



LEMUR NEWS

The Newsletter of the Madagascar Section
of the IUCN SSC Primate Specialist Group

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Front cover: Amber Mountain fork-marked lemur (*Phaner electromontis*) in Daraina Forest, northern Madagascar. This species is classified as Endangered on the IUCN Red List. © Nick Garbutt / naturepl.com

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Editorial

Since the last volume of *Lemur News* (Vol. 23) was published in early 2022, two full years have passed. I thus want to mention that we still aim to publish one volume of the newsletter per year as has always been the case. The two-year gap between Volumes 23 and 24 is merely a function of the relatively small number of articles and short communications that we received over these last two years, which simply did not make it economical to publish and print a full volume. The low number of contributions and the slowness of them trickling in may have been a result of the Covid hiatus of 2020 and 2021, and perhaps of the fact that foreign researchers weren't able to travel to Madagascar, and that domestic research was also suspended over longer periods of time. This may have led to a lower research output in 2022, which only started to pick up and gather pace again in 2023. An alternative explanation could be that researchers are submitting their work to other journals instead, perhaps because *Lemur News* does not have an ISI impact factor, or because other journals have higher publication frequencies or 'online first' facilities. Notwithstanding the relatively safe assumption that these researchers are probably not reading this editorial anyway, I nevertheless deem it worthwhile to stress that, in the most recent 5th edition of the mother of all lemur books, 'Lemurs of Madagascar', published by Re:wild (often referred to simply as the 'Lemur Field Guide'; Mittermeier *et al.*, 2023), *Lemur News* remains the most-cited journal, even ahead of the IUCN Red List. Therefore, my message to all those who *do* read this editorial is: If you want your paper to have an impact on lemur conservation, consider publishing it in *Lemur News*!



After this brief foray into promoting our newsletter, it would be only too easy to reflect on all the challenges that lemurs and Madagascar are facing, and to enlist the gloomy narrative that everything is going to hell in a handcart. However, on the contrary, it is with great pride and optimism that I want to reflect on the monumental achievements in lemur conservation in Madagascar over the past few years. Notably, the period of 2017 to 2023 saw the implementation of a significant number of innovative conservation strategies that focused on habitat restoration, community engagement, and scientific research. These initiatives were catalysed by the collaborative efforts of the IUCN SSC Primate Specialist Group's Madagascar Section, the IUCN SOS Lemurs Initiative, Re:wild's Lemur Action Fund, local communities, and international partners. They followed directly from the Primate Specialist Group's lemur action plan that we published in 2013 (Schwitzer *et al.*, 2013) and that, for the first time, brought together the Malagasy and international lemur conservation community with the IUCN SOS Fund in a joint fundraising effort that ultimately proved very successful.

Through three calls for proposals, the SOS Lemurs initiative provided 49 medium- to large-sized grants to 26 civil society organisations operating in Madagascar, contributing to the conservation of 63 lemur species. Primate Specialist Group members served as advisors to the SOS Lemurs programme. All projects supported, and worked with, local communities to reduce habitat destruction and lemur hunting through a combination of conservation actions, from species monitoring to strengthening law enforcement, and from habitat protection and restoration to alternative livelihoods. Community engagement was at the centre of all these activities. The vast majority of results could not have been achieved without the support and engagement of local communities, facilitated by long-lasting relationships and trust established with the grantees.

Several of the funded projects reported notable increases in lemur populations, the restoration and improvement of forest habitats, and strengthened food availability for local communities. While it may be too early to fully understand the impact that this initiative has had on wild lemur populations and protected areas, it is very exciting that, in 2023, the IUCN SOS Fund secured another 9.5 million Swiss Francs to continue SOS Lemurs until 2029. By then, the total amount channelled into lemur conservation as a direct result of the 2013 lemur action plan and the partnership with the SOS Fund will have been 17.2 million Swiss Francs. The continuation of SOS Lemurs is a testament to the relentless dedication of researchers, conservationists, and authors committed to preserving Madagascar's unique primate heritage.

The persistent threats of habitat loss, illegal logging and lemur poaching continue to loom large in Madagascar. It is thus crucial to carry forward the momentum gained between 2017 and 2023. I would like to encourage all readers of *Lemur News*, from researchers and conservationists to policymakers and local communities, to redouble their efforts in protecting Madagascar's lemurs.

Last but not least, I want to acknowledge the contribution of Heike Klensang, who has been doing the typesetting and layout for *Lemur News* since Volume 3 (1998) and is retiring from her position in the communications department of the German Primate Center in early 2024. On behalf of the entire editorial board, I wish Heike a happy and fulfilling retirement!

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Christoph Schwitzer
Senior Editor

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News and Announcements

Lynx Edicions and Re:wild: Lemurs of Madagascar, 5th edition

Published by Re:wild as part of the Re:wild Tropical Field Guide Series. Editors: Russell A. Mittermeier, Kim E. Reuter, Anthony B. Rylands, Edward E. Louis Jr., Jonah Ratsimbazafy, Lily-Arison Rene de Roland, Olivier Langrand, Christoph Schwitzer, Steig E. Johnson, Laurie R. Godfrey, Marina B. Blanco, Cortni Borgerson, Timothy M. Eppley, Tiana Andriamanana, Sylviane Volampeno, Sehen Andriantsaralaza, Patricia C. Wright & Serge Rajaobelina.

The fifth edition of this world-renowned guide provides detailed information on the origins, discovery, study, and conservation of Madagascar's lemurs and comprehensive species accounts for all currently known taxa. The guide is illustrated with more than 600 drawings, photos, and maps to assist in field identification. It also introduces the concept of primate-watching and primate life-listing to encourage readers to see as many primates as possible in the wild and to help conserve them in their natural habitats. Work on the book took place during 2022, and it was published in August 2023. The book is available from Lynx Edicions: <https://www.lynxeds.com/product/lemurs-of-madagascar>.

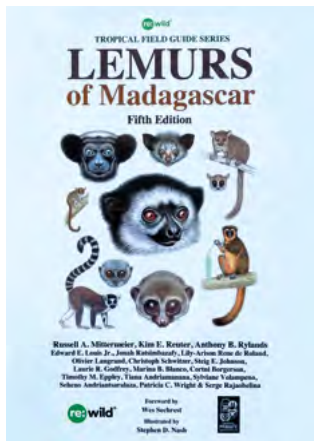


Fig. 1: The new 5th edition of the Lemur Field Guide.

Lemur News Submissions Must Adhere to Journal Guidelines

All journals, either prior to review or upon acceptance of a manuscript, mandate that authors format their submissions according to their guidelines to facilitate an efficient publication process. Lemur News is no different, yet many submissions do not adhere to these guidelines, leaving the Editorial Board with the time-consuming task of formatting. As most other journals and grant-giving bodies would not entertain that idea for a minute and would reject the submission outright, we must therefore stress that our contributors need to make a better effort to adhere to all guidelines and formalities for authors.

Dr. Jonah Ratsimbazafy Wins the Seacology Prize!

Dr. Jonah Ratsimbazafy, President of the International Primatological Society, was awarded the 2023 Seacology Prize, an international environmental prize, for his more than three decades of dedication to lemur and habitat conservation in Madagascar! The prize comes with a USD \$10,000 award and a trip to the USA. Please enjoy

watching Dr. Jonah's biographical film: <https://vimeo.com/874243482> as well as his Seacology Prize acceptance speech (October, 2023): https://youtu.be/Nt_f7nN6ss0?feature=shared.



Fig. 1: Seacology co-founders Ken Murdock (left) and Dr. Paul Cox (right) with Prize winner Dr Jonah Ratsimbazafy.

Short Communications

A case of hypomelanism in the northern giant mouse lemur (*Mirza zaza*)

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Colouration of skin, fur and eyes in mammals is influenced by the presence of melanin (Fertl and Rosel, 2002). Melanin deficiencies can cause a range of different pigmentation disorders in mammalian species, including hypomelanism (reduced pigmentation), leucism (partial pigmentation loss), and albinism (total pigmentation loss), and these result in atypical colouration (Krecsák *et al.*, 2008). Although a rare condition, atypical colourations have been observed in a number of mammals, including primates (e.g., Espinal *et al.*, 2016; Leroux *et al.*, 2021), pinnipeds (Acevedo *et al.*, 2009), cetaceans (Fertl *et al.*, 2004), carnivores (Eizirik *et al.*, 2003) and bats (Lucati and López-Baucells, 2017). In lemurs, cases of leucism or albinism have been documented for *Eulemur macaco* (Colquhoun, 1993), *E. collaris* (Eppley and Donati, 2017), *E. coronatus* (Le Pors *et al.*, 2020) and *Propithecus candidus* (Patel, 2014). In addition to the obvious physiological anomalies associated with atypical colourations, leucism and albinism, these phenotypes also result in increased skin sensitivity, compromised crypticity, and elevated predation vulnerability (Fertl and Rosel, 2002; Leroux *et al.*, 2021). In this communication, we provide a first

account of abnormal fur colouration and hypomelanism in the northern giant mouse lemur (*Mirza zaza*), a small-bodied, nocturnal, and non-gregarious primate that is endemic to Northwest Madagascar (Rode-Margono *et al.*, 2016; Seiler *et al.*, 2019).

Our observations took place in Anabohazo Forest (approximately 14°19S, 47°54E), a 1,169 ha transitional forest located in the Sahamalaza-Iles Radama National Park (Hending *et al.*, 2017; Hending *et al.*, 2021). Between March and August 2019, we conducted live-trapping along two 600 m transects using 56 live-traps (40 Sherman XLF15 and 16 Tomahawk Size 12) in order to investigate the physiological health of *M. zaza* at the study site. During this time, we captured and examined 63 separate *M. zaza* individuals ($N = 44$ males, $N = 19$ females). All males and 18 of the females exhibited greyish-brown pelage colouration, darker on the tail and lighter in ventral areas, which is the typical colouration of *M. zaza* (Kappeler *et al.*, 2005; Fig. 1). However, one female exhibited a unique gold colouration that was much lighter than all other individuals, with particularly lighter and whiter shades in ventral and facial areas (Fig. 2). Over the six-month study-period, we were able to capture this female individual 10 times, and her mean weight (182.6 g) was under that of the mean weight of the other 18 captured females (193.4 g). She also frequently appeared to look sickly, was often lethargic during capture and handling, and we observed her struggling to climb and negotiate tree branches upon her release, which suggests that she may have also been carrying an illness or infection. Additionally, she had a high frequency of injuries in comparison to the other captured *M. zaza* individuals (Fig. 2).

