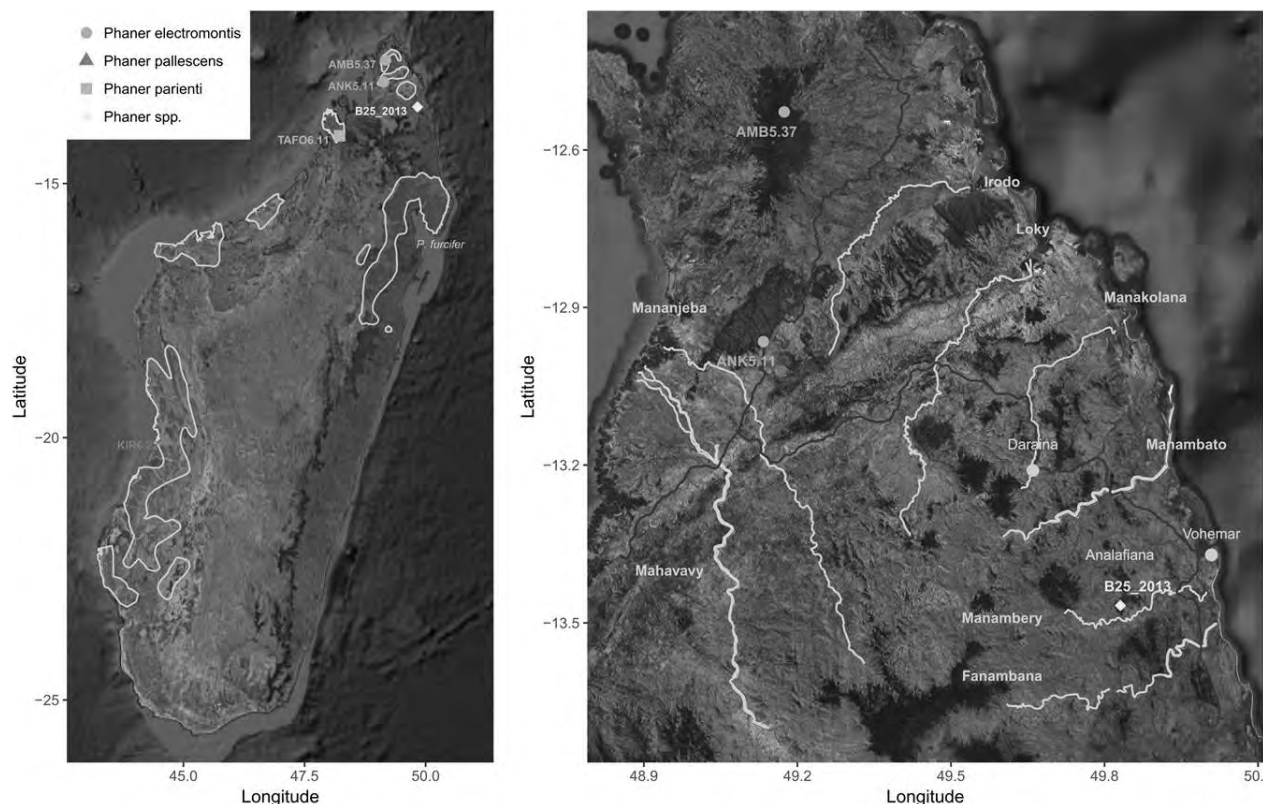


Fig. 1: Map of *Phaner* samples used in this study. The left panel represents the 5 samples used in the phylogeny reconstruction (see also Tab. 2). The samples B25_2013 correspond to the only juvenile *Phaner* individual captured in Analafiana in the present study. The right panel shows a closer view of Northern Madagascar allowing a better representation of the grassland/forest landscape and of the river system in the region. Rivers are represented in light blue, and roads in red. The figure was built using the R package RgoogleMaps (R CoreTeam, 2014). Distribution ranges of the left panel plot were downloaded from the IUCN red list pages (Andriaholinirina, et al., 2012a-d).

salli) can be found, hence supporting the idea that other taxonomic groups could have been isolated therein. Groves and Tattersall (1991) also identified a *Phaner* museum sample from Vohémar (Iharana), located south of the Daraina region, and thus further south than the possibly distinct *P. electromontis* population or putative species. However, the lack of samples and data from these regions have not allowed researchers to go beyond suggestions.

To summarize, it is unclear whether some of the gaps in the distribution (Fig. 1) reflect real discontinuities, or lack of knowledge from regions that are still poorly studied. Analyzing the few samples available from these regions for which little is known but where deforestation is taking place, is an increasingly important objective. In this study we present new genetic and morphological data obtained from one juvenile *Phaner* individual captured in Analafiana. Our report benefits from morphometric measurements and mitochondrial DNA material of a caught individual with precise locality and with the construction of a phylogeny placing it within the *Phaner* evolutionary tree.

Material and Methods

Study site and sample collection

Between the 25th and the 31st of August 2013 we visited the Analafiana dry deciduous lowland forest, located between the Manambato and Manambery rivers, ~20km west of the town of Vohémar, Eastern Madagascar (Fig. 1; <https://google/maps/analafiana>). The Analafiana forest is the southernmost dry forest of northern Madagascar. The closest dry deciduous forests are located north of the Ma-

nambato River. It is mainly surrounded by grasslands, open landscape, and montane humid forests, the closest being the Salafaina forest on the West. Few naturalistic reports mentioning the Analafiana forest exist, most of which focuses on plants and reptiles (e.g. Raxworthy et al., 2008; Leong Pock Tsy et al., 2013). Due to this isolation, the Analafiana forest is expected to host a unique fauna and flora diversity.

We visited the Analafiana forest to survey lemur populations. We used line transect visual and acoustic distance sampling, trapping, and other survey methods that are described in our previous works in Northern Madagascar (Meyler et al., 2012; Salmons et al., 2013; Sgarlata et al., 2017). We captured one individual of the genus *Phaner* by hand. We handled it after tranquilizing with an injection of Ketamine Hydrochloride (~3 mg/kg), collected ear biopsies and measured 18 morphological traits listed in Tab. 1. Field handling and sampling procedures followed Code of Best Practices for Field Primatology of the International Primatological Society, adhered to the legal requirements of France, Madagascar, and Portugal, and were approved by the Malagasy Ministry of Water and Forests.

Sample conservation and laboratory procedures

We stored the biopsies in Queens Lysis Buffer (Seutin et al., 1991) at ambient temperature during the fieldwork period and subsequently at -20°C. Genomic DNA was extracted from biopsies using a DNeasy Blood & Tissue Kit (QIAGEN #69506). Adaptations to the protocol included the addition of 20 µL of 1 M Dithiothreitol (Sigma-Aldrich #646563) during lysis and before eluting DNA in 80 µL of Buffer AE (QIAGEN).

Tab. 1: Morphometric measurements of the Alanafiana *Phaner* individual. This table shows the measures obtained for the juvenile individual sampled in Alanafiana together with published data for the other *Phaner* species.

Morphological traits (in mm)	<i>Phaner</i> spp. This study	<i>Phaner</i> spp. Vohémar	<i>P. furcifer</i>	<i>P. pallescens</i>	<i>P. parienti</i>	<i>P. electromontis</i>
Head length	50.3	59.5-54.6 ^b	-	53.1 ^b	55 ^b	56 ^b
Body length	124.0		-	-	-	-
Head-Body length	174.3		230-290 ^a	237 ^c -263 ^d	~238 ^d	272 ^d
Tail length	262.0		290-370 ^a	319 ^c -321 ^d	~401 ^d	344 ^d
Head width	26.4		-	-	-	-
Ear length	24.8		-	-	-	-
Ear width	15.9		-	-	-	-
Snout length	18.3		-	-	-	-
Intra orbital breadth	11.0		-	-	-	-
Inter orbital breadth	28.0	15.8-13.5 ^b	34.2 ^b	32.2 ^b	32.6 ^b	35 ^b
Tight length	48.3		-	-	-	-
Tibia length	60.5		-	-	-	-
Foot length	38.0		-	-	-	-
Radius length	35.0		-	-	-	-
Humerus length	34.2		-	-	-	-
3rd toe length	15.5		-	-	-	-
4th toe length	16.3		-	-	-	-
Tail circumference	26.0		-	-	-	-
Weight (g)	140.0		-	327 ^c -340 ^d	~360 ^d	387 ^d

References: a: Tattersall, (1982); b: Groves and Tattersall (1991); c: Schülke (2003); d: Mittermeier *et al.* (2010).

We amplified and sequenced two mitochondrial (mtDNA) loci: cytochrome b (*cyt b*; 1150 bp), (Irwin *et al.*, 1991); and the cytochrome c oxidase subunit II (*cox2*; 684 bp) (Adkins and Honeycutt, 1994). Amplification of *cyt b* was carried out in a 10 µl reaction with 2.5 µL of 5X GoTaqFlexi Buffer, 20mM of MgCl₂, 3 mM of each dNTP, 8 µM of each primer (L14724; H15915) and 1U of GoTaqFlexi DNA polymerase (Promega #M7801). Amplification of *cox2* was carried out in a 10 µL reaction comprised of 3.6 µL of 2X MyTaq HS Mix (BioLine #BIO-25045), and 2 µM of each primer (L17553 and H8320). In both reactions, 70 ng of DNA template was used. Standard PCRs were run with an initial denaturing temperature of 95 °C for 2 min, the *cyt b* reaction followed with 35 cycles of 1 min at 94 °C, 45 sec at 52.5 °C, and 90 sec at 72 °C (*cox2* followed with 28 cycles of 30 sec at 95 °C, 1 min at 45 °C, and 75 sec at 72 °C), and a final extension of 10 min at 72 °C (Guschanski *et al.*, 2006; Horvath *et al.*, 2008). PCR products were sequenced in an ABI 3130 XL Genetic Analyzer (Applied Biosystems #4359571) and edited using Geneious v10.1.3 (Kearse *et al.*; 2012).

Tab. 2: Sequences used in the phylogeny reconstruction (Accession: NCBI accession number).

Voucher	Species	Locality	Latitude	Longitude	Reference	Accession
AMB5.37	<i>Phaner electromontis</i>	Montagne d'Ambre	-12.5274	49.1742	Louis and Lei (2016)	KM112338.1
ANK5.11	<i>Phaner electromontis</i>	Ankarana	-12.9651	49.1336	Louis and Lei (2016)	KM112339.1
KIR6.22	<i>Phaner pallescens</i>	Kirindy	-20.0660	44.6549	Louis and Lei (2016)	KM112340.1
TAFO6.11	<i>Phaner parienti</i>	Antafondro	-14.0466	48.2248	Louis and Lei (2016)	KM112341.1
B25_2013	<i>Phaner</i> spp.	Analafiana	-13.4669	49.8311	current study	MG813795 - MG813796
MAS6.10	<i>Cheirogaleus major</i>	Masoala (Masiaposa)	-15.6719	49.9662	Louis and Lei (2016)	KM112323.1

Sequence alignment and phylogeny

We retrieved available mitochondrial genomes of the *Phaner* genus and of a *Cheirogaleus major* individual, KMI12323.1 (Tab. 2; Louis and Lei, 2016), from NCBI. We aligned *cyt b* and *cox2* and the above-mentioned mitochondrial genomes using MAFFT v7.031b (Kato and Standley, 2013), visually checked the alignment in GENEIOUS v7 (Kearse *et al.*, 2012) and subsequently truncate the alignment to keep the two aligned regions (*cyt b* and *cox2*). The final alignment consisted of two concatenated loci of 1346 bp. We used jModelTest v2.1.5.7 (Darriba *et al.*, 2012) to select the best-fitting model of nucleotide substitution for the concatenated loci (best model: GTR; Generalized Time-Reversed). We built a phylogeny using RAXML (Stamatakis, 2014), with 500 rapid bootstrap and 20 ML replicates, the GTR nucleotide sequence evolution model with CAT approximation of rate heterogeneity, partitions of each locus and codon positions and using the *Cheirogaleus major* sequence as outgroup (Tab. 2). The tree was graphically represented using the *ape* R package (Paradis *et al.*, 2004; R CoreTeam, 2014).

Results and Discussion

The captured individual was identified as a juvenile female (specimen B25_2013; Tab. 1 and Fig. 2). With its tail longer than its head-body length (Tab. 1), a darkening pattern limited to the last third of the tail, and the presence of clear fork mark and dorsal stripe (Fig. 2), the individual seems to best fit the description of *P. electromontis* than that of the other *Phaner* species, according to the determination key and species diagnosis proposed by Groves and Tattersall (1991). Unfortunately, out of the 18 measures that we obtained (Tab. 1), only two (head length and inter orbital breadth) were also used by Groves and Tattersall (1991) making quantitative comparisons tentative at best. However, we note that the head width and inter-orbital breadth of our individual are smaller than the values reported by these authors for *P. electromontis* (Tab. 1) and for the "doubtful subspecies" population of Vohémar. These differences can be attributed to the individual being a juvenile.

The phylogenetic tree represented in Fig. 3 was based on two DNA fragments with a total length of 1346 bp. Other *Phaner* species sequences published by Louis and Lei (2016) were much longer, however, the topology obtained here was consistent and our bootstrap values are generally high. The first point to notice is that the two *P. electromontis* sequences of Louis and Lei (2016) group together. Moreover the Alanafiana *Phaner* sequence forms a sister lineage to *P. electromontis* (Fig. 3). The Alanafiana *Phaner* sequence is divergent from the two *P. electromontis* sequences, but closer to these than other *Phaner* sequences. This suggests that if our individual belongs to a new species, it is genetically closer to *P. electromontis* than *P. parienti* in the north-west. Altogether, we identified for the first time a population of *Phaner* that is isolated, apparently genetically different from known populations of *Phaner*, and is likely under serious

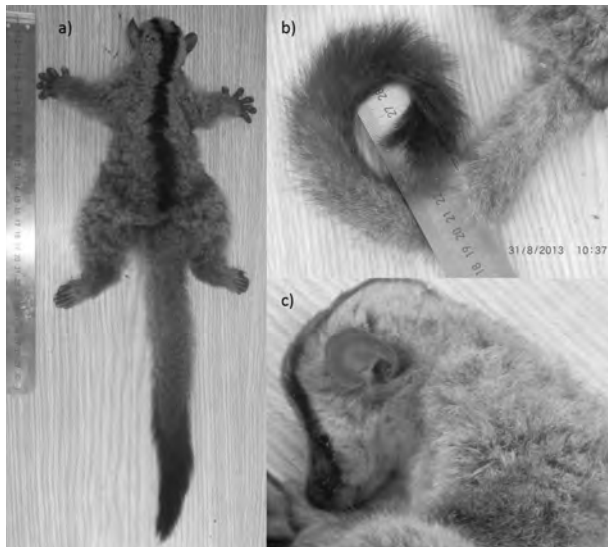


Fig. 2: Photographic illustrations of the coat color patterns of the juvenile *Phaner* specimen B25_2013. a) Dorsal view of the specimen; b) zoomed view of the specimen's tail coloration pattern and c) zoomed profile view of the specimen's head.

threat. Mittermeier *et al.* (2010) noted that *Phaner* are very vocal and it is easy to acoustically detect their presence. Surveys by our group over several field seasons provided very little support for *Phaner*'s presence in the surrounding humid forests (JS and LC, unpublished data), whereas their presence was obvious in Analafiana.