To our knowledge, this is the first observation of abnormal colouration and hypomelanism in *M. zaza*, and in any nocturnal lemur. Cheirogaleid lemurs such as *M. zaza* rely heavily on crypsis to avoid detection from predators such as owls, raptors and arboreal snakes (Rahlfis and Fichtel, 2010), and abnormal fur colourations are therefore highly likely to make the respective individual more visible to predators. Hypomelanism can also have negative impacts on fitness (Caro, 2005),



Fig. 1: Northern giant mouse lemur (*Mirza zaza*) individuals with normal greyish-brown fur pigmentation in Anabohazo Forest, Sahamalaza-Iles Radama National Park, Northwest Madagascar.



Fig. 2: A female northern giant mouse lemur (*Mirza zaza*) with golden body fur pigmentation and whiteish facial colouration in Anabohazo Forest, Sahamalaza-Iles Radama National Park, Northwest Madagascar. This female was found to be frequently injured or unwell.

which can subsequently affect the sufferer's ability to successfully forage. The female that we described here exhibited lower than average body mass, signs of illness, and physical injuries that were likely caused by predators or potential competitors; these observations may be due to compromised crypsis and poor physical health, both of which could be as a result of her unique pelage. Hypomelanism is an inherited trait (Fertl and Rosel, 2002) and *M. zaza* have a polygynandrous mating system (Hending *et al.*, 2020). This female individual will likely give birth to multiple offspring during her lifetime if she is able to survive long enough, and her offspring may inherit the hypomelanistic trait.

Acknowledgements

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The addition of dwarf lemurs (*Cheirogaleus* sp.) to the unusual assemblage of lemur species in the Itremo Protected Area

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The Protected Harmonious Landscape of Itremo (20°31'S 46°23'E, ~1500 m altitude), declared an IUCN Category V Protected Area in 2015, sits at the geographic center of Madagascar and is currently managed by Royal Botanic Gardens Kew (RBG-Kew) (Fig. 1). Harmonious landscapes, one of the newest types of protected areas in Madagascar, aim to integrate biodiversity conservation as well as cultural heritage and sustainable resource use (Beresford et al., 2005). With a total surface area of 24,788 ha, Itremo boasts pockets of sclerophyllous woodland, tapia (*Uapaca bojeri*), and pine trees surrounded by grasslands, but also several mid-altitude moist evergreen forest fragments found within valleys, with canopies that can reach ~25 m (Fig. 2). Due to its complex geological history, forest fragmentation, and fire-susceptible grasslands, Itremo is attractive to geologists, ecologists, and natural historians

Carte de localisation de la Nouvelle Aire Protégée d'Itremo

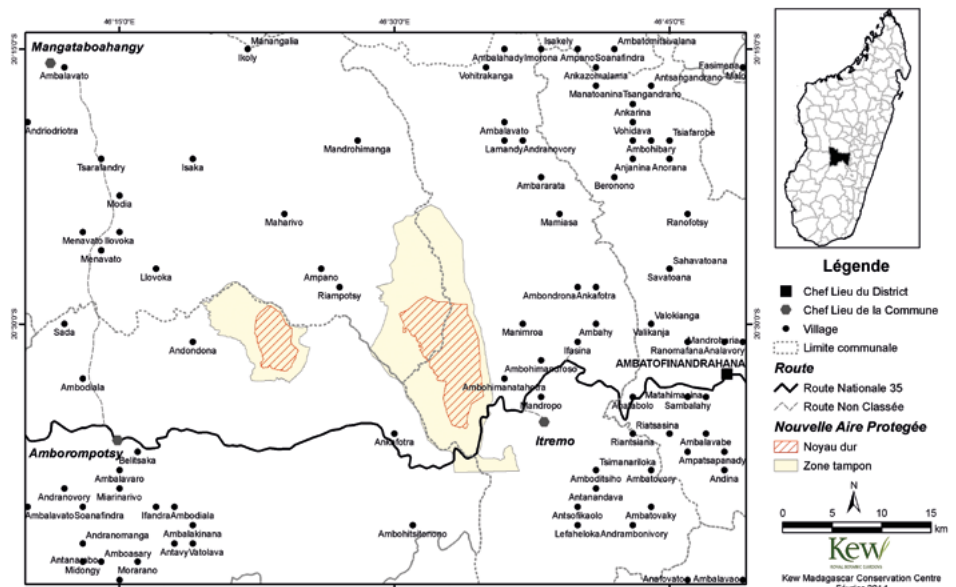


Fig. 1: Map of the Itremo Protected Area.

alike (Goodman *et al.*, 2018). The climate is sub-humid with a defined rainy season between November and April (~1,600 mm). Although temperatures can drop to ~6 °C during the coldest month of the year (July), there are no major temperature fluctuations between seasons, with values ranging between 13 °C and 26 °C year-round (Goodman *et al.*, 2018).



Fig. 2: Moist evergreen forest fragment at Itremo.

Previous faunal inventories acknowledged the presence of two lemur species at Itremo: Verreaux's sifakas (*Propithecus verreauxi*) and mouse lemurs (*Microcebus* sp.) (Goodman *et al.*, 2018). The presence of *P. verreauxi* at Itremo is notable because this species is primarily known to inhabit the dry deciduous, spiny, and low-altitude forests of western and southern Madagascar. That said, *P. verreauxi* is also reported from all areas of Andohahela National Park in southeast Madagascar, including the humid parcel (Goodman *et al.*, 2018; J. Ralison & A. Andriamahaiavana, personal communications), which, when coupled with their presence at Itremo, considerably extends the altitudinal range and habitat types that can host this species.

To the best of our knowledge, *P. verreauxi* has not been genetically confirmed at Itremo, although the individuals that our team observed on the east side of the protected area in June 2022 are visually indistinguishable from populations at other sites in Madagascar (Fig. 3). It is therefore curious that Itremo was removed as a geographic locale from the recent IUCN assessment for this species (Louis *et al.*, 2020).

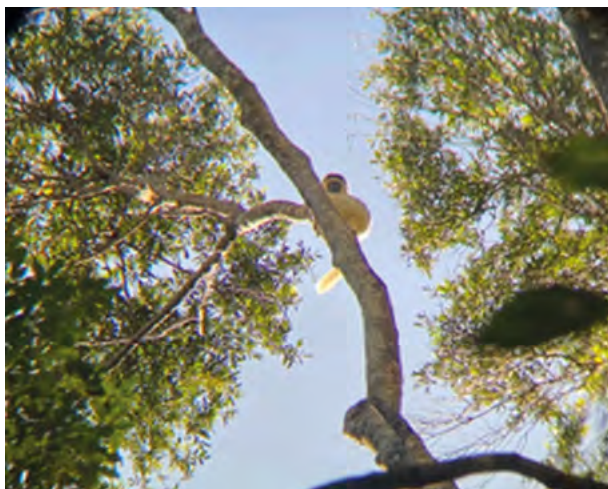


Fig. 3: Adult *P. verreauxi* in the eastern side of Itremo.

The mouse lemurs at Itremo have also not been genetically confirmed and are currently listed as an unknown species. With the purpose of collecting additional information about the Itremo mouse lemurs for a species assignment, our team conducted some live-trapping and nocturnal surveys on the east side of Itremo (June 2022) and nocturnal surveys on the west side of the protected area (October 2022).

Specifically, during the June expedition, we set up to 40 Sherman traps per night for 14 nights on three pre-established trails in the forest fragments next to camp, for a total of 1,102 trap nights. Moreover, we conducted seven night walks in total along the same trails between 6-7pm: We did not see any mouse lemurs during any of the night walks. During the October expedition, research teams conducted single night walks at four different forest fragments on the western side of Itremo. Although our efforts in June yielded not a single capture or sighting of a mouse lemur, the surveys conducted in October yielded more than 50 sightings of mouse lemurs and several individuals belonging to a dwarf lemur species (*Cheirogaleus* sp.) (Fig. 4, 5). These sightings are notable, as dwarf lemurs had not been included in previous faunal inventories at Itremo (Goodman *et al.*, 2018).

Of the nine currently recognized *Cheirogaleus* species, *Cheirogaleus crossleyi* and *C. grovesi* are the most likely identities of Itremo dwarf lemurs based on geographic proximity with their known ranges and general morphological similarities (Blanco *et al.*, 2020a, 2020b; McLain *et al.*, 2017). Until recently, *C. grovesi* was considered *C. crossleyi*, and the species are morphologically indistinguishable. Both species are medium-sized (~300-400 g), display brown-reddish dorsal coats, dark and “pointy” snouts, and dark and hairy ears. A “white mask” (like seen in Fig. 5) can be present in *C. crossleyi*, but this facial variation has not yet been reported in *C. grovesi*. *C. crossleyi* has a broad geographic distribution along eastern and central Madagascar, and is found across various habitat types, from lower elevation to high altitude rainforests, including secondary growths; it has also been found in other central highland localities like Ankafoabe to the north of Itremo (Blanco *et al.*, 2020a). Less is known of *C. grovesi*, currently restricted to Ranomafana and Andringitra



Fig. 4: Juvenile *C. crossleyi*-like dwarf lemur in the western side of Itremo.

forests below or up to 1000 m (Blanco *et al.*, 2020b).

Ultimately, for the sifakas, mouse and dwarf lemurs of Itremo, additional surveys and the collection of biological samples will be needed for species assignments and population assessments. However, based on the information reported here and in Goodman *et al.* (2018), this site adds a fascinating piece to the biogeographical lemur puzzle. Notably, we suggest that Itremo hosts an unusual faunal assemblage that includes a “central/eastern” dwarf lemur in sympatry with a “western/southern” sifaka, with clear implications for historical habitat connectivity in Madagascar’s highlands.

As a final note, although we failed to capture any mouse lemurs in June via standard Sherman traps, we did by-catch a small (~40-50 g), tufted-tail rodent, with dark brown coat and long black tail with black hairs, likely *Eliurus minor*. Thus far, *Eliurus tanala* has been the only Nesomyidae rodent listed at Itremo.

Acknowledgements

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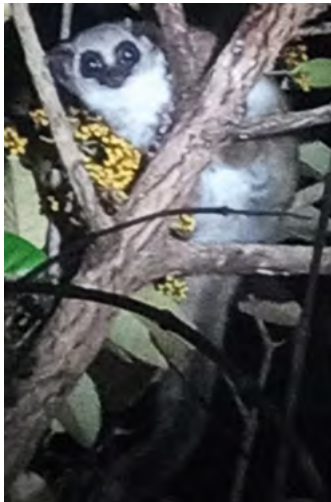


Fig. 5: Adult *C. crossleyi*-like dwarf lemur from Itremo.

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Ruffed lemurs on the edge: Recolonization of *Varecia variegata* in a disturbed forest

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Black-and-white ruffed lemurs (*Varecia variegata*) are often described as highly sensitive to habitat disturbance (White *et al.*, 1995; Balko, 1998; Ratsimbazafy, 2002; Ratsimbazafy, 2006; Herrera *et al.*, 2011). In fact, local habitat quality has been shown to be a major predictor of *Varecia* occupancy across the species’ range (Morelli *et al.*, 2020). In Ranomafana National Park, *Varecia* occupy several structurally and compositionally distinct sites. Disturbed sites—those previously subject to logging—have lower densities of shorter trees with smaller canopies and lower cover, as well as lower floristic diversity than undisturbed sites (Balko, 1998; Mancini, 2023). Resultantly, sites of lower quality habitat, particularly those with fewer large fruiting trees available, have lower population numbers of *Varecia*, with highly disturbed sites completely absent of this taxon (e.g., Herrera *et al.*, 2011). However, our recent observations of *Varecia* in a disturbed forest site in Ranomafana National Park suggests the latter is not always the case.

Talatakely (21°15'20" S, 47°25'15.3" E: Tan, 1999), is a mid-elevation secondary growth rainforest site in Ranomafana National Park, adjacent to Route National 25. This is a recovering forest previously subject to selective logging from 1986-1987, in addition to degradation along the forest edges (Balko, 1998; Tan, 1999). Talatakely has been slowly regenerating over the past few decades, but *Varecia* remained absent from this area of forest (Wright, 1997; Balko, 1998). Though the site remains structurally and floristically distinct from less degraded sites within this park (Mancini, 2023), since 2015, there have been reports of *Varecia* returning to Talatakely, with calls heard close to the park entrance and five individuals observed in the area in 2015.

In August 2022, we fitted three of the *Varecia* in Talatakely with GPS collars to begin monitoring their ranging, behaviour, and health. We have identified at least twelve animals living in five subgroups (Beeby, unpublished data), including three young juveniles which are likely offspring from the 2021 birth season. During August – November 2022, several individuals spent extended periods of time at the forest edge, as well as in banana plantations and mixed-use forest. Of the three focal subgroups, two

consistently range <100 meters from the forest edge, and frequently outside the National Park boundary. These individuals also appear to more frequently come down to the lower canopy, sometimes even to the ground, than is typical for this taxon (Tab. 1; Britt, 2000; Vasey, 2000; Balko and Underwood, 2005; Rafidimanana *et al.*, 2017; Beeby and Baden, 2021). In one extreme case, we followed an individual out of the forest and into a banana plantation to a single fruiting tree (*Ficus* sp.) beyond the continuous canopy. After feeding, this individual then travelled on the ground across an approximately 25 m patch of open grass to return to the main forest (Fig. 1). This individual spent over 6 hours of the day beyond the edge of the forest among banana plantations and crops.

These preliminary observations suggest *Varecia* may have a higher tolerance to habitat disturbance than previously thought. Though the population size is currently limited, the *Varecia* at this disturbed, forest-edge site appear to be successfully reproducing—a sign that conditions are, perhaps, not as suboptimal as we might expect. However, why *Varecia* recolonize some disturbed forest sites (e.g., Vatoharana: White *et al.*, 1995; Balko, 1998; Britt, 2000) long before others (e.g., Talatakely), remains unanswered. Resource availability and forest structure are strong predictors of this species' presence, and thus are likely driving the ability of individuals to return to areas of regenerating forest (Morelli *et al.*, 2020; Mancini, 2023).

Tab. 1: Total days observed, days observed within 100 meters and 20 meters of the forest edge, and below 2 meters from the ground, for three focal subgroups of *Varecia variegata* in Talatakely, Ranomafana National Park.

Subgroup	Days Observed	Days <100 m from Edge	Days <20 m from Edge	Times <2 m from ground
Silver	14	10	7	5
Pink	14	8	5	4
Green	12	6	0	4

However, other factors, such as competition with other frugivores (e.g., *Eulemur* sp.) that may be less sensitive to disturbance, may also impact the ability of *Varecia* to establish in regenerating forests. Data collected on range use, feeding behaviour, phenology, and interspecific interactions at this site over the next 12 months will enable us to examine the behavioural ecology of *Varecia* inhabiting this disturbed forest site and begin to answer these questions.

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Fig. 1: Photographs of *Varecia variegata* (left) spending an extended period foraging within a banana plantation, (centre and right) travelling on the ground through open habitat outside of forest.

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Eastern lesser bamboo lemur, *Hapalemur griseus*: Unique dietary observations in Analamazaotra Forest, Eastern Madagascar

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Madagascar is a region with a high level of biodiversity and endemism (Myers *et al.*, 2000). The island is well known for its richness in primates, with 100% endemism of the infraorder Lemuriformes. Five families of lemurs with more than 99 different species live all over the island (Schwitzer *et al.*, 2013). In Analamazaotra Reserve in the eastern part of Madagascar, 12 lemur species can be found (Mittermeier *et al.*, 2010). *Hapalemur griseus* (Eastern Lesser Bamboo Lemur) is one of the species that lives sympatrically with other species in this area.

Hapalemur griseus belong to the family Lemuridae. They are known to be diurnal and medium-sized (700g-1000g adult weight). They can be identified by their dark

reddish patches on the head and shoulders, and their coat colour ranges from grey to olivaceous to rust-brown (Mittermeier *et al.*, 2010). *H. griseus* is classified to be Vulnerable by the IUCN Red List (IUCN, 2020). It is also the smallest lemur species that is known to feed predominantly on species from the Poaceae family (bamboo), such as *Cathariostachys madagascariensis*, *Cephalostachyum cf. perrieri*, *Cephalostachyum cf. viguieri*, and *Nastus elongatus* (Andrianandrasana *et al.*, 2018). The species has also been observed feeding on non-bamboo plants like fruit of *Ficus* spp., *Psidium cattleianum*, *Streblus dimepate* etc. (Yamashita *et al.*, 2009). *H. griseus* in Ranomafana National Park have been observed to eat mushrooms, but the taxonomy of the fungi was never identified (Grassi, 2000).

On the morning of November 14th 2022, while collecting data on diets of diurnal lemurs in Mitsinjo Forest, a secondary forest that forms a part of the Analamazaotra Reserve, we found a group of five adult or subadult individuals of *Hapalemur griseus* at 08:53 am. After following them for some time, at approximately 10:30 am, we observed three individuals consuming mushrooms from the bark of a dead tree on the forest floor. The mushroom was identified to be a part of the *Auricularia* genus (Fig. 1). The feeding behaviour lasted for approximately 20 minutes. Total *H. griseus* dietary items observed during the research period by using an all-occurrence sampling (Altmann, 1974) are shown in Tab. 1.

Auricularia are edible fungi that are distributed worldwide (Wu *et al.*, 2015), and can be found especially in tropical, subtropical and temperate regions (Qui *et al.*, 2019). The genus belongs to the Auriculariaceae Family, Kingdom Fungi, and can be identified by its ear-like shape and brownish color (Phillips, 2013). The species is known in particular by its important property in terms of diet, as it contains an important source of protein and fiber (Bach *et al.*, 2017). This observation can allow us to better study the role played by fungi in the diets of *Hapalemur griseus*, as well as the distribution of *Auricularia* species in the forests of Madagascar.

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Tab. 1: Plant species consumed by *Hapalemur griseus* between November 12th 2022 and December 4th 2022 in Mitsinjo Forest and Analamazaotra National Park. FL=Flowers, FR=Fruit, LF=Leaves, SH=Shoot.

Common Name	Scientific Name	Family	Part of plant
<i>Belohalika</i>	<i>Justicia</i> sp.	Acanthaceae	LF
<i>Sofimboalavo</i> (mushroom)	<i>Auricularia</i> sp.	Auriculariaceae	Basidiocarp
<i>Vongo</i>	<i>Mammea bongo</i>	Clusiaceae	FR
<i>Dongovelona</i>	<i>Bakerella</i> sp.	Loranthaceae	FL
<i>Nonoka</i>	<i>Ficus</i> sp.	Moraceae	FR
<i>Volohosy</i> (Bamboo)	<i>Cathariostachys madagascariensis</i>	Poaceae	LF/SH
(Bamboo)	<i>Nastus elongatus</i>	Poaceae	LF



Fig. 1: *Auricularia* sp. in Mitsinjo Forest, Andasibe.

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Evidence of twinning in Coquerel's sifaka (*Propithecus coquereli*) in the Anjajavy Reserve

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Background

Sifakas (*Propithecus* spp.) are among the most charismatic and threatened lemurs in Madagascar. There are currently nine recognized species that inhabit different geographic areas and forest types across the island (IUCN, 2023). Compared to other lemurs, sifakas are famous for their “slow” life histories: Females delay sexual maturation but continue to reproduce later in life (Kappeler and Fichtel, 2012; Richard *et al.*, 2002). They have long gestation periods (Roulet, 2014; Wright, 1995; Zehr *et al.*, 2014) and typically only produce single infants yearly or every other year (Kappeler and Fichtel, 2012; Richard *et al.*, 2002; Wright, 1995). Infant sifakas continue to nurse and be transported at older ages (Ross and Lehman, 2016) and subsequently experience long juvenilities and sub-adulthoods. Yet, despite this maternal investment, infant mortality in sifakas is remarkably high (Kappeler and Fichtel, 2012; Richard *et al.*, 2002; Wright, 1995) perhaps due to a combination of lactational failure and infant failure to thrive in early life and the challenge of feeding and staying warm during the rainy season for recently weaned sifakas (Richard *et al.*, 2002). Sifakas have been described as bet-hedgers *par excellence* (Richard *et al.*, 2002). In unpredictable and heterogenous environments like Madagascar, when offspring survival is uncertain, females invest less in reproduction each year, but have more reproductive opportunities through a longer life.