Our data do not allow us to determine whether a new species has been discovered, and more work would be needed across all species of *Phaner* to increase our understanding of within and between populations, and species diversity. The population between the Loky and Manambato River was identified as a possibly distinct species; it has not yet been systematically investigated (Mittermeier *et al.*, 2010).

Additional research is needed to determine the exact taxonomic status of these new lineages. To be comprehensive and integrative, this research should include 1) extensive morphological, genetic and behavioral characterization of the *Phaner* species and populations (museum specimens should be revisited), 2) characterizing species distribution with presence-absence surveys (acoustic surveys at dusk are an efficient tool for *Phaner*; Charles-Dominique and Petter, 1980; Salmona, 2014) and 3) acoustic characterization of the populations (shown to be potentially informative criteria for nocturnal cryptic species differentiation; (Braune *et al.*, 2008). As noted above, *Phaner* are very vocal animals. Do we wish to hear the sound of silence (Simon and Garfunkel, 1964).

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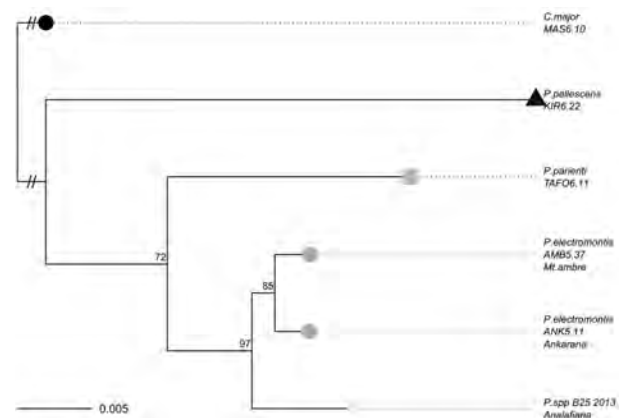


Fig. 3: Phylogeny of the *Phaner* genus obtained from *cyt b* and *cox2* mitochondrial loci. Hashed edges of the root (*C. major*) have been shortened for graphical purposes and its branch lengths are therefore not to scale. Tree tip symbols and colors correspond to those of figure 1. Bootstraps values are indicated as percentage derived from 500 replications.

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Effects of past logging on diet and behaviour of Milne Edward's sifaka in Ranomafana National Park

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Key words: *Propithecus edwardsi*, habitat disturbance, diet, activity, Ranomafana National Park

Abstract

A main cause of lemur decline across Madagascar is habitat degradation. Understanding how lemurs are affected by degradation of forests in Madagascar is vital to aid in conservation efforts. One mechanism may be that habitat loss limits available food sources, leading to dietary shifts and poorer overall health. I followed several groups of lemurs in Ranomafana National Park, Madagascar across a variety of forest types in order to understand how their forest condition affected behaviour and diet. I found that the sifaka spend the most time feeding on seeds in undisturbed forest and young leaves in the disturbed forests. There were few differences in behaviour found between the sites. These results suggest that fewer main food sources, such as large, seed-producing trees, are available in disturbed forests and young leaves are chosen in the absence of these resources. Long-term conservation measures need to focus on including preferred food groups in reforestation plans for lemur consumption. Additionally, the similarity in behaviour may indicate that lemurs in the disturbed areas are recovering and beginning to resemble those in the pristine sites.

Introduction

Of all the threats to lemurs, the most salient are the effects of deforestation and habitat loss (Schwitzer *et al.*, 2011). We know that deforestation limits the abundance of many large-bodied diurnal lemurs (Herrera *et al.*, 2011). However, the mechanisms through which habitat degradation affects lemur populations are still being explored. Deforestation may limit some lemur populations through loss of preferred food species. For example sifakas (*Propithecus* sp.) feed heavily on seeds and fruits (Irwin, 2008; Arrigo-Nelson, 2006) and may be affected by loss of fruit

trees when forests are logged. Large trees that provide fruits and seeds are often the first to be removed with selective logging (Wright *et al.*, 2005). Indeed, past studies of sifaka in Ranomafana National Park (RNP) in southeastern Madagascar have found that habitat disturbance decreases feeding on fruits and seeds and increases the number of leaves consumed (Arrigo-Nelson, 2006). The fruits that usually sustain sifaka in undisturbed forest are absent in the fragmented forest, resulting in a higher reliance on alternative food species such as mistletoe, *Bakerella* spp. (Irwin, 2008). These “fallback foods,” species that are over-emphasized in the diet because of loss of preferred foods, can have consequences on the physiology of some lemurs (Sauter and Cuozzo, 2009). Thus, it is important to examine dietary shifts in lemur populations to predict future health risks. Nearly a decade has passed since the diet and behaviour of sifaka in Ranomafana National Park have been analyzed in relation to habitat disturbance (Arrigo-Nelson, 2006). After almost ten years of protected regeneration, I re-examined the impact of past degradation on *P. edwardsi* diet and behaviour in RNP. The goal of this work was to better understand the current state of sifaka diet and behaviour in RNP, to better understand the timescale of the potential negative effects of degradation and for informing future strategies for their protection in the park and elsewhere.

Methods

Study Site and Species

I tested for the effect of forest disturbance on the behaviour and diet of *Propithecus edwardsi* in the rainforest of Ranomafana National Park (RNP), Madagascar (Fig. 1; 47°18' - 47°37'E, 21°02' - 21°25'S). RNP covers 41,000 ha of evergreen montane forest (Wright and Andriamihaja, 2002), with >330 known tree species (Razafindratsima and Dunham, 2015). This study was conducted in two disturbed secondary forest sites and in one natural primary forest site within RNP. The habitat in Vohiparara is characterized by secondary and moderately logged forest, while Valohoaka is intact, primary forest. Talatakely was heavily logged from 1986-1989, and now consists of heavily disturbed, secondary forest (Wright *et al.*, 2005).

The study focused on seven groups of Milne Edward's Sifaka, *Propithecus edwardsi* (hereafter sifaka), a large, sexually monomorphic, diurnal lemur (Glander *et al.*, 1992). Their diet is chiefly composed of leaves, whole fruits, and seeds, with preference towards fruits and seeds when they are available (Hemingway, 1998; Arrigo-Nelson and Wright, 2004). Data were collected from seven social groups: three in Vohiparara, two in Talatakely (one group sampled twice), and two in Valohoaka.

Data Collection

Three observers, Alicia Lamb from Stony Brook University, Jacob Krauss from Rice University and Noromalala Eliette from the University of Antananarivo, sampled each sifaka group for five consecutive days using focal-animal sampling. Field technicians Laurent (Raleso) Randrianasolo, George René Randrianirina, and Remi Rakotovoao from Centre Val-Bio aided observers in following sifaka and identifying food items consumed. Sites and groups were rotated each week from June until mid-August 2016. During group follows, adult focal individuals (n= 11) were randomly selected with replacement and observed from morning waking until they settled for the night. During each focal sample, the activity (ie. feeding, resting, traveling, grooming) was



Fig. 1: Location of study sites within Ranomafana National Park, Madagascar. Inset shows location of RNP relative to Madagascar.

recorded at three-minute intervals. Feeding observations were recorded *ad libitum* and included species identification, the part of plant consumed and its maturity. A total of 4105 focal samples were collected, amounting to 205 observational hours.

Statistical analysis

Analyses were conducted using RStudio (Version 0.98.1091. RStudio, Inc©, Boston, MA, 2009-2014). Activity and diet of the sifakas in degraded habitat were compared to those in the

primary forest (expected value) site using Chi-square tests. Tests were conducted overall and between specific variables.

Results

The only significant difference observed in sifaka activity between the sites was lower rates of grooming in the heavily disturbed forest than in the other two sites (Tab. 1; $\chi^2= 4.184$, $df= 1$, $P= 0.041$). Diets did vary significantly across sites. Seeds were chosen with greater frequency (44.5% of diet) in the predominately undisturbed forest, while young leaves (40%) were the second most common food item (Fig. 2). Young leaves, fruit, buds and flowers were consumed more often in both disturbed forests than in the undisturbed forest (Fig. 2; Tab. 2). However, there were some differences between the disturbed sites. More fruit was eaten in the Vohiparara forest than in either Talatakely or Valohoaka (Tab. 2, $\chi^2= 42.688$, $df= 1$, $P<0.001$). Furthermore, young leaves composed a higher percentage of sifaka diet in Talatakely (64%) than in Vohiparara (48%) (Tab. 2, $\chi^2= 7.51$, $df= 1$, $P= 0.006$). The complete list of differences in feeding with respect to plant part is described in Fig. 2. Additionally, the most commonly consumed plant was *Bakerella* spp., a hemiparasitic plant in the mistletoe family. This plant composed a significantly higher percentage of the diet in the heavily disturbed forest (24%) and moderately disturbed forest (19%) than in the primary forest (8%) ($\chi^2= 15.934$, $df= 1$, $P<0.001$, $\chi^2= 10.266$, $df= 1$, $P= 0.001$).

Tab. 1: Overall and specific differences in proportion of time spent consuming each food type in different habitats are shown for *Propithecus edwardsi* in Ranomafana National Park, Madagascar. Chi-square tests are used to compare values from the primary forest site to those in the moderately disturbed and heavily disturbed sites.

Food type	Moderately Disturbed			Heavily disturbed		
	χ^2	d.f.	P-value	χ^2	d.f.	P-value
Primary Forest						
Overall	98.93	6	<0.001	60.9646	11	<0.001
Buds	4.17	1	0.041	4.1764	1	0.041
Flowers	5.00	1	0.025	3.4457	1	0.063
Fruit	53.67	1	<0.001	2.239	1	0.135
Mature Leaves	4.00	1	0.046	0.925	1	0.336
Seeds	100.92	1	<0.001	10.866	1	0.001
Unripe Fruit	3.317	1	0.069	2.662	1	0.103
Young leaves	2.816	1	0.093	20.030	1	<0.001

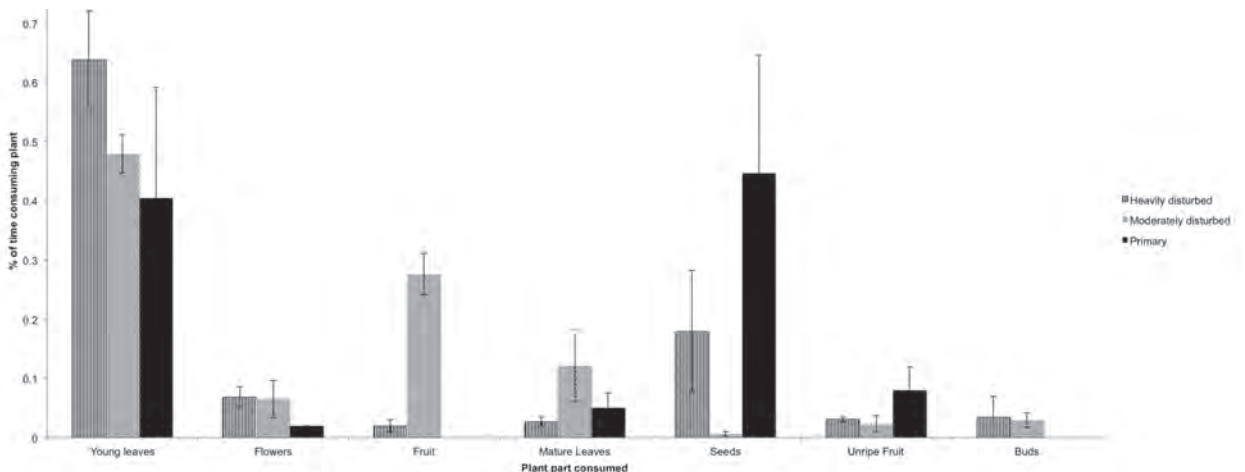


Fig. 2: Average percentage of time *Propithecus edwardsi* spent consuming each plant part in Ranomafana National Park, Madagascar in primary, moderately disturbed, and heavily disturbed forests.

Tab. 2: Overall and specific differences in proportion of time spent engaged in each behaviour are shown for *Propithecus edwardsi* in Ranomafana National Park. Chi-square tests are used to compare values from the primary forest site to those in moderately disturbed and heavily disturbed sites.

Primary Forest	Moderately Disturbed			Heavily disturbed		
	χ^2	d.f.	P-value	χ^2	d.f.	P-value
Overall	6.5	8	0.591	14.5916	8	0.068
Feeding	0.451	1	0.502	0.1523	1	0.696
Grooming	0	1	1.000	4.184	1	0.041
Mutual Grooming	0.379	1	0.538	0	1	1.000
Resting	0.680	1	0.410	0.3173	1	0.573
Self Grooming	0.409	1	0.522	0.689	1	0.407
Traveling	0.044	1	0.833	3.4955	1	0.062
Vigilance-Scan	0.367	1	0.543	2.2024	1	0.138

Discussion

The little variation in behaviour across sites is surprising, given that past studies have found sifaka engaged in less social behaviours and more resting in disturbed forests as compared to their counterparts in undisturbed forests (Arrigo-Nelson, 2006). The finding that there was less grooming in the heavily disturbed site (Tab. 2) may be a sign of stress. Lower time spent engaging in grooming may harm social bonds and lower future reproductive success (Dunbar, 1992). However, the strong overall similarity in activity between sites supports the idea that sifaka in the disturbed forests are slowly returning to “pristine” conditions, with those in the moderately disturbed forest strongly resembling those in the primary forest (Tab. 2).

The differences in diet between the sites of varying levels of disturbance may be reflective of the availability of resources at each site. The sifaka in primary forest consumed mainly seeds as part of their main food source together with young leaves in this study (Fig. 2). Fruit and seeds often come from large-bodied trees, but many of these were selectively logged in the study site forests (Wright *et al.*, 2005). The lower amounts of seeds consumed in the disturbed sites may mean that there are less of these resources available in the disturbed sites.

The much higher proportion of young leaves consumed in the disturbed forests may show preference towards these food resources in the absence of abundant seeds and fruits (Fig. 2). Of the species of young leaves consumed, the most common was mistletoe (*Bakarella* spp.), which was consumed more in the disturbed forests than in the primary forests. Reports from studies of sifaka diet in other parts of Madagascar show mistletoe to be an important fallback resource in disturbed sites, since it has a high reproductive rate and is consumed highly in the dry season (Irwin, 2008). Thus, mistletoe may serve as an important fallback resource for the sifaka in Ranomafana, especially in the heavily disturbed forest. A high reliance on the leaves of mistletoe may impact health negatively over the long term, leading to higher infant mortality (King *et al.*, 2005). For this reason, conservation strategies should focus on reforesting the disturbed areas with large fruiting trees that the sifaka prefer to eat. Over the long-term, the disturbed forests may recover and sifaka diet may resemble that of sifaka in the primary forests, ensuring high reproductive success and species longevity.

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Height and support use of three sympatric nocturnal lemurs in different habitats varying in disturbance on the Masoala Peninsula

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Abstract

Anthropogenic habitat disturbance of various levels is influencing many aspects of the ecology of lemur species. Yet, little is known concerning the effects of human-induced habitat disturbance on the habitat use of nocturnal lemurs. This two-month study (May-June 2014) aims to provide data on sympatric nocturnal lemurs' ecological responses in term of habitat use to different levels of anthropogenic habitat disturbance in Masoala Peninsula, northeastern Madagascar. We used nightly observations on transects to collect data on height on tree, support size and support angle of mouse lemur *Microcebus* sp., the Moore's woolly lemur *Avahi mooreorum* and the Scott's sportive lemur *Lepilemur scottorum* in four forest types (primary lowland, primary littoral, selectively logged and agricultural mosaic forests). We found *Microcebus* sp. at lowest height in the agricultural mosaic forest. *Avahi mooreorum* was higher and frequently used medium and large support in primary lowland forest. *Lepilemur scottorum* showed no difference in height, support size and support angle used between forest types. Our results suggest that anthropogenic habitat disturbance had different effects on the species studied, reflecting their different adaptations to varying habitat characteristics. Given the ongoing forest destruction coupled with illegal extraction of important trees for lemurs like rosewood on Masoala Peninsula, habitat management is a key for conservation of *Avahi mooreorum*, *Lepilemur scottorum* and *Microcebus* sp. inhabiting the peninsula.

Introduction

Human activities in the forests including logging and clear-cutting land lead to the fragmentation and destruction of forest integrity. Anthropogenic disturbance has been suggested to affect many aspects of lemur ecology (Petter *et al.*, 1977; Ganzhorn, 1995; Irwin, 2006; Lehman, 2007; Sawyer *et al.*, 2017). Lemurs' ecological responses to habitat disturbance are highly variable but in general a negative response is observed (Johnson *et al.*, 2003; Lehman *et al.*, 2006b; Irwin *et al.*, 2010; Schwitzer *et al.*, 2011). However, little information is available regarding the effects of human-induced habitat disturbance on the habitat use of lemurs, especially nocturnal lemurs. Understanding the habitat use of nocturnal lemurs living in such human-induced habitat disturbance is critical for their conservation.

Habitat use of primates is often measured via their use of resources; in terms of vegetation this has been measured

as how primates use different vertical levels (i.e. heights) of trees, and how supportive these levels are relative to their body mass (Warren, 1997; Nekaris *et al.*, 2005; Blanchard *et al.*, 2015). Primate species tend to use the lower stratum of the canopy in relation to their diet or predator avoidance (Li, 2007). Support size selection is based on body mass; small primates tend to use smaller supports than larger primates (Fleagle *et al.*, 1981; Harcourt and Nash, 1986; Cunha *et al.*, 2006). Support orientation used by lemurs is associated with their mode of locomotion. High-angled supports are largely used by vertical climber and leaper species, while quadruped species prefer horizontal or oblique supports (Warren, 1997). Selection of habitat to use by primate species may be constrained by the habitat disturbance and fragmentation. Anthropogenic activities in ecosystems such as agriculture, selective logging, or mining create habitat change and therefore lower the range of stratifications and supports available as compared to those in primary habitats (Irwin *et al.*, 2010). In addition, the differentiation in habitat use by sympatric primates, particularly those which are very ecologically similar, takes place to limit interspecies competition and allow coexistence (Case and Gilpin, 1974; Schoener, 1983; Amarasekare, 2003). However, the human activities that reduce habitat availability for primate species narrow their ecological niche and increase the potential for competition (Chesson, 2000a).

Among the seven nocturnal lemur species (*Microcebus* sp., *Cheirogaleus major*, *Allocebus trichotis*, *Phaner furcifer*, *Lepilemur scottorum*, *Avahi mooreorum*, and *Daubentonia madagascariensis*) inhabiting the Masoala National Park, northeastern Madagascar, three were observed in this study. Moore's woolly lemur *Avahi mooreorum* and Scott's sportive lemur *Lepilemur scottorum* are both currently classified as Endangered and locally endemic to Masoala by the IUCN Red List (Andriaholinirina *et al.*, 2014) whereas the IUCN Red List status of the mouse lemur *Microcebus* sp. remains unknown (IUCN, 2017). The aim of this study was to provide data of these three nocturnal lemurs' ecological response to different levels of anthropogenic habitat disturbance. We explored the height on tree, support size and support angle use of *Microcebus* sp., *A. mooreorum* and *L. scottorum* in four forest types of different levels of disturbance in order to understand their ability of using anthropogenic-influenced habitats and the potential for niche separation. Specifically we address the following questions: 1) how do the height on tree, support size and support angle of each species vary between habitat types? 2) Is there a niche overlap between ecologically similar species within each forest type?

Methods

Study site and species

The study was conducted around the village of Ambodiforaha on the southwestern part of the Masoala Peninsula in northeastern Madagascar (S15°42.728', E049°57.839'). Created in 1997, Masoala National Park is the largest protected area of the island consisting of 230,000 ha of rainforest and 10,000 ha of three patches of marine parks/marine zones. The Park ranges in altitude from 0 to 1300 m and contains a variety of habitats including humid forest, littoral forest, flooded forest, marsh and mangrove (Kremen *et al.*, 1999; Schwitzer *et al.*, 2013). Masoala National Park is characterized by four distinct seasons 1) hot-rainy (January-March), 2) transitional cold (April-May), 3) cold rainy (June-August), and 4) hot dry (October-December) (Vasey, 2000). Annual rainfall in the park ranges from 2,200 to 7,000 mm and average yearly temperature ranges from 21 to 24°C (Martinez, 2010).

Ten lemur species inhabit the Park, three diurnal or cathemeral species (*Varecia rubra*, *Hapalemur occidentalis*, and *Eulemur albifrons*) and seven nocturnal species (*Microcebus* sp., *Cheirogaleus major*, *Allocebus trichotis*, *Phaner furcifer*, *Lepilemur scottorum*, *Avahi mooreorum*, and *Daubentonia madagascariensis*). All nocturnal lemur species present at Masoala National Park were included in this study, although only *Avahi mooreorum* (Family Indriidae, ~920 g, folivore, pair-living), *Lepilemur scottorum* (Lepilemuridae, ~880 g, folivore, solitary living), and *Microcebus* sp. (Cheirogaleidae, average body weight between 39.5 and 47.9 g, omnivore, solitary forager) (Mittermeier et al., 2010) were observed.

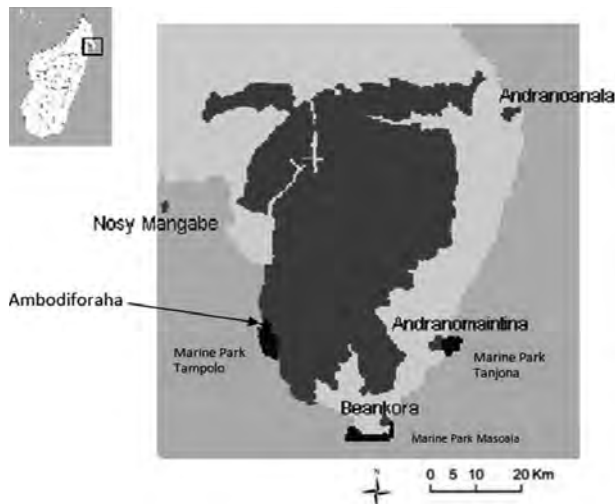


Fig. 1: Location of Ambodiforaha on the Masoala Peninsula.

Data collection

Data on habitat use of nocturnal lemur species were collected between the transitional cold and the cold rainy seasons (May and June 2014). We undertook lemur surveys along transect lines established in different types of habitat in the study site. Using pre-existing trails to minimize disturbance, we marked 11 transects of 750 m length flagged every 25 m within four study areas (3 transects in an area of primary lowland forest, 2 transects in an area of primary littoral forest, 3 transects in an area of selectively logged forest for construction materials by local people, and 3 transects in an area of agricultural mosaic forest used by local people) that were categorised based on their vegetation structure and human use. The vegetation characteristics of the study areas were based on the findings of Sawyer et al., 2017 who conducted research in the same site at the same time in order to assess the degree of disturbance of each habitat. Sawyer et al., 2017 found that agricultural mosaic forest is characterized by short trees, lower bole height, opened canopy and low tree density. Furthermore, Sawyer et al., 2017 found a high frequency of plant species indicators of disturbed habitats such as *Harongana madagascariensis*, *Syzygium* sp., *Symphonia* sp. (Ganzhorn et al., 1985; Lowry et al., 1997; Faulkner and Lehman, 2006) in the selectively logged forest and the agricultural mosaic forest. In contrast, the authors found that the primary lowland and primary littoral forests exhibited tall tree and higher bole height, high canopy cover, higher tree density which are structural characteristics observed in areas of lower disturbance (Hitimana et al.,

2004; Balko and Underwood, 2005; Malone et al., 2013). The primary lowland forest presented the tallest trees, the highest bole height and highest canopy cover among the four forest types (Sawyer et al., 2017).

We conducted daily lemur surveys either between 1800-2400 hours or 2400-0600 hours with a speed of 0.25-0.5 km per hour (Chapman et al., 1988; Norscia, 2008; Nekaris et al., 2014). We repeated the visit of each transect line four times over the study period (Rovero et al., 2006) resulting 44 nocturnal surveys giving a total survey effort of 33 km. We checked both sides of the transect line. One animal detected represented one sighting. Each time a lemur was detected in each visit of the transect, whether the animal was seen alone or in group, we recorded the following data at its first position on a tree (Nekaris, 2005): the date and time, study area and transect number, species, estimated vertical height up the tree measured from the ground, size and angle of the support used. Support can be trunk or branch of the tree. Support size and angle measurements were categorized as follows (Warren, 1997; Blanchard et al., 2015). Support size was grouped into four categories based on the diameter of the trunk or branch: small (S) ≤ 5 cm, medium (M) between 5 and 10 cm, large (L) between 10 and 15 cm, and extra-large (XL) > 15 cm. As for the angle, four categories were set according to the orientation compared to the horizontal plan: horizontal (H) $\leq 10^\circ$, oblique (O) between 10 and 45° , angled (A) between 45 and 80° , and vertical (V) between 80 and 90° .

Statistical analysis

After testing for normality using the Kolmogorov-Smirnov test, data on height on tree of the species were normally distributed and were compared among forest types using Analyses of Variance (ANOVA). Fisher's Least Significant Difference (LSD) post-hoc tests were used in the pairwise comparison of forest types that contributed to the significant result. Pearson Chi-Square tests were applied in comparing the support size and support angle used by the lemur species among forest types. The significance level α chosen for all tests was 0.05. Statistical analyses were run in R Studio.

Results

A total of 70 sightings of *Microcebus* sp., 51 sightings of *Avahi mooreorum*, 20 sightings of *Lepilemur scottorum* were observed over the study period. We found each species in the four forest types except for *L. scottorum*; we did not observe any individual of this species in the agricultural mosaic forest.

Height of the lemur species

Taking into account the effect of forest types in the height on tree of each lemur species (Tab. 1), the mean height on tree of *Microcebus* sp. was significantly different between

Tab. 1: Height on tree of the three lemurs in each forest type.

Species	Primary lowland forest	Primary littoral forest	Selectively logged forest	Agricultural mosaic forest	Average height
<i>Microcebus</i> sp. (n=70)	6.84 \pm 6.02 ^a	5.07 \pm 2.87	6.69 \pm 4.39 ^b	2.94 \pm 2.10 ^{ab}	5.46 \pm 4.61
<i>Avahi mooreorum</i> (n=51)	21.54 \pm 9.45 ^{c,d}	11.88 \pm 3.76 ^c	11.60 \pm 4.56 ^d	13.00 \pm 4.24	16.76 \pm 8.78
<i>Lepilemur scottorum</i> (n=20)	15.45 \pm 7.24	10.20 \pm 4.76	10.50 \pm 7.55	N/A	13.15 \pm 6.95

Values are mean \pm standard deviation expressed in meter (m). Cells with superscript letters in common differed significantly in LSD post-hoc comparisons from ANOVA ($P \leq 0.05$). n: total number of sightings. N/A: data are not available.

forest types (ANOVA, $F=3.129$, $df=3$, $P=0.031$). Post-hoc test revealed that the mean height on tree of *Microcebus* sp. was lower in the agricultural mosaic forest than in the primary lowland forest ($P=0.007$), and the selectively logged forest ($P=0.016$). The mean height on tree of *Avahi mooreorum* was significantly different between forest types (ANOVA, $F=7.380$, $df=3$, $P<0.001$). This species was higher in the primary lowland forest than in the primary littoral forest ($P=0.003$), and the selectively logged forest ($P<0.001$). Forest types appeared to not have an effect on the mean height on tree of *Lepilemur scottorum*. There were no significant differences of its mean height between forest types (ANOVA, $F=1.297$, $df=2$, $P=0.299$).

Support size used by three lemur species

Concerning the effect of forest types in the support size used by each lemur species (Tab. 2), there was no change in the support size used by *Microcebus* sp. in each forest type. *Microcebus* sp. mostly used small support with high proportion more than 60.00% in each forest type (primary lowland forest: $\chi^2=8.000$, $df=2$, $P=0.018$; primary littoral forest: $\chi^2=13.000$, $df=2$, $P=0.002$; selectively logged forest: $\chi^2=9.308$, $df=1$, $P=0.002$; and agricultural mosaic forest: $\chi^2=10.889$, $df=1$, $P=0.001$). Support size used by *Avahi mooreorum* varied among forest types. This species predominantly used medium and large supports in the primary lowland forest ($\chi^2=10.615$, $df=3$, $P=0.014$). Whereas *A. mooreorum* did not prefer a specific size of support in the primary littoral forest ($\chi^2=1.750$, $df=2$, $P=0.417$), in the selectively logged forest ($\chi^2=6.600$, $df=3$, $P=0.086$), and in the agricultural mosaic forest ($\chi^2=0.000$, $df=1$, $P=1.000$). *Lepilemur scottorum* did not prefer a specific size of support in each forest type. All support sizes were similarly used by this species (primary lowland forest: $\chi^2=3.182$, $df=3$, $P=0.364$; primary littoral forest: $\chi^2=0.200$, $df=1$, $P=0.655$; selectively logged forest $\chi^2=1.000$, $df=1$, $P=0.317$).