This phenomenon has been demonstrated in Verreaux's sifaka (*P. verreauxi*) at Beza Mahafaly, one of the harshest and most seasonal environments in Madagascar (Richard *et al.*, 2002). Demographic data collected over decades has shown that reproductive variability is normal within and between years. For example, some females reproduce every year while others skip a year. When faced with extreme climatic events like droughts, female fertility decreases, and in extreme cases, none may give birth (although see Lewis and Rakotonirainy, 2011). Thus, changes in resource availability under “good” or “bad” years have implications for female body condition and their ability to successfully raise offspring at a given time. In sifakas, body mass is greatest at the beginning of the dry season, and lowest at the end of it (King *et al.*, 2011; Lewis and Kappeler, 2005; Richard *et al.*, 2002).

Female Verreaux's sifakas that are heavier at the time of mating, at the end of the wet season, will be more likely to have infants in the following birth season (Richard *et al.*, 2000). Because energetically costly lactation occurs during the dry season for sifakas, females must rely on stored sources of energy to sustain reproductive costs. They are thus characterized as “capital” breeders (Richard *et al.*, 2002).

Although reports of individual female sifakas skipping reproduction in “bad” years have been documented in several species, we might expect evidence of enhanced reproductive output per female in “good” years or in “good” habitats, including via twinning. Like all lemurs, sifakas possess a bicornuate uterus and should, in theory, be capable of twinning. Nevertheless, twinning appears to be extraordinarily rare in sifakas. Indeed, a single occurrence of twinning was reported in Milne-Edwards' sifaka (*P. edwardsi*) in the humid eastern rainforests (Hemingway, 1995). Photos of Verreaux's sifakas from Berenty in southeast Madagascar and silky sifakas (*P. candidus*) in Marojejy in northeast Madagascar show females carrying two infants, though these events come with no additional data, and may be the result of allomaternal care between female group mates. Twinning has never been reported in captive sifakas, including in the long-term population of Coquerel's sifakas managed by the Duke Lemur Center (Zehr *et al.*, 2014).

Twinning at Anjajavy

Here, we present evidence of twinning in Coquerel's sifaka (*P. coquereli*) in the Anjajavy Reserve, northwestern Madagascar (14°58' 15°05' S 47°12' 47°20' E). Anjajavy, a dry deciduous forest, includes ~11,000 ha of protected area, of which ~9,800 ha are classified as an IUCN V Harmonious Landscape, and ~1,000 ha are classified as a private reserve. We specifically observed twinning in a group that, at the time of the event, comprised seven individuals: two adult females, two adult males, another adult individual of unknown sex (not always present in the group), and infant twins, tentatively sexed as males. This group occupies a territory that includes the Anjajavy Lodge, where they are prone to frequent and opportunistic observations by local guides and staff, as well as guests (Fig. 1). These sifakas are not provisioned any food by people and experience no close physical interactions with people.

On July 2nd 2023, local guides first noticed the presence of two, similarly-sized infants placed ventrally on one of the adult females of the group. The group was intensively followed from 8:00 to 16:00 for four days from July 5th to 8th 2023, and opportunistically every afternoon from the rest of July and August 2023 by local research assistants. Local assistants always observed the two infants nursing from the same female, despite a few occasions of transport of one of the infants by another adult. Starting at the end of July, the infants began to cling from the ventral location to the dorsum of the female (Fig. 2). Three weeks later they were on their mother's back (Fig. 3) and beginning to cling more often to other members of the group, including the adult male and presumed father. Not surprisingly, as the infants grew, transport sharing became more common. By late September, both infants had been observed exploring branches in proximity to adults and testing leaves for consumption.

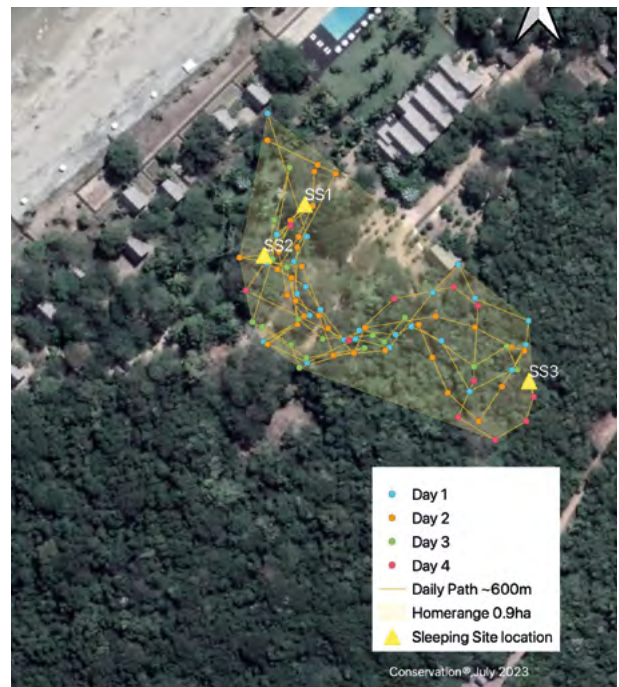


Fig. 1: Home range of the sifaka group with twins.

During this period of observations, the group's range was small, totalling ~0.9 ha, and always in proximity to the Lodge. Other sifaka and brown lemur groups (*Eulemur fulvus*) were also observed in this area, though in the case of other sifaka groups, at different times of the day. Furthermore, Anjajavy staff have reported additional sightings of female sifakas with twins in the last few years. For example, in 2022, research assistants found three sifaka groups with females presumably carrying twins in different areas within the private reserve. Although twinning may not happen every year, and although infants may not always survive, these observations suggest twinning in sifakas at this location may have been under-reported and perhaps is more common than in other sifaka populations across Madagascar.

Implications

The density of Coquerel's sifakas is greater at Anjajavy than in other dry deciduous forests (e.g., Ankarafantsika) that harbor this species (Kun-Rodrigues *et al.*, 2014, Salmona *et al.*, 2014). Even within Anjajavy Reserve, the density of sifaka groups close to the Lodge in the private reserve seems much greater than in the larger protected area (ER, pers. obs.). One explanation relates to the availability of water, as the grounds and gardens close to the Lodge are frequently watered. Another explanation relates to the rich number of introduced trees, like kapok and tamarind that exist near the Lodge. Unlike endemic trees, these species tend to favor bud and leaf growth earlier in the season, which in turn, provides the sifakas with nutritionally rich foods at a time of the year where strong energetic stress can constrain reproductive success. Indeed, diverse wildlife across northwest Madagascar shows similar reliance on Kapok and other introduced trees with extended phenology (Hending *et al.*, 2021; Sussman and Tattersall, 1976). Perhaps the availability of water and food enables female sifakas to more frequently produce twins, particularly in “good” years.



Fig. 2: Adult female with twins, photo taken on July 31st 2023.



Fig. 3: Adult female with twins, photo taken on August 22nd 2023.

However rare, our observations highlight the flexible nature of sifaka reproduction, where females can perhaps afford multiple infants under favorable conditions. Whether these juveniles survive to adulthood, or whether the fate of multiple offspring born in a “good” year will be auspicious in the long term, is beyond the scope of this note.

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Articles

Perspectives on research in Madagascar

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The following is a conversation between two colleagues, from different generations and cultural backgrounds, who share the same research interests. Madagascar is at the core of the conversation, neither as a biodiversity paradise nor a monolith of people, but as a place that both “humans” and wildlife call home, literally and figuratively. This piece is both an exploration of personal purpose, as well as a redefinition of the role of research and researchers in an ever-changing societal landscape. In the end, this account aims to spark conversations among colleagues rather than impose another set of arbitrary rules or guidelines. First, a foreigner tells an anecdote of a recent field project; second, a Malagasy researcher shares an experience from the field; third, both authors propose suggestions, learned from their mistakes and reflecting on perspectives different from their own.

I. As we arrived at the drop-off site, after three days traveling by 4x4 from the capital, we were told the campsite was just down the hill. We were completely surrounded by grasslands and wondered where the “forests” were that we were supposed to explore. In our city clothes and inadequate shoes, we picked up as many bags of food and supplies as we could, almost running down the hill with naïve excitement. Along the way, our balance failed, and we became scared of falling. We were embarrassed. Bags were dropped for the local team members to pick up after us. Earlier that day, we had parted with some food items brought from the capital, as their consumption was a local fady (taboo). Even before we set foot in camp, we already realized we were less prepared- physically, logistically, and culturally- than we thought for this research expedition.

Some on our team have had the privilege of working in Madagascar for nearly two decades. We have made our own decisions about where to go and what to study, depending on available funding and logistics from the USA,

rather than questioning whether our research was fair or worthwhile to the Malagasy science community and to the local communities. We have fiercely defended the slogan “We are contributing to the production of knowledge” and data collected will “inform other scientific fields from ecology to conservation”. For some of us, it was just short of saying we come here with big dreams, to figure out how to fix *your* environmental crisis. A crisis we assumed to be somebody else’s doing.

We are now sitting around a smoky fire, some of us wearing winter jackets and gloves, some wearing shorts and T-shirts, all equally cold, it seems. In the mix of languages and backgrounds, ideas and concepts can morph into caricatures of themselves. “They think you are crazy” our Malagasy research assistant said, loosely translating perceptions of us, the “vazaha” (foreigners), from our local research guides. We laughed with incredulity, obviously not seeing anything wrong with our research choices. Upon closer thought, however, the way our strange obsession with lemur feces had brought us all the way from the USA to that specific spot in the middle of the central highlands could, in fact, seem odd.

The first impulse was to explain ourselves, to delve into Madagascar’s biodiversity and how Madagascar is seen around the world as the quintessential example of nature’s experiment. Or we could talk about the links between gut microbiomes (thus, the fecal collection) and lemur ecological flexibility and even health. But no words came out of our mouths, as we sipped instant coffee (another luxury at camp) from our metal cups. Later attempts at discussing were well-intended but still clumsy, and we wondered if we made sense. At worst, we wondered if our research was just more materials for academic “Conferences” and if it mattered anywhere else. We, scientists, are generally pretty bad at describing our work to non-scientists; also, in this case, there is a language barrier, and it’s hard to find accurate replacements for the terminological jargon we are familiar with. Most importantly, would it be okay to argue that, in the name of Western science, we can place our flags all around the world and occupy land? Or demand “data” because science production is a societal priority? These thoughts were not only challenging for us to articulate but also hard to come to terms with.

I stand by science, as it is the path I chose to follow. I also acknowledge that our actions are biased and sometimes misguided. Science, at its core, is following a recipe, though the menu selection, attributes and evaluations are very much subjective. Who gets to cook, or taste the food is at its best arbitrary, and at its worst, utterly unfair.