Tab.2: Percentage of support size used by each nocturnal lemur among forest types.

Forest type	<i>Microcebus</i> sp. (n=70)				<i>Avahi mooreorum</i> (n=51)				<i>Lepilemur scottorum</i> (n=20)			
	S	M	L	XL	S	M	L	XL	S	M	L	XL
Low	60.00	20.00	20.00	0.00	3.85	42.31	38.46	15.38	9.09	45.46	27.27	18.18
Litt	78.57	14.29	0.00	7.14	0.00	37.50	50.00	12.50	0.00	40.00	60.00	0.00
SL	92.31	7.69	0.00	0.00	13.33	53.34	13.33	20.00	0.00	75.00	25.00	0.00
Agri	88.89	11.11	0.00	0.00	0.00	0.00	50.00	50.00	N/A	N/A	N/A	N/A
Overall	S 77.14% (n=54 out of 70)				M 43.14% (n=22 out of 51); L 33.33% (n=17 out of 51)				M 50.00% (n=10 out of 20); L 35.00% (n=7 out of 20)			

Low: primary lowland forest, Litt: primary littoral forest, SL: selectively logged forest, Agri: agricultural mosaic forest. S: small, M: medium, L: large, XL: extra-large. n: total number of sightings. N/A: data are not available.

Tab. 3: Percentage of angle of the support used by each nocturnal lemur among forest types.

Forest type	<i>Microcebus</i> sp. (n=70)				<i>Avahi mooreorum</i> (n=51)				<i>Lepilemur scottorum</i> (n=20)			
	H	O	A	V	H	O	A	V	H	O	A	V
Low	28.00	12.00	32.00	28.00	11.54	0.00	42.31	46.15	9.09	9.09	45.46	36.36
Litt	0.00	14.29	21.42	64.29	0.00	37.50	25.00	37.50	0.00	0.00	40.00	60.00
SL	7.69	15.38	30.78	46.15	13.34	0.00	53.33	33.33	0.00	0.00	25.00	75.00
Agri	5.56	11.11	44.44	38.89	0.00	0.00	50.00	50.00	N/A	N/A	N/A	N/A
Overall	V 41.42% (n=29 out of 70); A 32.86% (n=23 out of 70)				V 41.18% (n=21 out of 51); A 43.14% (n=22 out of 51)				V 50.00% (n=10 out of 20); A 40.00% (n=8 out of 20)			

Low: primary lowland forest, Litt: primary littoral forest, SL: selectively logged forest, Agri: agricultural mosaic forest. H: horizontal, O: oblique, A: angled, V: vertical. n: total number of sightings. N/A: data are not available.

Angle of support used by lemur species

Concerning the effect of forest types in the support angle used by each lemur species (Tab. 3), there was a variation in the use of orientation of support by *Microcebus* sp. in each forest type. In the primary littoral forest, *Microcebus* sp. used vertical support ($\chi^2=6.143$, $df=2$, $P=0.046$), while vertical and angled were mainly used in the agricultural forest ($\chi^2=8.222$, $df=3$, $P=0.042$). In contrast, *Microcebus* sp. did not prefer an orientation of support in the primary lowland forest ($\chi^2=2.360$, $df=3$, $P=0.501$) and in the selectively logged forest ($\chi^2=4.538$, $df=3$, $P=0.209$). Forest types did not influence the angle of support used by *Avahi mooreorum*. This species did not prefer an orientation of support in each of the forest type (primary lowland forest: $\chi^2=5.615$, $df=2$, $P=0.060$; primary littoral forest: $\chi^2=0.250$, $df=2$, $P=0.882$; selectively logged forest: $\chi^2=3.600$, $df=2$, $P=0.165$; agricultural mosaic forest: $\chi^2=0.000$, $df=1$, $P=1$). Like *Avahi mooreorum*, forest types did not influence the angle of the support used by *Lepilemur scottorum*. Statistically, this species did not prefer an orientation of support in each of the forest type (primary lowland forest: $\chi^2=4.636$, $df=3$, $P=0.200$; primary littoral forest: $\chi^2=0.200$, $df=1$, $P=0.655$; selectively logged forest: $\chi^2=1.000$, $df=1$, $P=0.317$).

Discussion

In this study, we aimed to provide data on the three sympatric nocturnal lemurs' ecological responses in term of habitat use to different levels of anthropogenic habitat disturbance in Masoala National Park. We found that habitat disturbance had different effects on the three lemurs. *Microcebus* sp. was at lowest height and used vertical and angled supports in the agricultural mosaic forest. *Avahi mooreorum* was found higher up the vegetation, and preferred medium and large supports in primary lowland forest. *Lepilemur scottorum* showed no difference in height, support size and support angle used between forest types.

Microcebus sp. in Masoala was at an average level of around 5 m of height. This is a little higher than the height on tree of *Microcebus* in Mandena around 3 m (Lahann, 2008) but *Microcebus* was still in lower stratum. This might be due to its omnivorous mainly insectivorous diet. Insects are particularly abundant in the lower stratum of forest. Disturbed forests are opened areas but characterized by the dense understory shrubs and dense forest floor. Such habitats tend to contain invertebrates including insects in abundance and which are important resources for insectivorous primates like *Microcebus* (Heck Jr and Wetstone, 1977; Ganzhorn, 1995; Atsalis, 2007). In our study, *Microcebus* sp. was found in lower stratum and at lowest height in Agricultural forest likely for insects foraging. Support size frequently used by *Avahi mooreorum* was medium and large. It is argued that support used by primates is in association with their body mass (Fleagle et al., 1981; Cunha et al., 2006). *Avahi* is a medium-sized lemur among the extant lemur species in Madagascar with 900g average weight so it used medium support size. However, we found that there was no difference

in the proportion of use of all support size in habitat with human influence. In fact *Avahi occidentalis* in western of Madagascar had a preference for a particular support but did not randomly use all available supports (Warren, 1997). In our study, the choice of support of *Avahi mooreorum* in selectively logged and agricultural mosaic forests might be restricted compared to the primary lowland forest that contains a large diversity of supports. These facts suggest that *Avahi* is likely to choose and use the appropriate support size for its weight when such support choice is not limited within a habitat.

Lepilemur scottorum used frequently vertical and angled supports. This is in accordance with the support orientation used by *Lepilemur edwardsi* in the western of Madagascar which frequently used vertical supports (Blanchard et al., 2015). This can be explained by its resting posture and locomotor mode as *Lepilemur* is a vertical clinging and leaping (VCL) lemur (Napier and Napier, 1967). Although no difference in the proportion of orientation of support used by *Lepilemur scottorum* was found in all habitat types, this might be due to its ecological flexibility since ecologically flexible lemur species seem to be less affected by habitat alteration as they do not rely on specific habitat characteristics (Ganzhorn and Schmid, 1998; Andrianasolo et al., 2006; Schwitzer et al., 2007b). For example, *Lepilemur* can move between trees of greater distance in a less intensive logged forest. But due to energetic constraints, this tolerance has a limit in very disturbed forests which have further increased tree distances (Ganzhorn, 1993). Furthermore, during such travel like other VCL primates such as *Avahi* and *Tarsius* different orientations of support could be used by *Lepilemur scottorum* depending on the length of leap (Warren, 1997; Crompton et al., 2010).

The habitat use of *Microcebus* sp., *Avahi mooreorum* and *Lepilemur scottorum* indicates some degree of niche overlap. We found that there was a difference in the general mean height and the frequently used support size for the three lemurs. Findings elsewhere for ecologically similar or closely related sympatric lemurs showed a difference in their habitat use (Warren et al., 1997; Lahann, 2008). Such difference could be the reason of facilitating sympatric species coexistence. Habitat type may however influence habitat use of sympatric species particularly those ecologically similar. *Avahi* sp. and *Lepilemur* sp. are ecologically similar lemurs but *Avahi* sp. are canopy dwelling species compared to *Lepilemur* sp. (Warren and Crompton, 1997). This difference in height use is obvious in primary lowland forest that presented taller trees since we found *Avahi mooreorum* in the highest level. In contrast, in disturbed forest there is a potential for niche competition between *Avahi mooreorum* and *Lepilemur scottorum* as these species require similar needs but habitats present lower range of habitat supports.

The results on the habitat use of *Avahi mooreorum*, *Lepilemur scottorum* and *Microcebus* sp. presented here provide data of their respective response to anthropogenic habitat disturbance. Ongoing destruction of forests resulting in decrease of forest area particularly rainforests is one of the threats for lemur populations. In Masoala National Park, logging including illegal extraction of rosewood *Dalbergia* sp. may have a negative impact on the ecology of lemur species which frequent the higher stratum. Those trees may be important for lemurs like *Lepilemur* sp. and *Avahi* sp. for their locomotion. Also, in our study, we collected a small sample size for *Lepilemur scottorum* with no individual detected in agricultural mosaic forest. It would suggest that this species is not adapted for heavily disturbed forests or it could be

the result of the outcompetition of *Avahi mooreorum* over this species. Thus, consideration of habitat management as well as long term lemur monitoring would provide further details in implementing conservation strategies of *Avahi mooreorum*, *Lepilemur scottorum* and *Microcebus* sp.

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Estimation de la taille des populations d'*Eulemur macaco* (Linnaeus, 1766) dans la nouvelle aire protégée de Galoko-Kalobinono, Nord-Ouest de Madagascar

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Mots clés : *Eulemur macaco*, population, abondance, densité, structure de la végétation, Galoko-Kalobinono, région de Sambirano, Madagascar

Résumé

La région Sambirano du Nord-Ouest de Madagascar est connue comme refuge du lémurien *Eulemur macaco*. Une nouvelle aire protégée nommée Galoko-Kalobinono a été créée et reste encore relativement peu étudiée, seulement un inventaire de référence a été effectué. Dans le but d'estimer la taille de la population de *Eulemur macaco* dans le site, nous avons utilisé la méthode «line transect distance-sampling». Nos résultats ont montré une densité de 386 individus/km² et une abondance de 45313 individus pour l'ensemble de la Galoko-Kalobinono. Afin de compléter les lacunes, il s'avère nécessaire de mener d'autres investigations dans les autres secteurs de l'aire protégée. Il est aussi à suggérer d'approfondir l'étude sur la dynamique de la population dans le site.

Key words: *Eulemur macaco*, population, abondance, densité, végétation structure, Galoko-Kalobinono, Sambirano region, Madagascar.

Abstract

The Sambirano region of the northwest Madagascar is known as refuge of the lemur *Eulemur macaco*. A new protected area named Galoko-Kalobinono has been created yet is relatively under studied; only a reference assessment has been realised. To count the size of the *Eulemur macaco* population in the site, we used the line-transect distance-sampling method. Our results showed a density of 386 individuals/km² and an abundance of 45,313 individuals for the whole Galoko-Kalobinono. In order to fill the gap from this study, we recommend investigating other parts of the protected area. We also suggest further studies such the population dynamics of Black lemurs.

Introduction

Dans le domaine de la conservation, le terme population est l'un des plus prononcés. La population est l'unité biologique sur laquelle la plupart des questions de

conservation et de gestion sont focalisées (Caughley, 1994). Si une espèce est reconnue en danger, l'objectif consiste souvent à maintenir ou à augmenter la taille de la population et la distribution de la population sur le long terme est à procéder. Les intérêts portés sur l'étude des populations sont donc importants dans le domaine de la conservation de la biologie. Dans une population, les êtres vivants répondent à la modification de leurs milieux naturels par leur propre manière. Parmi la biodiversité, les lémuriens font partis de l'objet de nombreuses recherches depuis plusieurs décennies. Pour poursuivre les recherches dans les zones méconnues, une contribution sur l'étude de la population de lémurs noirs (*Eulemur macaco*) a été entreprise en 2016 dont le but d'estimer la taille de la population de l'espèce.

Site d'étude

L'étude a été menée dans la chaîne Galoko-Kalobinono, partie Nord-Ouest de Madagascar qui est situé dans l'ex-province Antsiranana, région Diana. La chaîne Galoko-Kalobinono est partagée entre deux districts: Ambilobe et Ambanja. Elle se situe à 13°35'19,2" de latitude Sud et 48°42'33,9" de longitude Est (Fig. 1). C'est la seule région à basse altitude de la côte Ouest de Madagascar présentant un climat tropical humide favorable au développement d'une forêt dense ombrophile (Gautier *et al.*, 1996). D'une superficie de 11739 ha, Galoko-Kalobinono est le plus gros bloc de la relicte forestière du domaine de sambirano où la végétation est généralement composée de formations dégradées, de forêts humides et de forêts sèches occidentales (Moat and Smith, 2007).

Methodologie

La méthode de «line transect distance-sampling» a été utilisée pour l'évaluation de la densité de la population (Buckland *et al.*, 2004; Meyler *et al.*, 2012; Rantoharijaona *et al.*, 2014). Dix transects de 1 km de longueur ont été effectués. Les transects sont espacés d'au moins 0,5 km et ont été parcourus entre 8h30 à 12h et 14h à 17h pendant trois jours.

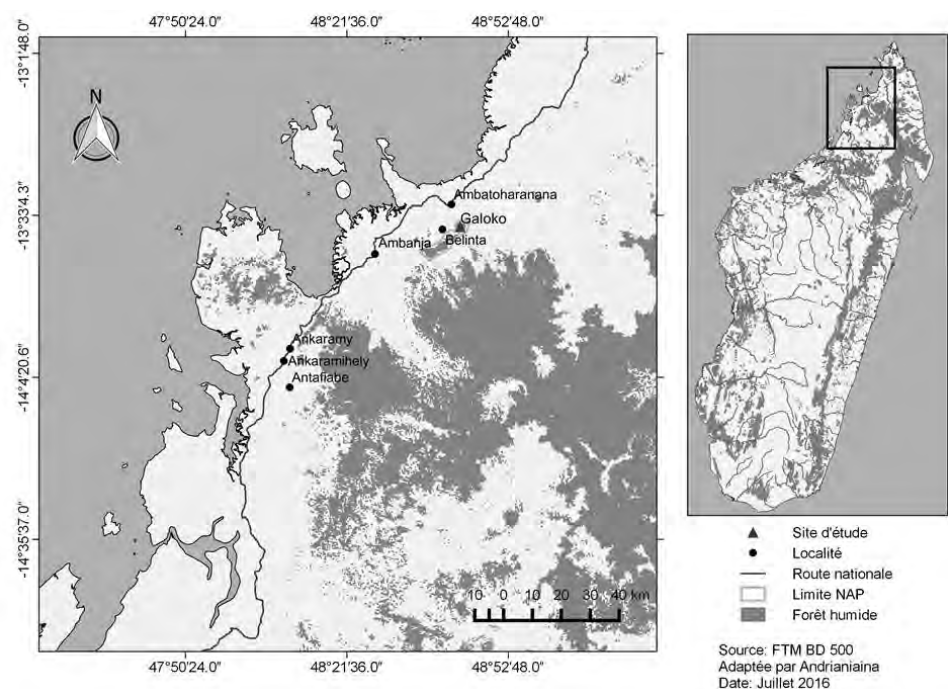


Fig. 1: Carte montrant la localisation du site d'étude Galoko-Kalobinono, Nord-Ouest de Madagascar.