In Madagascar, particularly, Western science gave the Island’s biodiversity, and its evolutionary and ecological uniqueness, a global showcase. Western science has also highlighted its vulnerability, the biodiversity crisis, historically putting forward narratives stressing the mismanagement and destruction of land by the hands of local people, while failing to stress narratives that hold colonial powers and foreign interests accountable. Although the role of humans in changing landscapes, at present, is undeniable, the narratives often have been simplistic and unnuanced. Perhaps a classic example would be that of prominent naturalists Perrier de la Bâthie (1873-1958) and Humbert (1887-1967), who argued that

Madagascar was originally fully forested and poor land use by Malagasy people converted the central highlands to grasslands. This justified French policies to retain control of the forests. Simplistic narratives create rifts between locals and foreigners (i.e., outsiders coming to Madagascar to “save” the land from its local inhabitants or “teach” them how to manage it), but also between scientists/researchers and the general public. Today, the savior complex may result in more subtle behavior, but it can underlie the implementation of activities or practices without cultural or other types of considerations. For researchers, science is oftentimes considered the only valid method of knowledge production, and it trumps traditional methods when in conflict.

That brings the question: What is our role as scientists in Madagascar today, and how permeable should we be in negotiating our contract and our research with Malagasy colleagues and local communities? How should research collaborations be built without assuming a “savior complex” attitude or erasing other non-scientific values, all while maintaining scientific integrity? How can we, as a community, listen to less represented voices and move beyond assigning blame and setting unilateral agendas? Perhaps, humility and curiosity would serve as an antidote to cynicism and despair. Understanding that a lot of what we do, we do for ourselves, rather than for others is a good start.

II. For the first time in five years, I had a new research technician on my field team. He had worked in the forest for more than a decade, but this was our first collaboration together. Before heading to the forest, we had a short conversation about the project activities and data collection. I thus assumed that he understood what the project was about. One night, during a huge storm that prevented us from leaving camp, he asked me “What are you going to do with all of these data that we collect?” That was when I realized I had mistakenly skipped some important aspects when describing the project. I started explaining that those data will contribute to my PhD work, but then I was asked to narrow down the question to “What are your *specific objectives* with these data?” I discussed my research questions, hypotheses, and variables... Everybody listened carefully, and I started noticing the change in their facial expressions from totally clueless to understanding the project. One of the local guides then asked: “That is cool, but how can all of that help us protect the lemurs and the forest?” I tried to explain that if we know what is at stake, we can better plan for the protection and preservation of wildlife. Yet, it did not make sense to them as it was not a tangible result, something they could see materialize in the next few years. I felt that I had failed not only to show my project’s purpose and explain the conservation implications of my project, but also to express my research in non-scientific terms, even though I talked to them in my native language, Malagasy.

I could have blamed it on the dialect differences, but internally, I knew that I had provided little context about the research to be conducted in their “backyard”. I started drawing things on a piece of paper to show the steps to follow to have concrete conservation action from research findings. Drawings turned into words, and words into dialogues. Dialogues into different

perspectives, on how the project could directly affect the local community and the forest. Malagasy researchers and students are better suited than are foreign researchers to engage and discuss with the local communities to promote understanding of what is going on in the local environments and how research can help biodiversity protection.

It became apparent that, because of the language barrier, most Malagasy team members could not discuss projects with foreign researchers. Thus, they are left to just execute assigned tasks and, for that reason, they fail to experience any personal benefits from working on different projects besides receiving monetary compensation. Unfortunately, language barriers are not the only ones: some Malagasy researchers underestimate Malagasy local and traditional knowledge because of the superiority bestowed upon higher education. If scientific-based knowledge, as learned in universities is the only acceptable “language”, local technicians and guides find themselves passively executing tasks. What a lost opportunity! Malagasy researchers and students can communicate the nuances and intricacies of life in their native language, which can facilitate communication about concerns, opinions, and knowledge in different forms and thereby provide the opportunity to decolonize science so that we all have something to contribute to and benefit from working together.

III. What can we do to embrace decoloniality, e.g., consider non-Western modes of thinking, while conducting research in Madagascar? Where we come from and what we can offer is different for everybody, and perhaps this is the starting point for conversations with peers and team members, rather than the justification for what we do without questioning and informing. Let the following suggestions spark conversations among all of us, across cultures, generations, backgrounds, and motivations to work in Madagascar, and maybe gradually change our opinions and behaviours towards Malagasy communities.

- Discuss research priorities with Malagasy counterparts, *before* designing and implementing projects. At a minimum, consider sharing funding and resources for projects that are inception and developed by Malagasy colleagues, and consider participating as an assistant and or collaborator instead of Principal Investigator. This is particularly relevant for foreign researchers leading labs.
- If you are leading a project, dedicate time to explain the research program to the local people throughout the project implementation and execution, adjusting the language according to who is on the other side. Firstly, acknowledge that we are working in *their* forest: they deserve to know what the plan is and how research may be beneficial to their communities. Secondly, value hands-on knowledge and local practices that can help facilitate the work. Thirdly, establish clear communication with local participants about their benefits, including fair payment for services, training, and guaranteed protection if physical risks are involved in the required work.
- Make the effort to go back to the field site and share research findings with the local communities after the project is over. This is a tremendous opportunity to

engage local participants in biodiversity conservation and management. It is a chance to discuss their interests and concerns and discuss ways to contribute pragmatically. These exchanges are also an opportunity to show appreciation for their collaborations. Prioritize local team members in country to avoid unsustainable emission costs associated with transportation.

- Acknowledge local participants' contributions and include them as much as possible, in the decision-making process, e.g., field protocols, activities and conditions, and authorship. Fieldwork never goes as planned, and in challenging times, insights from local people can be particularly relevant for how to address crises. At a minimum, the field team should be active participants and should be given the opportunity to express their concerns and suggest alternative solutions, rather than serve as passive recipients taking directives. Respect their point of view and, if there are disagreements, respectfully discuss differences of opinion.
- Respect local Malagasy culture and superstitions. Scientific training does not give us the right to discredit local communities' beliefs and taboos. Even if taboos are rooted in misconceptions and fears, they are intrinsic to the fabric of Malagasy society. Our respect should supersede our incredulity. Incidentally, local knowledge rooted in superstition could be integrated into the research program or discussed in a broader context. Perhaps, myths and legends can help us understand some aspects of how biodiversity has been valued (or the opposite) in those regions.
- Please, stop thinking that money is always the solution in a developing country. Most foreign researchers in Madagascar come to the island with a preconceived idea that money can solve all the existing problems. In fact, the opposite may be true. On the one hand, offering money to speed up services, or to circumvent administrative requirements, perpetuates corruption in the local administrations, which most of us have witnessed and complained about. More importantly, it perpetuates inequality with local researchers who cannot afford to do the same. On the other hand, when you are in locations far from large towns, local villagers may prioritize access to balanced foods, medicine and health care, tools or items needed for their subsistence, while cash may be saved for bigger investments later. Finally, the sporadic giving of cash without context and without respecting local and socially acceptable terms can create confusion and false expectations, and thereby undermine the work of our colleagues.
- Follow and respect socially accepted ethical behaviours. We should not feel entitled to break or ignore local rules because they do not align with our own standards. Beliefs and traditional knowledge are important components of heritage and ignoring them is harmful and detrimental. We should also acknowledge that expeditions are impossible to carry out without local people, who are not only familiar with wildlife – which is critical to our data— but also help us navigate forests safely.
- Be legal. Follow local laws and regulations, whether it makes sense to you or not. This is particularly relevant

for researchers attempting to enter protected areas and collect data without valid research permits and local authorizations. These behaviours are a form of neocolonialism. Plan ahead and contact local official and academic institutions for procedural details to avoid unnecessary delays. Incidentally, all relevant paperwork may be required by scientific Journals prior to manuscript submissions.

- Engage Malagasy students in your project, include them as members of your research team, provide mentorship, share the project rationale, objectives, and activities, and ask for feedback. Be prepared to adjust or change plans if students voice reservations or concerns. Establish a professional relationship that goes beyond collecting high-quality data and see students as potential long-term research collaborators and the emerging new generation of scientists and conservationists. In other words, mentor them. As much as possible, please work with the students to help them develop a side project integrated or not with the main project, a project that they can lead and/or publish. Such mentoring can tremendously increase their self-esteem and confidence in leading and disseminating their scientific results, and/or in developing new research projects and grant applications, and ultimately increase diversity in the current and future scientific workforce.
- Please, do not tokenize Malagasy students/ collaborators. Take the time to seek people who are good matches for the proposed projects, ensuring their best interests are served, without assuming anybody could do the job just fine. Acknowledge their contributions with fairness and transparency, avoiding under- or overestimating their roles and responsibilities.

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New genetic evidence from the Ambatotsirongorongo / Petriky complex in southeast Madagascar calls for an immediate re-evaluation of conservation strategies focusing on the Bemanasy mouse lemur (*Microcebus manitatra*)

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Abstract

The diverse forest habitats of southeastern Madagascar support a complex arrangement of five putative species of mouse lemur (genus *Microcebus*). One of these species, the Critically Endangered Bemanasy mouse lemur (*Microcebus manitatra*), requires urgent evaluation. In this short article, we present findings from a series of expeditions to the Ambatotsirongorongo massif and the nearby littoral forest of Petriky. Genetic results confirm that the range of *M. manitatra* is extremely limited. Notably, we find that two *Microcebus* species (*M. manitatra* and the Anosy mouse lemur, *M. tanosi*) occupy the remaining forest fragments of the massif, with seemingly discreet distributions. We observed and captured *M. tanosi* in the remaining intact humid fragments, whereas we only found *M. manitatra* in degraded habitats on the lower eastern slopes. The forest fragment that comprised the original type locality of *M. manitatra* has been all but cleared in recent years. We further confirm the identity of the mouse lemur species present in nearby Petriky as *M. manitatra*, making this forest the foremost remaining habitat for the species. These findings have substantial implications for species conservation and management strategies at both sites.

Résumé

Les divers habitats forestiers du sud-est de Madagascar abritent un arrangement complexe de cinq espèces putatives de lémuriers souris ou microcèbes (genre *Microcebus*). L'une de ces espèces, le microcèbe de Bemanasy *Microcebus manitatra*, en danger critique d'extinction, nécessite une évaluation urgente. Dans ce court article, nous présentons les résultats d'une série d'expéditions dans le massif d'Ambatotsirongorongo et dans la forêt littorale voisine de Petriky. Sur la base des résultats génétiques, il est maintenant clair que l'étendue géographique de *M. manitatra* est plus restreinte que préalablement envisagée. Il est évident que deux espèces de microcèbes (*M. manitatra* et le microcèbe d'Anosy, *M. tanosi*) occupent les fragments forestiers restants du massif, avec des répartitions apparemment discrètes. Nous avons observé et capturé *M. tanosi* dans les fragments humides intacts restants, et *M. manitatra* dans les habitats dégradés des pentes inférieures orientales. Le fragment de forêt qui constituait la localité type d'origine de *M. manitatra* a été pratiquement défriché ces dernières années. Nous confirmons en outre l'identité de l'espèce de microcèbe présente à Petriky comme étant *M. manitatra*, faisant de cette forêt le principal habitat restant de l'espèce. Ces découvertes ont des implications substantielles pour l'espèce et les stratégies de gestion de la conservation sur les deux sites.

Introduction

The extreme southeast of Madagascar is characterized by marked environmental gradients (humidity, precipitation, and temperature) and consequently, notable habitat heterogeneity (Goodman *et al.*, 2018). Beyond the large National Parks and reserves, many smaller relict forest habitats support important biodiversity. However, many of these forests are now disconnected and degraded as a consequence of long-term natural phenomena (Burney, 1992; Virah-Sawmy *et al.*, 2010) and intensive anthropogenic practices (Harper *et al.*, 2007; Vieilledent *et al.*, 2018). The result is a highly fragmented landscape, with

isolated islands of forest supporting unique assemblages of flora and fauna which reflect their positions along these gradients. These forests now serve as crucial refuges for species displaced by habitat loss.

The genus *Microcebus* is well represented in the southeast region, with five putative species occupying a range of habitats within 50 km² (Rasoloarison *et al.*, 2013; Hotaling *et al.*, 2016). Although each species is largely constrained by habitat type (e.g., the Grey-brown mouse lemur *M. griseorufus* in dry spiny forest and *M. tanosi* in humid forest), two species appear to have particularly restricted ranges (*M. ganzhorni* and *M. manitatra*). Whilst Ganzhorn's mouse lemur (*M. ganzhorni*) is known only from the few remaining littoral forest fragments at Mandena, the precise distribution of the Bemanasy mouse lemur, *M. manitatra*, remains unclear. Despite being listed as one of the world's 25 most endangered primate species (Donati *et al.*, 2019), and recognized as Critically Endangered by the IUCN (Blanco *et al.*, 2018), a high degree of uncertainty surrounds our understanding of the geographic distribution and ecological needs of this species. Most significantly, its current conservation status is based on a series of distributional assumptions that require urgent validation.

Microcebus manitatra (Hotaling *et al.*, 2016) has only officially been recognized from a single patch of forest on the Ambatotsirongorongo massif (Blanco *et al.*, 2018), in the extreme southeast of Madagascar. The massif consists of a series of humid forest fragments that form the Nouvelle Aire Protégée Ambatotsirongorongo (decree 2015-792). Once a continuous habitat, these remaining forests now persist only on the south-facing, most inaccessible mountain slopes. Three main fragments remain; Lavasoa (54 ha; 300-800m a.s.l.), Bemanasy (33 ha; 100-400m a.s.l) and Ambatotsirongorongo (< 5ha; 200-400m a.s.l). Despite recent protections, all fragments remain under severe human pressure (Donati *et al.*, 2019), and logging is chronic at all elevations. In recent years, and notably during the Covid-19 pandemic, the forest fragment Ambatotsirongorongo has been greatly diminished and now exists as just a small cluster of trees (S. Mara, pers. comm., 2023). Crucially, this forest fragment represents the type locality for *M. manitatra*, based on the GPS data that accompanies the original species description (although the locality is commonly, but erroneously referred to as Bemanasy in the literature). Whilst it is widely assumed that *M. manitatra* occupies each of the three forest fragments (Blanco *et al.*, 2018; Donati *et al.*, 2019), previous work has suggested otherwise. Hapke *et al.* (2012) reported two *Microcebus* species from the massif, *M. cf. rufus* and *M. murinus*, each with discreet distributions. However, this report preceded two taxonomic revisions that bear directly on our understanding of *Microcebus* distributions in the region. First, the '*murinus*' species complex has been expanded to include *M. manitatra* and *M. ganzhorni*, and second, *M. tanosi* has been described as distinct from *M. rufus*. Following the description and naming of *M. manitatra* (Hotaling *et al.*, 2016), all subsequent accounts omit the earlier observation of Hapke *et al.* (2012) and assume instead that all remaining forests support the new form, *M. manitatra*, exclusively.

Beyond the Ambatotsirongorongo massif, it is further hypothesized that the nearby (~5 km) littoral forest block

of Petriky (800 ha) also supports *M. manitatra*, based on mtDNA analyses (Hapke *et al.*, 2012). Petriky represents a particularly important and highly threatened habitat type in itself, characterized as a sub-category of evergreen forest occurring on a sand substrate (Dumetz, 1999). Like other littoral forests, Petriky supports a rich biodiversity and is noted for its high floristic value (Consiglio *et al.*, 2006; Temple *et al.*, 2012). Petriky is the most southerly intact littoral forest patch in the region and is considered a transitional ecosystem, supporting a biota typical of both dry and humid littoral forest formations (Rabenantoandro *et al.*, 2007). Notably, the composition of the lemur communities at both sites varies considerably, underscoring the specialized nature of both habitats. In this report, we aim to clarify the spatial distribution of the Critically Endangered *M. manitatra*.

Methods

Sample collection

As part of a broader sampling effort for mouse lemurs across the southeast, the Ambatotsirongorongo massif and the coastal forest of Petriky were sampled during three expeditions between October 2022 and June 2023. Animals were captured using a combination of Sherman trapping and direct hand capture. Animals were sedated using a standardized dose of ketamine (1 µl), administered into the quadriceps muscle. Lidocaine (5%) was applied topically to the ear pinna, and skin biopsies (ear clips) were collected and stored in 99% ethanol. All animals were released back to their initial capture sites after a period of post-operative monitoring, ensuring the effects of sedation had completely passed.

Genetic analysis

Whole genome re-sequence data was generated for two mouse lemurs sampled at Bemanasy forest (Am 2, Am10) and two mouse lemurs sampled at the Petriky (P1, P2) forest. The libraries for sequencing were built

with illumina DNA prep workflow, with sequencing using an illumina Novaseq 6000 instrument at an approximate coverage of 10X. The read length was 150bp. We trimmed the raw reads to eliminate adaptors with Trimmomatic version 0.4 (Bolger *et al.*, 2014). Clean reads were aligned to the *Microcebus murinus* reference genome version Mmur_3.0 (Genebank accession GCF_000165445.2) using BWA mem version 0.7.17 (Li and Durbin, 2009). The resulting BAM files were indexed and subsetted to the specific region of the cytochrome B gene (cytB), NC_028718.1:14222-15361. We then used SAMTOOLS version 1.7 (Li *et al.*, 2009) to call SNPs and index the resulting vcf file. The consensus command of BCFTOOLS version 1.17 (Danecek *et al.*, 2021) was used to extract the consensus sequence of each individual. The resulting fasta sequences were then concatenated together with all the cytB sequences used in Hotaling *et al.* (2016) to create a multi-fasta file used to build the phylogenetic tree. A maximum likelihood phylogenetic tree was created using the software iQtree version 1.6.12 (Nguyen *et al.*, 2015) and visualized with Figtree version 1.4.4.

Results

We captured a total of 10 mouse lemurs on the Ambatotsirongorongo massif and 14 in the littoral forest of Petriky. We found two distinct morphological phenotypes on the Ambatotsirongorongo massif (Fig. 1) with the 'rufus' form genetically corresponding to *M. tanosi* (Fig. 2). The second phenotype corresponds both by morphology and location to *M. manitatra*, as described by Hotaling *et al.* (2016). In Petriky, we observed a single phenotype which also corresponds both morphologically and genetically to *M. manitatra*. Observations of other lemur species were recorded opportunistically at both sites during the expeditions (Tab. 1).

Discussion

The findings of this study have clear implications for

Tab. 1: Lemur inventories for the Ambatotsirongorongo massif and Petriky forests. Species lists derived from earlier works (Ganzhorn *et al.*, 2007; Eppley *et al.*, 2019), with contemporary observations included.

Locality	Species	Activity Pattern	Typical Affinity	Observed
Petriky	<i>Avahi meridionalis</i>	Nocturnal	Humid forest	Y
	<i>Cheirogaleus cf. thomasi</i>	Nocturnal	Humid forest	Y
	<i>Microcebus manitatra</i>	Nocturnal	Dry forest	Y
	<i>Lemur catta</i>	Diurnal	Dry forest	Y
	<i>Propithecus verreauxi</i>	Diurnal	Dry forest	X
Ambatotsirongorongo Massif	<i>Avahi meridionalis</i>	Nocturnal	Humid forest	Y
	<i>Cheirogaleus lavasoensis</i>	Nocturnal	Humid forest	Y
	<i>Cheirogaleus thomasi</i>	Nocturnal	Humid forest	X
	<i>Daubentonia madagascariensis</i>	Nocturnal	Humid forest	X
	<i>Microcebus manitatra</i>	Nocturnal	Dry forest	Y
	<i>Microcebus tanosi</i>	Nocturnal	Humid forest	Y
	<i>Eulemur collaris</i>	Cathemeral	Humid forest	X
	<i>Haplemur meridionalis</i>	Cathemeral	Humid forest	Y
	<i>Lemur catta</i>	Diurnal	Dry forest	Y
	<i>Propithecus verreauxi</i>	Diurnal	Dry forest	X