Lors d'une rencontre avec un ou plusieurs individus, l'heure d'observation, le nombre d'individus rencontrés, la distance perpendiculaire de l'individu à l'observateur ou la distance moyenne pour les groupes, la hauteur de l'animal par rapport au sol, le sexe, le nom d'identification du transect et les coordonnées géographiques du milieu étaient notés. La densité de la population a été calculée par la formule de Whitesides *et al.* (1988):

$$D = \frac{N}{2WL}$$

D = Densité relative; N = Nombre total des individus rencontrés; L = Longueur totale de transect; W = moyenne des distances perpendiculaires de l'animal à l'observateur
L'abondance relative (Ar) des individus a été obtenue par la formule de Hattour *et al.* (2004): $Ar = D \times S$; Ar = Abondance relative, D = Densité relative; S = Superficie du milieu

Résultats et discussion

L'étude a pu recenser 86 *Eulemur macaco* répartis dans 14 groupes, soit une densité de 386 individus/km². L'abondance des individus a été calculé à 19 007 pour le partie nord du site d'étude et 45 313 individus dans l'ensemble du complexe Galoko-Kalobinono. Ainsi, la densité d'*Eulemur macaco* est assez élevée.

Cette situation peut être relevée en présence de conditions favorables pour l'espèce, comme la qualité de la couverture végétale, confirmée par les études de Donati *et al.* (2012) et Ossi et Kamilar (2006). Ceci pourrait également être due à l'abondance et la qualité de la nourriture (Lehman, 2006). Dans son ensemble, Galoko-Kalobinono présente encore des conditions favorables à l'espèce.

La population d'*Eulemur macaco* dans la forêt Galoko-Kalobinono est dense (386 individus/km²) et est de ce fait comparable aux plus fortes densités de lémurs noirs estimées dans la péninsule de Nosy Faly et dans la Réserve Spéciale de Manongarivo qui varient de 48,35 à 398,93 individus/km² (Rakotoarinivo *et al.*, 2011).

Irwin (2006) et Johnson et Overdorff (1999) ont confirmé que les modifications de l'habitat affectent la densité de plusieurs espèces de lémuriens. Cela dit, en général, si les lémuriens ne sont pas chassés, ils peuvent s'adapter à la modification du milieu, ceci n'affectant pas leurs abondances (Mittermeier *et al.*, 1994). Durant notre collecte de données, aucun piège à lémuriens n'a été repéré. Selon les responsables du site venant du gestionnaire de l'aire protégée ou Missouri Botanical Garden (MBG), la coupe de bois illicite reste la menace la plus importante dans le milieu, mais la chasse serait devenue moins prononcée. La stratégie de conservation adoptée dans le site par ce gestionnaire traite déjà différentes alternatives, telles que l'existence des activités régénératrices de revenus, pour aider la population locale améliorer leur condition de vie (MBG, 2015). Tout ceci peut ainsi contribuer à l'explication de cette forte densité de lémurs noirs à Galoko-Kalobinono.

Conclusion

La densité élevée d'*Eulemur macaco*, qui est de 386 individus/km² peut être expliquée par les conditions environnementales favorable pour l'espèce et par la quasi-absence de chasse dans le site. Ces informations pourraient donc servir d'outils d'aide à la conception d'une stratégie adéquate pour la gestion et la préservation de la biodiversité du complexe. En effet, le renforcement de la sensibilisation et de la responsabilisation des villageois par des éducations et des formations environnementales est primordial pour la réduction des menaces anthropiques dans la forêt. Le rajout

des activités et des infrastructures qui sont utiles à la vie quotidienne constitueront aussi des moyens qui pourraient réduire les pressions anthropiques dans la forêt. Un suivi de la population suivant les saisons serait intéressant pour modéliser le taux d'accroissement des populations et établir la tendance de la population de lémurs noirs à Galoko-Kalobinono. Ceci permettrait un suivi sur le long terme de l'espèce en connaissant les valeurs des coefficients de changement: les taux de natalité et de mortalité, les taux d'immigration et d'émigration.

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Terrestrialité et domaine vital chez *Prolemur simus* d'Ambalafary

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Mots clés: *Prolemur simus*; terrestrialité, domaine vital, Ambalafary, Madagascar

Résumé

Pour les espèces de primates notamment les lémuriens arboricoles, rare voire inexistantes sont les activités au sol. Pour *Prolemur simus*, des données de comportement ont été enregistrées en supposant que pour toutes ses activités *P. simus* habitant le site d'Ambalafary utilise les mêmes niveaux de strates forestières. Nous avons suivi l'espèce pendant une année entière dans ce site en utilisant la méthode de «focal sampling» et «scan sampling» toutes les 5min. Quant à l'étude du domaine vital, le logiciel Quantum GIS a été utilisé. Il en résulte que pour chacun de ses activités, *P. simus* adopte des niveaux forestiers différents et statistiquement la différence est très significative quel que soient les activités considérées ($\chi^2=16.17$; ddl=2; $P<0.005$). Selon les saisons, la surface du domaine vital occupée par l'espèce est différente (saison chaude et humide, surface=9.206ha; saison froide et sèche, surface=6.033ha). Quant à la terrestrialité, elle s'observe surtout à partir du mois de décembre au mois de mars où l'espèce passe jusqu'à 28.63% de son temps au sol. La conservation de *P. simus* et la sensibilisation de la population locale sont très recommandées vu le type de comportement adopté par l'espèce où probablement d'éventuels prédateurs terrestres pourraient rôder à l'intérieur de son habitat provoquant des dangers tant pour l'espèce elle-même que la communauté locale qui gère le site pouvant ainsi annihiler les efforts de conservation déjà entamés.

Introduction

De nombreux facteurs influencent l'arboricolisme ou la terrestrialité chez les espèces de primates: la prédation (Altmann, 1974a; Cheney et Wrangham, 1987; Hart, 2007; Isbell, 1994; Janson et Goldsmith, 1995), la distribution et la qualité des ressources (Cant, 1992; Campbell et al., 2005; Janson, 1990; Jolly, 1985; Xing et al., 2009). Par exemple les babouins chacma (*Papio ursinus*), fréquentent le sol même si les nourritures y sont pauvres en qualité plutôt que les arbres où les risques de prédation sont plus élevés (Cowlshaw, 1997). Parmi les primates strepsirrhini-

niens de Madagascar, le *Lemur catta* est l'espèce de lémurien qui fréquente le plus souvent le sol à un taux d'environ 30 à 40% (Jolly, 1966; Sussman, 1974; Sauther et al., 1999; Cameroun et Gould, 2013). En ce qui concerne les lémuriens de bambous, certaines espèces comme l'*Haplemur meridionalis* passe environ 70% de leurs temps au sol à la recherche de lianes de bambous et ceci surtout lors de la saison froide (Eppley et Donati, 2009; Eppley et al., 2011). Pour *P. simus* qui est également un lémurien de bambou et qui constitue l'objet de notre étude, parfois elle est strictement arboricole et parfois elle passe la plupart de leur temps au sol (pers. obs.) ce qui nous a conduit à poser comme hypothèse que la fréquentation du sol et des arbres se fait dans la même période pour *P. simus* habitant le site d'Ambalafary qui est un site récemment découvert par The Aspinnall Foundation (Ravaloharimanitra et al., 2011) et dans lequel aucune étude concernant *P. simus* n'a été encore entamée. Quant au domaine vital, il se définit comme l'espace occupé et défendu par un individu ou un groupe contre d'éventuels envahisseurs afin de maintenir exclusivement l'accès aux ressources pour pouvoir s'alimenter et se reproduire convenablement (Burt, 1943).

Pour *P. simus*, son domaine vital est conditionné principalement par sa distribution en bambous à des altitudes plus ou moins élevées (King et al., 2013). De plus, environ 90 à 96% de l'alimentation de *P. simus* est composée de parties de bambous répartis en jeunes pousses, jeunes feuilles, feuilles matures et tige aussi bien de l'espèce *Cathariostachys madagascariensis* (Tan, 1999) que des espèces *Bambusa vulgaris* et *Valiha diffusa* (Mihaminekena et al., 2012; Randriahaingo et al., 2014). Seulement peu d'études ont pu mettre en évidence l'utilisation spatiale de *P. simus* lors de l'exploitation de ses ressources alimentaires (Tan, 1999; Tan, 2000). Ainsi une étude préliminaire concernant le domaine vital de *P. simus* selon les saisons, l'utilisation de l'espace verticale et la terrestrialité seront présentés afin de mieux comprendre d'autres aspects de la vie de ce grand haplemur pour pouvoir envisager une conservation à long terme de l'espèce.

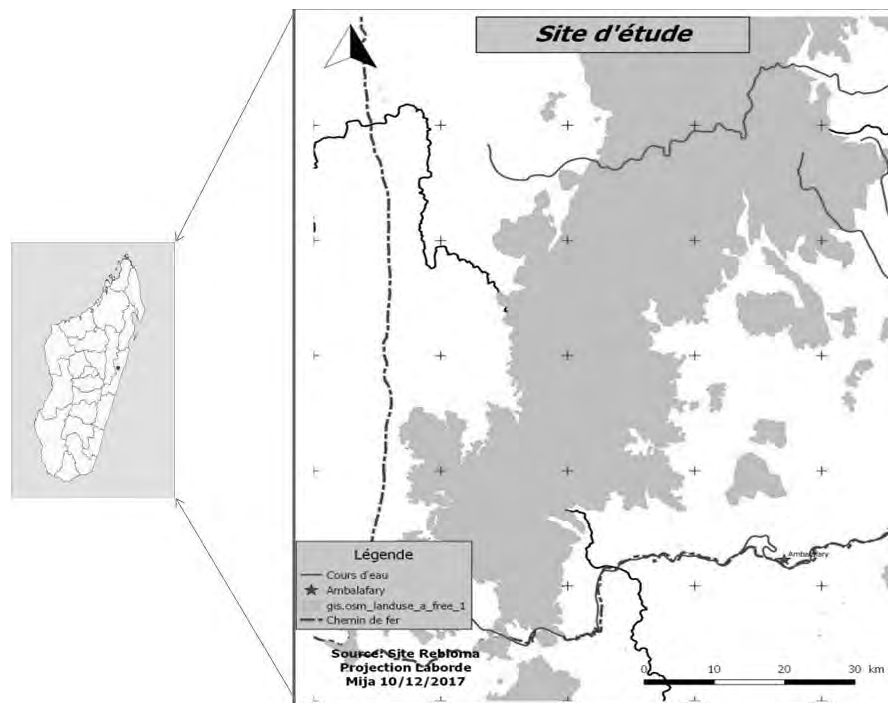


Fig. 1: Carte montrant la localisation du site d'étude.

Méthodologie

Description du site

Le site d'Ambalafary est un site isolé de la Commune Rurale de Fanasana gare, district de Brickaville (Mihaminekena et al., 2012). Il a comme coordonnées géographiques (S18, 8008°, E48, 8092°) et se trouve entre le chef lieu de la Commune Rurale de Fanasana gare à l'ouest et le fokontany de Mangabe à l'est sur la rive nord du fleuve Ivohitra. Le site est géré par le COBA Ainga Vao II créé exprès par la population locale lorsque la présence de *P. simus* a été confirmée dans la région (Ravaloharimanitraet King, 2012; Ravaloharimanitraet al., 2013). C'est un site dominé par le bambou des espèces *Bambusa vulgaris* et *Valiha diffusa*.

Méthode utilisée concernant le domaine vital

Pour délimiter le domaine vital de *P. simus* à Ambalafary nous avons utilisé les deux types de saison, la saison chaude et humide (novembre à avril) et la saison froide et sèche (mai à octobre). Concernant le suivi du groupe, nous avons enregistré les coordonnées du groupe lorsqu'il se déplace d'une distance ou égale à 10m et lorsqu'il mange. Le logiciel Quantum GIS 2.8 a été utilisé. En plus de cela le centre qui sépare la distance des différentes zones des domaines vitaux ont été mesurées avec le même outil GPS et après avoir reliées les points, on les rapporte directement dans le logiciel Quantum GIS 2.8 pour le traitement.

Méthode concernant l'utilisation verticale et la terrestriabilité

Nous avons employé la méthode du «focal animal sampling» d'Altmann (1974b) pour enregistrer les activités du focal animal toutes les 5 min et par la même occasion la hauteur fréquentée par l'animal pour ses activités et lorsqu'il s'alimente. Néanmoins comme l'espèce est en partie arboricole, une unité de mesure a été prise en compte pour estimer la hauteur des animaux sur les arbres par rapport au sol ainsi elle a été :

«Unité de mesure»= taille moyenne des adultes (sans la queue)*2=1m

Quant à la terrestriabilité, elle se définit comme le déplacement d'un individu ou d'un groupe au sol pour se reposer ou pour chercher de la nourriture. Les calculs statistiques, ont été fait à l'aide du logiciel statistique SPSS et comme le traitement des données est seulement pour une année entière, l'effectif est donc réduit à 12 mois (n=12) d'où l'utilisation de tests non paramétriques.

Temps d'observation

L'étude a été faite durant l'année 2013. Le tableau 1 exprime le total d'heure d'observation lors de l'utilisation verticale de l'espace et la terrestriabilité observée chez *P. simus* dans le site d'Ambalafary. Lors de cette étude le groupe de *P. simus* d'Ambalafary l'étude l'est composée d'un groupe de 24 individus, composé de 3 mâles, 11 femelles, 6 juvéniles et 4 bébés.

Tab. 1: Tableau montrant la totale d'heure d'observation par mois.

Mois	Heure d'observation	Mois	Heure d'observation
Janvier	40	Juillet	64
Février	48	Août	56
Mars	40	Septembre	64
Avril	32	Octobre	56
Mai	40	Novembre	40
Juin	64	Décembre	40

Résultats

Utilisation de l'espace verticale

La Fig. 2 exprime la hauteur moyenne annuelle utilisée par *P. simus* pour ses «trois principales activités: repos, alimentation, déplacement». Notons que la différence de la hauteur est hautement significative pour ses activités ($\chi^2=16.17$; $ddl=2$; $P<0.05$).