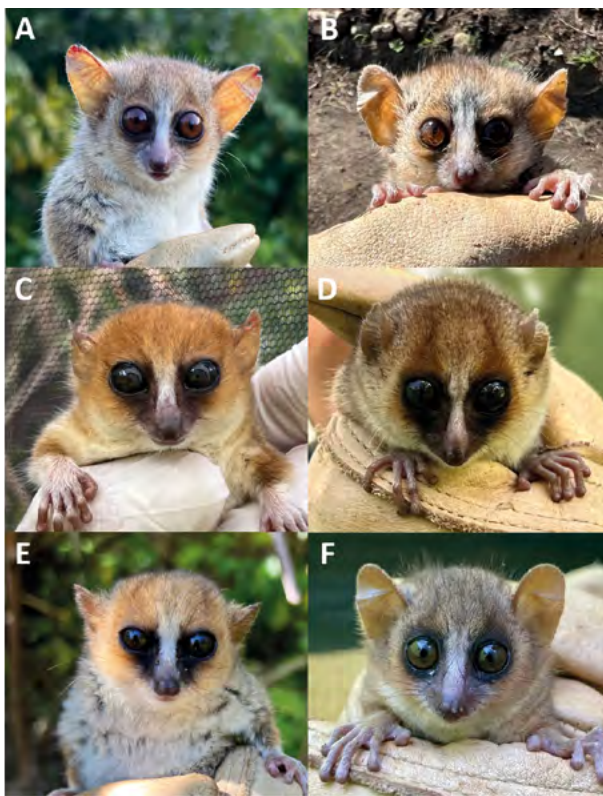


Fig. 1: Representative phenotypes from the study area. A+B) *Microcebus manitatra*; Ambatotsirongorongo / Sakoamaso forest. C+D) *Microcebus tanosi*; Bemanasy forest. E) *Microcebus tanosi*; Lavaso forest. F) *Microcebus manitatra*; Petriky. All photographs by SHR.

the conservation of *Microcebus manitatra* and for the wider conservation management strategies at both the Ambatotsirongorongo massif and Petriky sites. First, we confirm the presence of two mouse lemur species in the Nouvelle Aire Protégée of Ambatotsirongorongo massif. Despite previous observations of *M. cf. rufus* reported on the massif (Hapke et al., 2012), recent population estimates, and distributional assessments are based on the premise that *M. manitatra* occupies the entire range of fragments (Blanco et al., 2020). However, we have determined that the remaining intact fragments at higher altitudes (Bemanasy and Lavaso) support only *M. tanosi*, a humid forest species normally associated with the rainforests of Andohahela and Tsitongambarika. Whilst *M. manitatra* does evidently occur on the mountain (the area represents the type locality for the species), it appears to be distributed at lower altitudes and outside of intact standing forest, thus existing solely within the heavily degraded and secondary connective habitats on the eastern slopes (e.g., Ambatotsirongorongo and Sakoamaso). The forest fragment (Ambatotsirongorongo) from which *M. manitatra* was originally described (erroneously referred to as Bemanasy in Hotaling et al. (2016) and repeated in subsequent publications), has now been cleared. No individuals matching the *M. manitatra* phenotype were observed in either Bemanasy or Lavaso, upholding the earlier observation of Hapke et al. (2012) that can now be interpreted as *M. manitatra* and *M. tanosi* having discrete distributions. Thus, the type locality of *M. manitatra* (Bemanasy mouse lemur), appears to have been incorrectly assigned. These findings suggest that the area of occupancy for *M. manitatra* on

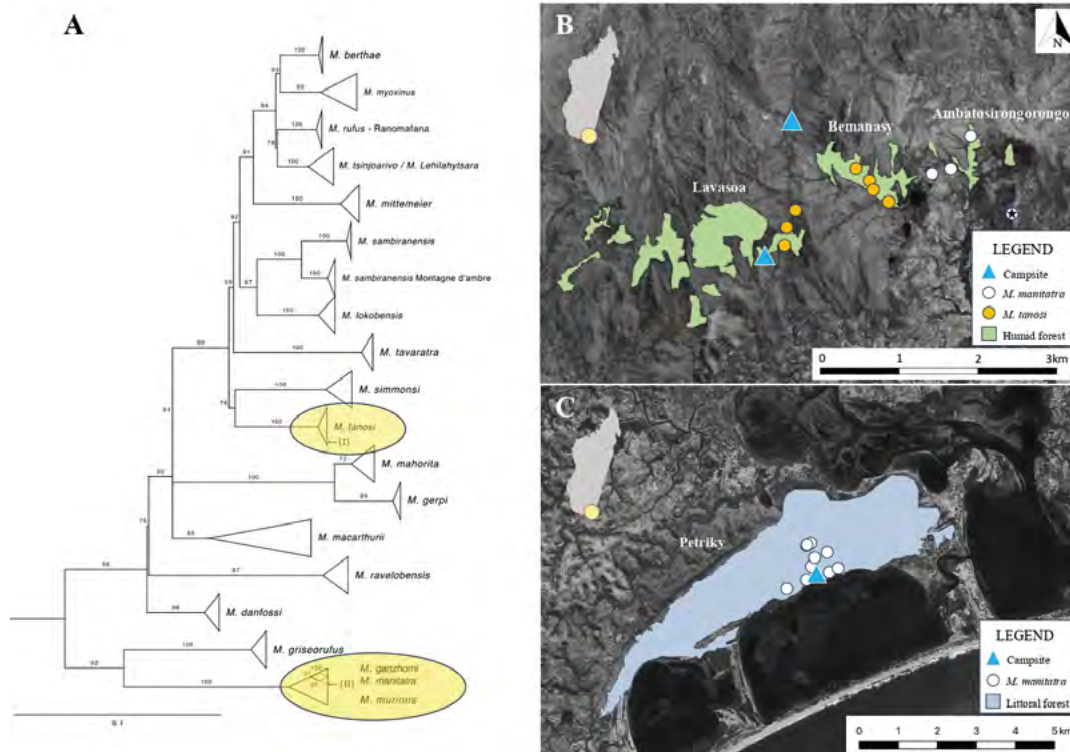


Fig. 2: A) Phylogenetic placement of sequenced individuals. Animals captured in Bemanasy (I) forest cluster with *M. tanosi* and individuals from Petriky (II) cluster with *M. manitatra*. *Cheirogaleus* samples (K133A, K152A and K180A) used as outgroups. B) Distribution of captured individuals on Ambatotsirongorongo massif (starred individual shows capture site of *M. manitatra* type specimen (Hotaling et al., 2016). Forests in this Ambatotsirongorongo region are now heavily degraded. C) Distribution of individuals captured in Petriky.

the Ambatotsirongorongo massif is instead restricted to a series of highly degraded patches of connective and secondary forest, likely totalling ca. 10-15ha.

In the field, the two species (*M. tanosi* and *M. manitatra*) are clearly discernible by phenotype, with pelage coloration and ear size being clear diagnostic features (Fig. 1). Given the ease of visual identification, we can say that there does not appear to be any area where the two species are sympatric on the massif, although some interaction may occur towards the southern end of the Bemanasy forest fragment. We observed and captured several *M. tanosi* individuals in connective habitat outside of the Lavasoa forest fragment, indicating that the species readily utilizes degraded habitat beyond the sharp humid forest boundary. This distributional pattern may also be mirrored in the other Cheirogaleid species present on the massif; with the Lavasoa dwarf lemur *Cheirogaleus lavasoensis* occupying the intact rainforest blocks Lavasoa and Bemanasy, and Thomas' dwarf lemur *C. thomasi* present in degraded forest habitats (e.g., Vohisampa) on the lower eastern slopes (J. Rakotonranary, pers. obs., 2020).

Importantly, we further conclude that Petriky now represents the critical remaining habitat for *M. manitatra*. This roughly 800 ha littoral forest block is expected to undergo extensive mining in the coming years, reducing the remaining habitat to a 120 ha Conservation Zone (Temple *et al.*, 2012), thus calling for urgent conservation evaluation of this locality. The proposed mining operation is anticipated to place extreme pressure on all plant and animal populations at the site. Whilst QIT Madagascar Minerals (QMM), along with Nature Based Solutions, are committed to partly restoring mined areas (c.225 ha) (Temple *et al.*, 2012), their strategies, schedules and methodologies must be shared with wider stakeholders for transparency and constructive scrutiny. Confirmation that the *Microcebus* form present in Petriky corresponds to the Critically Endangered *M. manitatra* should invite local area managers at QMM to revisit their proposed biodiversity strategies, especially given that operations have not yet begun. Expansion of the existing Conservation Zone should be considered as an important strategy in Petriky, since *M. manitatra* population density appears to be highest in the protected areas (Malone *et al.*, 2013). Of pressing concern, littoral habitats are poorly represented in the country's protected area network at present (Goodman *et al.*, 2018), yet it is now clear that the three major littoral forest blocks in the southeast (Sainte Luce, Mandena and Petriky) each support a distinct form of *Microcebus* (*M. tanosi*, *M. ganzhorni* and *M. manitatra*, respectively).

Whilst the two sites, Ambatotsirongorongo and Petriky, are only separated by approximately 5 km, the intervening habitat is heavily modified, consisting mainly of rice paddies and pastures. Two small tomb forests (Amporoforo and Loharano) persist in between the two sites, although it is unclear whether these fragments still support any lemur species given their restricted size (9 ha and 4 ha, respectively). Under current strategies, once mining operations are completed, *M. manitatra* may only occupy a fragmented range of <150 ha. Although some slight phenotypic and genetic differences may exist between the populations on Ambatotsirongorongo massif and Petriky, these are likely explained by isolation

and topographical effects and clearly do not extend to species delimitation.

We wholeheartedly echo the call for urgent conservation actions on the Ambatotsirongorongo massif (Eppley *et al.*, 2019), given it clearly supports a diverse and unusual assemblage of lemur species, as well as numerous other threatened and range-restricted taxa (e.g., *Chrysalidocarpus prestonianus*, the Madagascar fruit bat *Eidolon dupreanum*, the eastern falanouc *Eupleres goudoti*, and *Phelsuma antanosy*). However, we further urge that attention be immediately directed towards the littoral forests of Petriky. The IUCN Red List assessment for *M. manitatra* urgently requires updating in light of these new findings.

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Ethics and permissions

All field work was carried out with permission from the Malagasy authorities (Permits: No.290/22 and No.167/23/MEDD/SG/DGGE/DAPRNE/SCBE.Re). All animals were handled and treated according to IACUC protocol A163-22-09, registered to the corresponding author.

Data availability

The code and multi fasta file with the sequences used to build the phylogenetic tree are available at: https://github.com/CaroSegami/Ambatotsirongorongo_mouse_lemurs. New cytB sequences are available at NCBI under accession numbers OR754226 (Am10), OR754227 (Am2), OR754228 (P1) and OR754229 (P2).