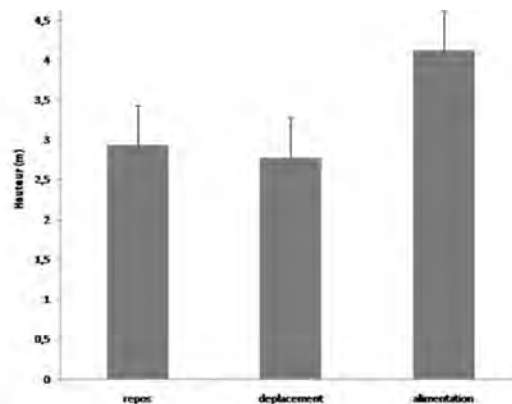


Fig. 2: Hauteur annuelle des principales activités de *Prolemur simus*.

Lors de l'activité repos, la hauteur baisse surtout pendant le mois de mars mais commence à s'élever à partir du mois de juillet à moyenne novembre (Fig. 3). La hauteur moyenne annuelle pour le repos est de $4.74 \pm 1.60m$.

Concernant l'alimentation, la hauteur est en général plus élevée lors de la saison sèche $5.38 \pm 1.99m$ par rapport à la saison humide $2.38 \pm 1.56m$ et cette différence de la hauteur est significative ($Z=-2.023$; $N=12$; $P<0.05$). Néanmoins la hauteur moyenne annuelle utilisée par *P. simus* pour s'alimenter est de $4.13 \pm 2.33m$. Pour plus de détails cf. Fig. 4.

Quant au déplacement la hauteur annuelle est de $2.73 \pm 1.50m$. Ainsi c'est pendant l'activité de déplacement que *P. simus* choisit un niveau plus faible par rapport aux deux autres activités de repos et d'alimentation (voir Fig. 5 pour plus de détails).

Terrestriabilité

En dehors de l'alimentation (surtout de jeunes pousses de bambous), *P. simus* pratique d'autres activités au sol ainsi la Fig. 6 montre le pourcentage de terrestriabilité observé chez *P. simus*. Cette espèce est surtout terrestre à partir du mois de décembre à mars, c'est-à-dire qu'à cette période de l'année, l'espèce passe entre 15 et 30% de son temps au sol. Par contre elle choisit une hauteur plus élevée des supports (arbres ou bambous) à partir du mois d'avril (0%) jusqu'au mois de novembre (0%) donc durant ces mois, la terrestriabilité est nulle chez l'espèce: c'est-à-dire qu'elle ne descend pas au sol.

Domaine vital

La surface vitale pour cette espèce varie selon les saisons. Le Tab. 2 résume la surface occupée par le groupe de *P. simus* selon les saisons. Elle a été déterminée en utilisant un logiciel SIG Quantum GIS 2.8.

Tab. 2: Superficie du domaine vital de *Prolemur simus* pendant les deux saisons.

	Saison chaude et humide (novembre à avril)	Saison froide et sèche (mai à octobre)
Surface (ha)	9,206 ha	6,02 ha

Ainsi la surface occupée est beaucoup plus faible pendant la saison humide contrairement à la saison sèche.

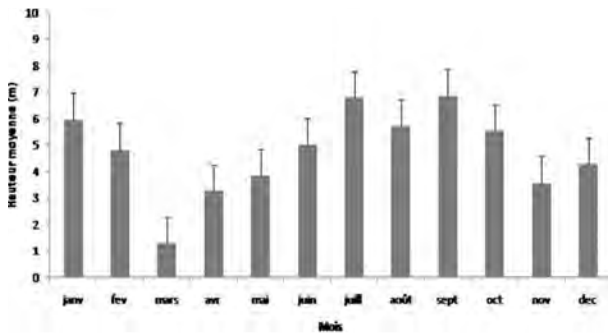


Fig. 3: Hauteur mensuelle de *Prolemur simus* lors de l'activité repos.

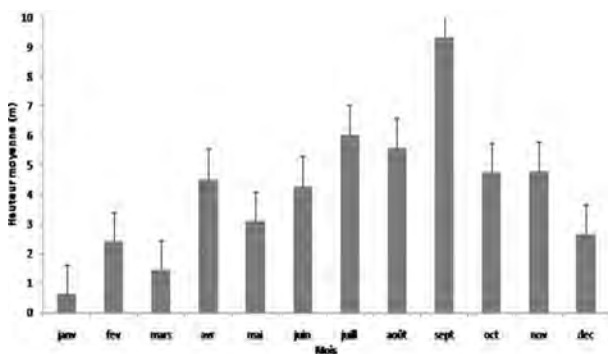


Fig. 4: Hauteur mensuelle de *Prolemur simus* lors de l'activité alimentation.

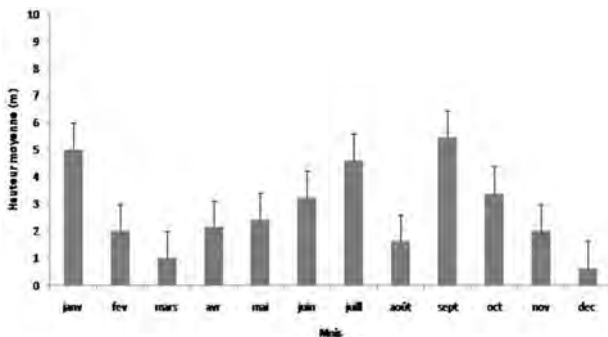


Fig. 5: Hauteur mensuelle de *Prolemur simus* lors de l'activité déplacement.

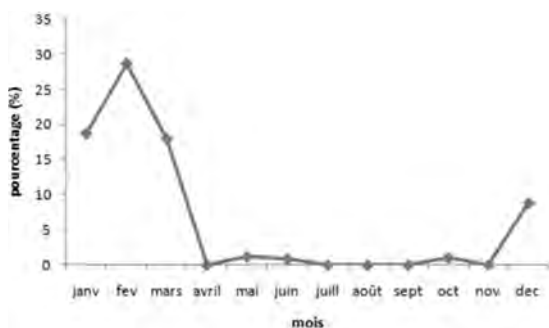


Fig. 6: Pourcentage de la terrestriality observé chez *Prolemur simus*.



Fig 7: Carte montrant le domaine vital de *Prolemur simus*: la ligne tiret-pointillée indique le domaine vital lors de la saison chaude et humide; la ligne continue indique le domaine vital lors de la saison froide et sèche (Carte de fond© Google Earth).

Discussion

Utilisation de l'espace verticale

Concernant les 3 principales activités de *P. simus*, la hauteur moyenne du déplacement annuel est plus faible $2.73 \pm 1.50m$ par rapport à la hauteur moyenne des autres activités repos et alimentation respectivement $4.74 \pm 1.60m$ et $4.13 \pm 2.33m$. Néanmoins comparés aux autres lémuriniens de bambous comme *Haplemur griseus* dont la hauteur annuelle pour s'alimenter est $5.5 \pm 0.6m$ (Tan, 1999), le *P. simus* semble moins arboricole que ses autres congénères. Cette attitude révèle l'avantage de vivre dans un large groupe car il y aura de nombreux yeux et de nombreuses oreilles pour détecter la présence d'éventuels prédateurs (Hamilton, 1971; Bertram, 1978). Par conséquent même lors du déplacement, les *P. simus* cherchent encore de la nourriture surtout les jeunes pousses de bambous (pers. obs.).

Terrestrialité

La terrestriality est un phénomène observé chez les lémuriniens. Selon les espèces étudiées, elle est pratiquée seulement pour s'alimenter comme le cas chez *Haplemur griseus* et *Haplemur aureus* (Tan, 1999) ou pour exercer d'autres activités tels que des activités sociales observées chez *Lemur catta* qui dépense 15 à 36% de son temps au sol (Jolly, 1966; Sussman, 1974) ou *P. simus* de Talatakely (Parc National de Ranomafana) qui consacre 24.1% de son temps au sol surtout pendant le mois de février (Tan, 2000). Quoiqu'il en soit, la terrestriality observée chez le *P. simus* d'Am-balafary (Figs 8-10) coïncide avec la saison d'abondance des pousses des bambous.

Domaine vital

Comme *P. simus* dépend énormément de bambous, son domaine vital se concentre avec la disponibilité des bambous. Néanmoins il a été remarqué que d'une manière plus générale le domaine vital des lémuriniens frugivores tend à être



Fig. 8: Une femelle *Prolemur simus* en train de manger un fruit mûr d'Ampalibe (*Arthocarpus heterophilus*) au sol (Photo: Mihaminekena).



Fig. 9: Un adulte *Prolemur simus* en train d'extraire une pousse de bambous (*Bambusa vulgaris*) au sol (Photo: Mihaminekena).



Fig. 10: Un jeune *Prolemur simus* en train d'extraire une pousse de bambous (*Bambusa vulgaris*) au sol (Photo: Mihaminekena).

beaucoup plus larges que ceux des folivores (Clutton-Brock et Harvey, 1980) car les arbres fruitiers sont beaucoup plus éparpillés que les arbres à feuilles. A Ambalafary, il ya une différence entre la surface du domaine vital lors des 2 saisons. En effet, lors de la saison humide les pousses de bambous sont nombreuses et comme il existe au moins 3 espèces de bambous dans le site situées à des endroits éloignés les uns des autres, le groupe de *P. simus* devrait exploiter chaque



Fig. 11: Une mère *Prolemur simus* en train d'allaiter son petit au sol (Photo: Mihaminekena).

espèce de bambous à la recherche de ces pousses ce qui explique la longueur de la distance parcourue par conséquent l'élargissement du domaine vital.

Conclusion

Une étude préliminaire concernant l'utilisation de l'espace vertical, la terrestrialité et le domaine vital d'un groupe de *P. simus* pendant une année a été réalisée dans le site de basse altitude d'Ambalafary. Ainsi selon les saisons, une différence a été toujours notée selon ces trois paramètres. D'abord pour l'utilisation de l'espace verticale, surtout lors de l'alimentation, le *P. simus* choisit un niveau plus élevé des supports pendant la saison froide et sèche contrairement à la saison chaude et humide. Ensuite concernant la terrestrialité, c'est surtout à partir du mois de décembre à mars que *P. simus* passe du temps au sol, c'est-à-dire pendant la saison chaude et humide et le maximum observé a été au mois de février (28.63%). Pendant la saison froide et sèche le *P. simus* est rarement observé au sol et durant cette période la terrestrialité se résume à 0% surtout au mois de juin, juillet jusqu'en septembre. Finalement toujours selon la saison, le domaine vital de *P. simus* à Ambalafary lors de la saison froide et sèche est d'environ 6.03 ha tandis que pendant la saison chaude et humide elle est estimée à 9.21 ha. Ainsi presque la totalité du mode de vie de *P. simus* varie selon la saison et par conséquent cette dernière influencera en grande partie ses activités. Une étude concernant les activités de *P. simus* selon la saison combinée avec son mode de vie en partie cathémérale serait à envisager pour comprendre d'autres aspects de la vie de ce lémurien mangeur de bambous afin de mieux orienter sa conservation à long terme.

Remerciements

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Edge effects on indri and black-and-white ruffed lemur distribution in the Andriantantely lowland rainforest, eastern Madagascar

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Key words: Edge effects, *Varecia variegata*, *Indri indri*, fragmentation

Abstract

Andriantantely is a large fragment (4000 ha) of lowland rainforest in eastern Madagascar and contains several Critically Endangered lemur species, including black-and-white ruffed lemur (*Varecia variegata*) and indri (*Indri indri*). The Aspinall Foundation (TAF) has been working with local communities to reduce pressure on the forest from agricultural encroachment and hunting. Locally-based teams have been conducting regular transect surveys for lemurs in Andriantantely since 2012. We used this lemur observation data to determine if edge effects influence lemur habitat use within the fragment. We found that two sympatric species used different areas within the fragment, with a significantly higher number of black-and-white ruffed lemur observations >850 m from the forest edge. For indri the opposite was true, with significantly more observations <850 m from the forest edge. These results have conservation implications, with indri at higher risk from anthropogenic threats and black-and-white ruffed lemurs restricted to the core of the fragment, limiting the carrying capacity of the site. This illustrates the importance of long term monitoring in conserving the Andriantantely lowland forest fragment.

Introduction

Primates are in decline throughout their geographic range; in 2012, almost half (49.5%) of all recognised primate species were classified as either Vulnerable, Endangered or Critically Endangered under the IUCN Red List of Threatened Species (Oates, 2013). Human population growth is above the global average within primate-inhabited countries, increasing hunting, habitat conversion and disease transmission pressures on primate populations (Estrada et al., 2012). With very few exceptions, primates are dependent on tropical forests for their survival and are therefore highly susceptible to deforestation and forest degradation (Mittermeier and Cheney, 1987; Cowlishaw, 1999). Despite deforestation rates falling globally, they remain disproportionately high in the tropics compared to other regions, reducing suitable primate habitat (Bala et al., 2007).

In Madagascar, the unprecedented level of threat to the Malagasy primates has led the IUCN SSC Primate Specialist Group to initiate a three-year lemur conservation strategy (Schwitzer et al., 2013). The strategy contains action plans for 30 different sites throughout the country, aimed at halting threats in priority areas, establishing infrastructure for long-term lemur conservation, expanding research and providing livelihoods for rural people through ecotourism (Schwitzer et al., 2013). One of these action plans, proposed

by The Aspinnall Foundation (TAF), is focused on the Andriantantely lowland forest fragment in the central east of the island (King *et al.*, 2013). The largest known population of the Critically Endangered greater bamboo lemur (*Prolemur simus*) inhabits the bamboo thickets surrounding Andriantantely (Randriahaingo *et al.*, 2014), whilst within the forest, populations of three Critically Endangered large-bodied lemurs occur sympatrically: indri (*Indri indri*), black-and-white ruffed lemur (*Varecia variegata*), and diademed sifaka (*Propithecus diadema*) (King *et al.*, 2013).

Andriantantely has become isolated from the main Ankeniheny-Zahamena rainforest corridor due to habitat fragmentation caused by slash-and-burn agriculture (King *et al.*, 2013; Ravaloharimanitra *et al.*, 2015). Habitat fragmentation can have deleterious effects on primate populations through many processes, such as population isolation (resulting in subsequent loss of genetic diversity), change in local ecology and increased accesses for anthropogenic disturbance, such as hunting, logging and agriculture (Irwin, 2007). Species vulnerability to fragmentation is not homogenous across the lemur taxonomic order, but varies with both species-specific and local ecological factors, making estimating species' reactions to disturbance difficult (Gillespie and Chapman, 2008). Craul *et al.* (2009) analysed genetic samples from Milne Edwards's sportive lemur (*Lepilemur edwardsi*), occupying 13 fragmented sites across north western Madagascar. Significant differences were found in genetic diversity associated with random genetic drift between each population, suggesting dispersal between fragments is limited (Craul *et al.*, 2009). Habitat disturbance will often affect the floral species composition of an area, with disturbance caused by logging often leading to a reduction in mature fruiting trees, but increasing overall leaf biomass (Herrera *et al.*, 2011). As a result, folivorous species are predicted to cope better with habitat disturbance than frugivorous species (Herrera *et al.*, 2011). An example can be seen with black-and-white ruffed lemurs in Ranomafana National Park, which were negatively affected by forest disturbance due to a reduction in mature fruiting trees, with the species totally extirpated in areas with the highest levels of anthropogenic disturbance (Balko and Underwood, 2005).

Edge effects are particularly relevant to lemur conservation, as high levels of habitat degradation in Madagascar have led to their populations becoming increasingly fragmented (Quéméré *et al.*, 2010). Edge habitats are often very different from the forest interior, with altered abiotic (higher temperature and lower humidity) and biotic (altered plant community composition) factors (Lehman *et al.*, 2006a). In the 2000 ha Vohibola III forest fragment, greater dwarf lemurs (*Cheirogaleus major*) have been observed to be negatively affected by edge habitats; their population density rises significantly with increased distance from the edge of the forest, until reaching a peak at 1700 metres (Lehman *et al.*, 2006b). In the same fragment, other species, such as the eastern woolly lemur (*Avahi laniger*), red-bellied lemur (*Eulemur rubriventer*) and eastern lesser bamboo lemur (*Hapalemur griseus griseus*) were edge-tolerant, showing no significant variation in density with increased distance from the forest edge (Lehman *et al.*, 2006a).

To monitor the diurnal lemur populations of Andriantantely, TAF teams have been carrying out transect surveys since 2012 within the forest, to obtain population density estimates. Members of the local communities are trained and funded to conduct surveys of lemurs within the forest, supervised by a primatologist. In this study, we use transect data collected between 2012 and 2014 by the TAF team on the two most frequently recorded diurnal species in

Andriantantely, indri and black-and-white ruffed lemur, to investigate the potential influence of edge effects on their distribution within this fragmented habitat. As ruffed lemurs are primarily frugivorous (Morland, 1991; Rigamonti, 1993; Vasey, 2000), we predicted that a loss of fruiting trees near the forest edge is likely to result in black-and-white ruffed lemur intolerance to edge-habitat, and therefore this species would have a higher population density towards the forest interior (Lehman *et al.*, 2006a). Conversely, due to their folivorous diet, we expected indri to be edge tolerant and to be evenly distributed throughout the site (Lehman *et al.*, 2006a).

Methods

Study Site

The study was carried out in the east of Madagascar, in the Andriantantely lowland forest (18.7638°S, 48.9468°E, elevation 300 to 700 m) which, although fragmented, is included within the 550,000 ha Ankeniheny-Zahamena Corridor (CAZ) (Fig. 1). The CAZ is relatively narrow at approximately 30 km wide but stretches 180 km from its northernmost to southernmost points and includes high, mid and low altitude rainforests (Randrianasolo *et al.*, 2013). The Andriantantely forest fragment is located in the Brickaville District and is surrounded by a matrix of agricultural land but has remained largely intact due to the spiritual importance of the site. Despite this, the forest is still under pressure from surrounding human populations through *tavy* (slash-and-burn agriculture), illegal timber harvesting and hunting (Ravaloharimanitra *et al.*, 2015). The fragment itself is approximately 4000 ha and is one of only a few remaining areas of lowland forest (<800 m elevation) in Madagascar (King *et al.*, 2013).

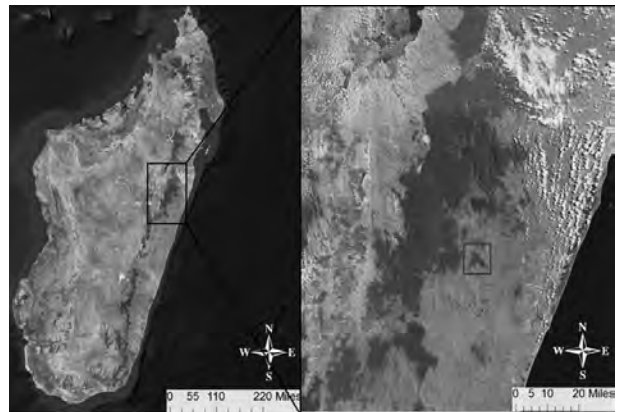


Fig. 1: Map of Madagascar (left) showing location of the Ankeniheny-Zahamena rainforest corridor (CAZ; right) and the Andriantantely lowland rainforest fragment (box in right panel).

Study species

Indri are the largest extant primate in Madagascar, with a body weight of 6-10 kg, and are highly specialised to a clinging and leaping form of locomotion, with only a vestigial tail (Mittermeier *et al.*, 2008). They have home ranges of up to 40 ha, which they defend with a complex set of calls, and they usually live in groups, consisting of a monogamous pair with up to four offspring (Geissmann and Mutschler, 2006; Mittermeier *et al.*, 2008). Fragmented populations generally have larger average group sizes and smaller home ranges, which may reduce to as little as 18 ha (Glessner and Britt, 2005). Indri are almost exclusively folivorous, only occa-

sionally supplementing their diet with seeds, bark and fruit, depending on the season (Andriaholinirina *et al.*, 2014a). A severe decline in both suitable habitat and population (projected >80% over the next three generations), has led indri to be classified as Critically Endangered on the IUCN Red List (Andriaholinirina *et al.*, 2014a). Indri have traditionally not felt the same pressures of hunting as other lemurs, due to *fadys* (traditional taboos) prohibiting hunting of the species. However, cultural erosion has led to a decline in the tradition and hunting is increasingly becoming a major threat to the species (Harcourt and Doherty, 2005). Black-and-white ruffed lemurs have been considered Critically Endangered on the IUCN Red List since 2008, due to a population decline of >80% over three generations resulting from continued loss of habitat and high hunting pressures (Andriaholinirina *et al.*, 2014b). This lemur has a large but narrow distribution across most of the eastern forest belt, although taxonomic classification of this species remains an area of contention; three sub-species are now recognised, *Varecia variegata editorum*, *V. v. subcincta* and *V. v. variegata* (Mittermeier *et al.*, 2008). The Andriantantely lowland rainforest site supports populations of the subspecies *V. v. editorum* (King *et al.*, 2013). Ruffed lemurs also call, but unlike indri, their calls appear to be used more for intragroup communication than defending a territory (Geissmann and Mutschler, 2006). This species is frugivorous; having limited dietary plasticity compared to other lemur species and as a result, is highly sensitive to habitat disturbance and the abundance of fruit trees (Balko and Underwood, 2005). Unlike most other primates, ruffed lemurs do not carry their young, but have nursery nests that can contain litters of multiple offspring which develop rapidly (Balko and Underwood, 2005).

Transect surveys

Two transects, A and B, were consistently surveyed over the three-year period (2012 to 2014) while six additional transects were added subsequently, C and D in 2013 and E – H in 2014. Transects ranged in length from 1.4 to 2km and each were surveyed between 15 to 20 times per year. All transects were located within the eastern portion of Andriantantely, in the areas managed by three local community associations based in the villages of Lanonana, Ambodimanga and Amboditavolo. Transects began on the edge of the forest, and although best efforts were made to establish straight transect lines, the complex topography of the site meant it was impossible for transect lines to be completely straight.

Transect walks were undertaken by trained rangers from surrounding villages, in groups of two or three. Surveys started in the morning between 8am and 9am, or in the afternoon between 12pm and 1pm, and were walked at a steady pace of approximately 0.5km/hour. At the end of each survey, rangers waited for a minimum of one hour before repeating the transect in the opposite direction. When an individual or group of lemurs was encountered, we recorded information of species, number of individuals, perpendicular distance from the transect line to the nearest individual, location (using a Garmin eTrex H Handheld GPS) and observation time. We also recorded data on the species and diameter at breast height (DBH) of the tree the animal was observed in, as well as the height of the animal within the tree and their activity.

Data analysis

We were unable to calculate accurate annual population density estimates, as the necessary number of observations

(>60), as recommended by Marshall *et al.* (2008), was not achieved for any species in any given year, except for indri in 2012. Therefore, we calculated linear encounter rates as an index of relative abundance. These were calculated for each species by dividing the number of individual lemurs observed by the length of the transect (ind/km). To provide an overall encounter rate for each year, the mean of all individual transects was used.

Edge effects were assessed from Transect B, as this was the only transect to take a perpendicular route from the edge of the forest towards the interior. GPS waypoints were plotted into ArcMap 10.2.1 (ESRI, 2015) and the measuring tool was used to divide the transect into 100 m bands. The number of observations for each band was calculated and plotted onto a histogram for visual inspection. Due to the lower number of observations for black-and-white ruffed lemurs, we grouped data into two bands (<850 m from the edge and >850 m from the edge) for further analysis. Chi square (X^2) tests were then used to determine whether the differences in abundance between the two bands were significant.

Results

Over the three year period, a total of 192 km of transects was surveyed. A total of $n = 412$ indri, $n = 141$ black-and-white ruffed lemur and $n = 58$ diademed sifaka individuals were observed. Three other species were also observed over the study period, but at much lower frequencies: eastern woolly lemur (*Avahi laniger*), brown lemur (*Eulemur fulvus*) and at least one species of dwarf lemur (*Cheirogaleus* sp.). Annual encounter rates for the three most frequently observed species ranged from 1.14 to 3.43 individuals/km for indri, 0.59 to 0.85 ind/km for black-and-white ruffed lemur, and 0.22 to 0.41 ind/km for diademed sifaka.

The edge effect analysis from transect B showed indri ($n=50$ observations) to be observed within every sampling distance from the forest edge, but to be more frequently observed towards the edge of the forest (Fig. 2). Black-and-white ruffed lemurs ($n=26$ observations) were observed most frequently within the forest interior and were only once observed close to the forest edge (Fig. 3). Indri were observed significantly more frequently <850 m from the edge of the forest than >850 m from the edge ($X^2 = 5.120$, $df = 1$, $P = 0.024$). In contrast, black-and-white ruffed lemurs were observed significantly more frequently >850 m from the edge of the forest ($X^2 = 3.846$, $df = 1$, $P = 0.050$).

Discussion

Due to their folivorous diet and the traditional *fadys* preventing hunting, we predicted indri to be the most abundant of the large-bodied lemur species in Andriantantely. This was supported by the results of this study, which showed them to be the most frequently observed species along the transects. More surprisingly, black-and-white ruffed lemurs were the second most frequently observed species.

Black-and-white ruffed lemurs rely primarily on five fruiting tree species for most of their food items and these are found at relatively low densities within Madagascar's landscape (Herrera *et al.*, 2011). These fruiting trees have been reported to be rare or absent from other disturbed forests (Balko and Underwood, 2005; Irwin *et al.*, 2007) and this has been proposed as the cause of ruffed lemur population decline within the fragmented areas of Ranomafana National Park (Herrera *et al.*, 2011). Although no data is currently available on the density of large fruiting trees within the Andriantantely forest, the rare trees are likely to be present due to the large size of the fragment. This may explain the

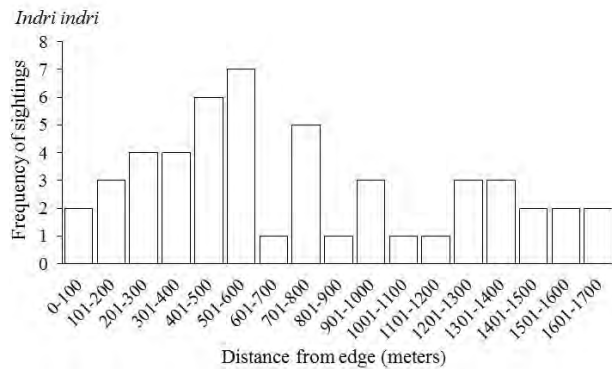


Fig. 2: Histogram of indri sightings with increasing distance from the forest edge.

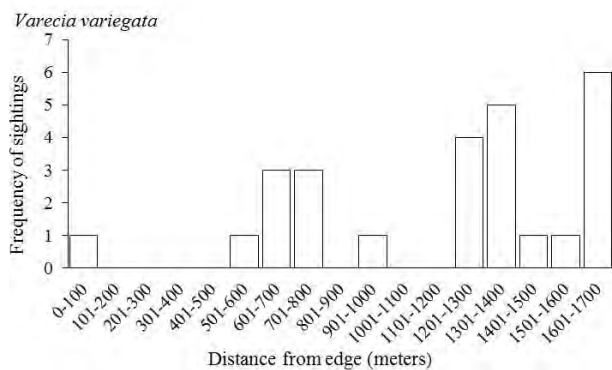


Fig. 3: Histogram of black-and-white ruffed lemur sightings, with increasing distance from the forest edge.

presence and relatively high abundance of black-and-white ruffed lemurs within the forest, despite their intolerance of other fragments elsewhere.

As predicted, black-and-white ruffed lemurs do appear to be edge-intolerant, with a significantly lower frequency of observations of this species <850 m from the forest edge. Unlike indri, black-and-white ruffed lemurs are not protected by traditional *fadys* and are therefore, more likely to avoid areas of human disturbance, explaining their edge avoidance (Golden and Comaroff, 2015). For indri, the prediction of their edge-tolerance appears to be accurate, although our study suggests they might have an actual preference for edge habitats, with highest frequencies of this species observed <850 m from the forest edge. Edge habitats are likely to differ from the forest interior structurally, having a lower percentage of canopy cover, increasing light permeation and promoting leaf growth (Godfrey and Irwin, 2007). This increase in leaf availability, and therefore food availability, may explain preference for edge habitats in the folivorous indri. This study raises several conservation concerns and implications for the indri and black-and-white ruffed lemur. As indri appear to prefer areas near to the forest edge, they would be vulnerable to human activity and disturbance. Although indri have been protected from hunting by traditional *fadys*, in other areas of Madagascar, these cultural traditions have begun to erode (Golden and Comaroff, 2015). When encountered in Andriantantely, indri displayed a marked lack of fear to humans, which would make them susceptible to hunting if similar cultural change were to happen here. Similarly, snares which would kill indiscriminately were also found during transect surveys. Reports from national parks suggest that hunting pressure is highest around the edge of protected areas (Wato *et al.*, 2006) and therefore the indri can be assumed to be at a greater risk from hunting

compared to forest interior-dwelling species. Their apparent edge-tolerance also puts them at more risk of novel pathogens and parasites from anthropogenic sources, which may negatively affect fitness (Junge *et al.*, 2011). Although the black-and-white ruffed lemur's edge-intolerance may shelter them from human disturbance, the complex shape of the Andriantantely forest fragment may reduce the area of available forest interior habitat, despite the fragment's large size (Lehman *et al.*, 2006b). This would reduce the carrying capacity of the area for black-and-white ruffed lemurs and limit population growth. These findings also illustrate the importance of covering a representation of the study area when surveying species; if the area surveyed includes a disproportionate area of edge habitat, this may inflate population density estimates for edge tolerant species, such as indri, or underestimate population densities of edge-intolerant species such as black-and-white ruffed lemur.

An additional conservation concern is reports that lemur predation is higher in fragmented forests in comparison to intact forest (Goodman *et al.*, 1993; Irwin *et al.*, 2009). The fossa (*Cryptoprocta ferox*) is the largest predator in Madagascar and regularly preys on lemurs (Irwin *et al.*, 2009). In continuous forests, fossa home ranges encompass numerous lemur groups, spreading the pressure of predation over a wide area. However, in forest fragments, their ranges are likely to be restricted, aggregating predation pressure onto fewer groups (Irwin *et al.*, 2009). Scat analysis has revealed that lemurs make up a higher proportion of fossa diets within forest fragments in comparison to continuous forests (Irwin *et al.*, 2009). Furthermore, the limited dispersal and immigration ability of fragmented populations (Irwin, 2008) means the effect of predation is likely to have a large impact on the demographic of local lemur populations (Irwin *et al.*, 2009). Fossa are known to inhabit the Andriantantely fragment but there has been no research on them within this study site thus far (H. Randriahaingo, pers. obs.). As black-and-white ruffed lemurs have a relatively large number of offspring (Herrera *et al.*, 2011), they are likely to endure more offtake through fossa predation than other species. Diademed sifakas are reported to constitute a large proportion of fossa diet in Tsinjoarivo Forest in eastern Madagascar, with higher predation rates in fragmented areas than continuous forest (Irwin *et al.*, 2009). Fossa predation has also been reported to be a contributing factor for group extinctions of Milne Edwards' sifaka (*Propithecus edwardsi*) in Ranomafana National Park (Irwin *et al.*, 2009). Fossa appear to focus hunting efforts within a small area of their home range until potential prey populations are depleted, before shifting hunting effort to other areas with higher densities of prey species (Irwin *et al.*, 2009). If similar processes are occurring in the Andriantantely forest, this could be impacting the densities of the local lemur populations. Therefore, assessing fossa densities within the fragment may help understand the viability of current lemur populations and should be a priority for future research at the study site. Similar methods to Gerber *et al.* (2010) could be employed, using camera trapping, to estimate predator abundance, and then be used to investigate predator-prey interactions within the fragment.

Conclusion

The Andriantantely lowland forest fragment is an important area for lemur conservation, containing at least three Critically Endangered lemur species (King *et al.*, 2013). Although the forest fragment is considered a sacred site by local people, and thus receives a level of protection, encroachment by the surrounding communities continues to be a problem

(King *et al.*, 2013). Our results have two potential implications concerns for conservation within the fragment. Firstly, indri appear to prefer edge habitats, putting them at higher risk from hunting and novel diseases. Secondly, black-and-white ruffed lemurs prefer forest interior habitat, and whilst this apparent edge-intolerance may buffer them against anthropogenic threats, this limits the area within the fragment which they are able to occupy. Further research within the fragment focussing on predation pressure and fruit tree densities is likely to give further insight into the long-term survival of these threatened lemur species and inform future conservation decisions. Due to the limited accuracy of modelling and forecasting lemur species' responses to fragmentation (Irwin, 2008) and the continued anthropogenic pressure (King *et al.*, 2013), long term monitoring will continue to be a vital part of conserving the Andriantantely lowland forest fragment.

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Funding and Training

AEEL Small Grants

Since 2009, AEEL awards two small grants of up to €1,000 each year to graduate students, qualified conservationists and/or researchers to study lemurs in their natural habitat. Priority is given to proposals covering conservation-relevant research on those species red-listed as Vulnerable, Endangered, Critically Endangered or Data Deficient by the IUCN. We support original research that helps with establishing conservation action plans for the studied species. Grants are normally given to recent graduates from Malagasy universities to help building local capacity. We may also, in special circumstances, support studies on Malagasy species other than lemurs if the proposal provides satisfactory information as to how lemurs or the respective habitat/ecosystem as a whole will benefit from the research. All proposals will be assessed by the Board of Directors of

AEEL and/or by external referees. The deadline for applications is February 15th of each year. Successful applicants will be notified by June 1st. More information can be found on the AEEL website, www.aeel.org.



The Mohamed bin Zayed Species Conservation Fund

Announced at the World Conservation Congress in Barcelona in 2008, The Mohamed bin Zayed Species Conservation Fund is a significant philanthropic endowment established to do the following:

- Provide targeted grants to individual species conservation initiatives;
- Recognize leaders in the field of species conservation; and
- Elevate the importance of species in the broader conservation debate.



The fund's reach is truly global, and its species interest is non-discriminatory. It is open to applications for funding support from conservationists based in all parts of the world, and will potentially support projects focused on any and all kinds of plant and animal species, subject to the approval of an independent evaluation committee. Details on this important source for species conservation initiatives and research can be found at <http://www.mbzspeciesconservation.org>.

Theses completed

Rostant, Y. 2017. Comportement écologique et social d'une mère de *Daubentonia madagascariensis* et de sa progéniture dans la Forêt Classée de Kianjavato, Sud-Est de Madagascar. Mémoire de Master d'ANDRIAMALALA Mention: Anthropologie et Développement Durable, Domaine: Sciences et Technologie, Université d'Antananarivo, Madagascar. Pour une meilleure connaissance de l'histoire naturelle de *Daubentonia madagascariensis*, une étude sur les activités et le comportement social d'une mère et de sa progéniture a été menée dans la Forêt Classée de Kianjavato, au Sud-est de Madagascar, de Janvier 2016 à Février 2017. Plusieurs méthodes ont été adoptées pour pouvoir atteindre les objectifs spécifiques, telles que: la capture pour pouvoir identifier les individus cibles, la radio télémétrie et le « instantaneous focal animal sampling » dans le but de collecter des données sur le comportement des animaux. Les méthodes « Minimum Convex Polygon » et « Kernel Density Estimate » ont été aussi utilisées, et les pieds de *Canarium*

dans le territoire de la femelle ont été recensés afin de pouvoir examiner l'utilisation de l'habitat par les deux individus. Les résultats ont montré que les fréquences des activités effectuées par l'enfant ne diffèrent pas de celles réalisées par sa mère. Les deux individus ont consommé les mêmes types de nourriture, telles que: des graines de *Canarium*, des larves, des insectes et du nectar de *Ravenala madagascariensis*. Ils les ont mangés avec des proportions différentes. Diamond (l'enfant) s'est nourri davantage de larves; et Bozy (la mère), des graines de *Canarium*. Chez chaque individu, une variation mensuelle de la fréquence de leurs activités et de la composition de leur alimentation ont été constatées. L'utilisation de l'habitat par la femelle semble être régie par la disponibilité de certaines nourritures, autre que le *Canarium*, et par la présence de sa progéniture. Avant le 19^{ème} mois de l'enfant, les deux individus ont utilisé 44 nids et ont toujours partagé le même nid pour dormir; et leurs territoires ont couvert une superficie de 87,71 ha (pour la mère) et 47,05 ha (pour l'enfant). Après cette période, les deux animaux ont commencé à se séparer de nid et à se déplacer en dehors de leur territoire habituel; mais Diamond s'est toujours resté dans le territoire de Bozy. Comparé à son enfant, la mère a beaucoup investi dans les interactions sociales: émission fréquente de cris pour se communiquer avec son enfant, jeu et toilettage. Ces faits ont nettement affaibli quand l'enfant a atteint l'âge d'un an et a fini par disparaître à son 20^{ème} mois. La qualité de la relation mère-enfant dépend de plusieurs facteurs.

Narcisse, A. 2017. Contribution à une écoéthologie de la population de *Varecia variegata editorum* introduite dans la Réserve Spéciale d'Analamazaotra, Est de Madagascar. Mémoire de Master de RAHAJANIRINA Mention: Anthropobiologie et Développement Durable, Domaine: Sciences et Technologie, Université d'Antananarivo, Madagascar.

Varecia variegata editorum s'est localement éteinte dans la Réserve Spéciale d'Analamazaotra (RSA), à l'Est de Madagascar, vers les années 1970. Ainsi, une réintroduction de quelques individus a été effectuée en 2006 et 2007 par l'ONG MBP/OHDZA. La population actuelle de *V. v. editorum* vivant dans cette Réserve mérite d'être suivie pour examiner comment elle vit maintenant. La présente étude contribue à l'étude de ses activités, son alimentation et son territoire. Les travaux sur le terrain ont été menés de juillet 2015 au juillet 2016. Pour atteindre le but de la recherche, plusieurs méthodes ont été utilisées, à savoir: l'instantaneous focal sampling, la collecte des coordonnées géographiques de l'emplacement de l'animal à chaque intervalle de 15 minutes et le marquage des sources de nourriture de l'animal dans son habitat. Quinze individus formant quatre groupes ont été suivis. Les résultats montrent que durant les deux saisons, le «repos» prédomine dans toutes les activités de la population, suivi de l'alimentation, du déplacement et des activités sociales. Durant toute l'année, *V. v. editorum* de cette réserve se nourrit d'une grande quantité de fruits. Une variation saisonnière a été constatée dans la consommation des autres compléments de son alimentation, qui sont des fleurs, des feuilles et des bulbes d'orchidées. Quelques individus ont été aussi observés pratiquer la géophagie et boire de l'eau d'un ruisseau. La taille du territoire des quatre groupes varie de 21,62 à 33,49 ha; et elle est fortement corrélée à l'abondance des sources de nourriture. Les territoires se chevauchent entre eux, surtout pendant la saison chaude. Les groupes semblent s'organiser entre eux, en pratiquant la stratégie de «fission-fusion», pour des raisons encore floues.

Guidelines for authors

Lemur News publishes manuscripts that deal largely or exclusively with lemurs and their habitats. The aims of *Lemur News* are: 1) to provide a forum for exchange of information about all aspects of lemur biology and conservation, and 2) to alert interested parties to particular threats to lemurs as they arise. *Lemur News* is distributed free of charge to all interested individuals and institutions. To the extent that donations are sufficient to meet production and distribution costs, the policy of free distribution will continue. Manuscripts should be sent to one of the editors electronically (see addresses for contributions on the inside front cover). *Lemur News* welcomes the results of original research, field surveys, advances in field and laboratory techniques, book reviews, and informal status reports from research, conservation, and management programs with lemurs in Madagascar and from around the world. In addition, notes on public awareness programs, the availability of new educational materials (include the name and address of distributor and cost, if applicable), and notification of newly published scientific papers, technical reports and academic theses are all appropriate contributions. Readers are also encouraged to alert *Lemur News* to pertinent campaigns and other activities which may need the support of the lemur research and conservation community. Finally, *Lemur News* serves as a conduit for debate and discussion and welcomes contributions on any aspect of the legal or scientific status of lemurs, or on conservation philosophy.

Manuscripts should be in English or French, double spaced with generous margins, and should be submitted electronically in Word (*.doc or *.docx) or rich text format (*.rtf). They should generally be 1-8 pages long, including references and figures. Submissions to the "Articles" section should be divided into Introduction, Methods, Results and Discussion and should include a list of 4-6 key words. Short reports and other submissions do not need subheadings or key words. Ideally, English articles should include a French abstract and vice versa. Articles should include a map of the area discussed, including all major locations mentioned in the text. Macros, complex formatting (such as section breaks) and automatic numbering as provided by text processing software must be avoided. The corresponding author's affiliation and full address must be provided, including e-mail and telephone number. For all other authors, affiliation and address should be provided. Use superscript numerals for identification. Tables should include concise captions and should be numbered using roman numerals. Please give all measurements in metric units. Please accent all foreign words carefully.

Maps should always be made as concise as possible and should include an inset showing the location of the area discussed in relation to the whole of Madagascar.

Photographs: Black-and-white photographs are ideal. Color photographs are acceptable if they can be printed in greyscale without losing any of the information that they are supposed to convey. Please send only sharply-focused, high quality photographs. Please name each file with the photographer credit and the number of the identifying caption (e.g. "Schwitzer_Fig.1"). We are always interested in receiving high quality photographs for our covers, especially those of little known and rarely photographed lemurs, even if they do not accompany an article.

All figures should include concise captions. Captions should be listed on a separate sheet, or after the References section of the manuscript. Subtle differences in shading should be avoided as they will not show up in the final print. Maps, photographs and figures should be sent electronically in any one of the following formats: EMF, GIF, TIFF, JPG, BMP, XLS. Please name all files with the name of the first author of the manuscript to which they belong. Do not send figures embedded in the text of the manuscript.

References: In the text, references should be cited consecutively with the author's surname and year of publication in brackets (e.g. Schwitzer *et al.*, 2010; Kaumanns and Schwitzer, 2001). The reference list should be arranged alphabetically by first author's surname. Examples are given below.

Journal article

Ranaivoarisoa, J.F.; Ramanamahefa, R.; Louis, Jr., E.E.; Brenneman, R.A. 2006. Range extension of Perrier's sifaka, *Propithecus perrieri*, in the Andrafiomena Classified Forest. *Lemur News* 11: 17-21.

Book chapter

Ganzhorn, J.U. 1994. Les lémuriens. Pp. 70-72. In: S.M. Goodman; O. Langrand (eds.). Inventaire biologique; Forêt de Zombitse. Recherches pour le Développement, Série Sciences Biologiques, n° Spécial. Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, Madagascar.

Book

Mittermeier, R.A.; Konstant, W.R.; Hawkins, A.F.; Louis, E.E.; Langrand, O.; Ratsimbazafy, H.J.; Rasoloarison, M.R.; Ganzhorn, J.U.; Rajaobelina, S.; Tattersall, I.; Meyers, D.M. 2006. Lemurs of Madagascar. Second edition. Conservation International, Washington, DC, USA.

Thesis

Freed, B.Z. 1996. Co-occurrence among crowned lemurs (*Lemur coronatus*) and Sanford's lemur (*Lemur fulvus sanfordi*) of Madagascar. Ph.D. thesis, Washington University, St. Louis, USA.

Website

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Call for voluntary contributions

As most readers of *Lemur News* are certainly aware, fundraising has become more difficult. We will continue to distribute *Lemur News* free of charge to all interested individuals and institutions. However, we would like to ask subscribers for voluntary contributions to cover production costs. Please contact one of the editors for information on how to make contributions.

Drawing by Stephen D. Nash



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