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***Phaner furcifer* - The ghost lemur of northeastern Madagascar?**

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Abstract

Fork-marked lemurs (*Phaner*) are a group of four medium-sized, gummivorous lemur species belonging to the Cheirogaleidae family, representing one of the least-studied primate genera in Madagascar. This study focuses on elucidating the presence and local knowledge of the Endangered *Phaner furcifer* in the Analanjirofo region of northeastern Madagascar. Field surveys included more than 300 km of nocturnal transect surveys across varying forest degradation stages, and 243 household interviews to gather local knowledge about this species. Results indicate the absence of *P. furcifer* in the study region, including areas with historical anecdotal reports. This species was not detected visually or acoustically during the extensive surveys, and only 1.6% of interviewees mentioned occasional sightings, but only in areas of previous anecdotal reports. This suggests either a recent decline of the population due to anthropogenic pressures and deforestation, or a genuinely disjunctive distribution of the species, potentially representing two distinct lineages. The study highlights the critical conservation status of *P. furcifer* and emphasizes the urgent need for conservation measures in the face of ongoing deforestation and climate change in Madagascar. Furthermore, it underscores the importance of taxonomic research to better understand the diversity and distribution of these enigmatic lemurs and the ecosystems they inhabit. Immediate action is imperative to safeguard the future of *P. furcifer* and other sympatric lemur species within this threatened region.

Introduction

Fork-marked lemurs (*Phaner*) from the Cheirogaleidae

family are medium-sized, nocturnal and gummivorous lemurs and among the least-studied of all Malagasy primates (Mittermeier *et al.*, 2023). This genus had long been considered to be monotypic until Groves and Tattersall (1991) defined four subspecies based on morphological differences. These were elevated to species rank by Groves (2001), although this classification was disputed later on (Tattersall, 2007). These four species, *P. furcifer*, *P. parienti*, *P. pallescens* and *P. electromontis*, occur in allopatry in a discontinuous range that does not include the southeastern rainforests and the spiny forests (Fig. 1). Moreover, they have not been reported from areas in between their known distributions (Hending, 2021; Mittermeier *et al.*, 2023). From a biogeographical perspective, this is puzzling, and the barriers that determine and limit these distributions remain unclear, which is in contrast to other lemurs (*Microcebus*: Olivieri *et al.*, 2007; van Elst *et al.*, 2023; *Lepilemur*: Craul *et al.*, 2007). Molecular studies have been very limited so far and mainly inconclusive (e.g., Salmona *et al.*, 2018).

Recent efforts have aimed to elucidate the distribution of *Phaner electromontis* in northern Madagascar, highlighting the potential for another undescribed lineage within this genus (Hending *et al.*, 2020; Hending, 2021; Salmona *et al.*, 2018). Other research has focused primarily on behavioural and ecological aspects of *P. pallescens* (e.g., Petter *et al.*, 1971; Charles-Dominique and Petter, 1980; Schülke, 2003, 2005), while some studied the ecology and habitat use of *P. parienti* (Forbanka, 2018a; Webber *et al.*, 2019). With the exception of two studies (i.e., Forbanka, 2018a, 2018b), the fourth species of *Phaner*, *P. furcifer*, remains the most poorly-studied species from this genus. It has only rarely been observed in the wild and is assumed to occur throughout the humid forests of northeastern Madagascar, between Zahamena National Park (NP) in the south and the Masoala/Makira region in the north (Mittermeier *et al.*, 2023). Its estimated range is based on opportunistically gathered observations from the northern and southern limits of its assumed distribution (as summarized in Mittermeier *et al.*, 2023). However, the ranges in between have not been surveyed for the presence of this species so far.

Here, we report on nocturnal field surveys and interviews with local community members on the presence of, and the local knowledge on, Endangered *Phaner furcifer* (Louis *et al.*, 2020a) from multiple sites located between Zahamena NP and Masoala NP in the Analanjirofo region of northeastern Madagascar.

Methods

Study region

This study was conducted in the humid lowland and montane forests of northeastern Madagascar, stretching from the boundary of Masoala National

Park in the northeast, to the Maningory River in the south (see Schübler *et al.*, 2020; Fig. 1). A total of 22 study sites were visited along this 200 km long stretch of Madagascar's east coast, of which all were located in unprotected forests (Fig. 1).

Nocturnal surveys

We conducted nocturnal transect surveys, using existing pathways crossing undegraded and differently degraded stages of humid primary forests, and also including secondary habitats that resulted from shifting cultivation and agroforestry plantations. Transects were equally distributed across the different degradation stages and walked 1–3 times at an average speed of 0.5 km/h with 2–3 observers, using forehead lamps to locate lemurs by the reflection of their eye shine. A total of 109 transects or 303.73 km were surveyed for *P. furcifer* between August and September 2017, August and October 2019, September and December 2021, and March and May 2022 (see Schübler *et al.*, 2023).

Household interviews

We interviewed a total of 243 adult local community members from 22 different villages, all located in the proximity of forests. Similar to the study of Randimbiharirinina *et al.* (2021), all interviews were conducted by a native speaker in Malagasy. Before any interview was conducted, the village leaders were approached to explain the objectives of the research (i.e., to learn about local knowledge and interactions with lemurs, local land use strategies, and that all data is anonymized and not traceable to the communities) and to ask for permission. We explained to each respondent

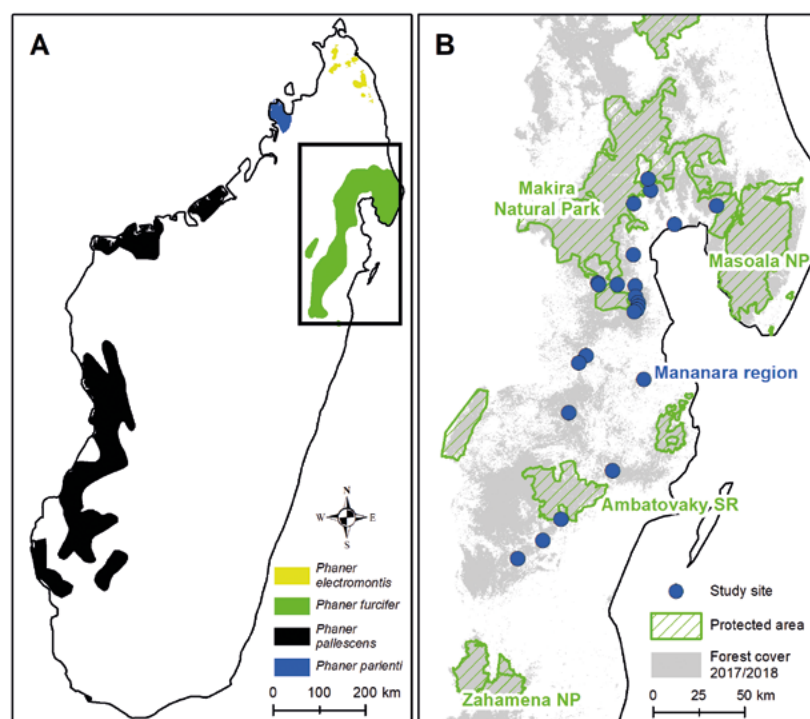


Fig. 1: A: IUCN ranges of *Phaner* spp. in Madagascar (Borgerson, 2020; Louis *et al.*, 2020a, b; Sgarlata *et al.*, 2020). B: Estimated distribution of *P. furcifer* with study sites, protected areas (UNEP-WCMC, 2023) and forest cover of 2017/18 (Schübler *et al.*, 2020). Sightings of *Phaner furcifer* are reported from Zahamena National Park (NP), central and western Masoala National Park and the northeastern and central part of Makira Natural Park (Mittermeier *et al.*, 2023; Rasolofson *et al.*, 2007). NP = National Park, SR = Special Reserve.

(adults of >18 years) that participation was voluntary, and participants could end the interview at any time or deny certain answers. After giving their informed consent, we presented participants with photographs of different lemur species, including *P. fuscifer*, and asked whether this species was seen before and whether it could be named. Among these species were also other elusive lemurs like *Allocebus trichotis* (Schüßler et al., 2023) and *Daubentonia madagascariensis* (Randimbiharinarina et al., 2021). In a second step, we asked specifically for *P. fuscifer* (Malagasy name: Tantana, Tanta or Vakiandrina; Mittermeier et al. (2023)), whether it is known and in which densities it occurs in the surroundings of the village. This study was conducted under research permits 197/17/MEEF/SG/DGF/DSAP/SCB.Re, 169/19/MEDD/SG/DGEF/DGRNE, 349/21/MEDD/SG/DGGE/DAPRNE/SCBE.Re, and 030/22/MEDD/SG/DGGE/DAPRNE/SCBE.Re., issued by the Direction Générale de l'Environnement et des Forêts of Madagascar and approved by the ethics committee of the University of Hildesheim (Germany). We adhered to ethical standards proposed by Wilmé et al. (2016) and the World Medical Association (2013).

Results

Besides sightings of several other lemur species, *Phaner fuscifer* was not observed during our surveys. The vocalizations of *P. fuscifer* were also not heard at any of the sites throughout the whole duration of the study. None of the 243 interview participants could provide a name for this species when presented with a photograph, and only 4 respondents (1.6%) mentioned that this species is rarely seen in the forests surrounding the village. Three of these four answers came from Makira, and one from the surroundings of Ambatovaky Special Reserve.

Discussion

Reports of the presence of *P. fuscifer* in the northeastern forests of Madagascar have been rare and mostly anecdotal (see Mittermeier et al., 2023). They furthermore originate from the two endpoints of its estimated geographic distribution, the Makira/Masoala region and Zahamena NP (Fig. 1). Although we invested a considerable amount of standardized survey effort and spent long periods of time near and inside the forests, we failed to provide any evidence for the presence of this species in between Masoala NP and Zahamena NP. This is quite surprising for a species that is highly vocal and easy to acoustically detect and distinguish from heterospecifics (Hending et al., 2020; Markolf et al., 2022). In accordance with our own nocturnal surveys, none of the participants of our interviews could recall having seen this species when presented with a photograph, and only four out of 243 participants expressed that this species occurs in the forests surrounding their village, yet being considered rare. Interestingly, these assessments came from regions (i.e., Makira Natural Park, Ambatovaky Special Reserve) that already had anecdotal occurrence records, but not from the areas in between. One recent study (i.e., Schüßler et al., 2018) conducted in the Mananara region (Fig. 1) found *P. fuscifer*. However, this presence record is based on a single sighting of one individual in September 2017. Although unambiguously identified as *Phaner* spp. by its prominent fork-shaped facial mask, seen from about three meters distance (by D.S.), this occurrence

remains questionable, as it could not be confirmed in a 2022 survey in the same forests and interviews with the local community.

Our findings can be interpreted in two ways: *P. fuscifer* is absent from the entire region in between the previous anecdotal reports, or it was present there before but has vanished under the recent degree of anthropogenic pressure on the forest and the high levels of deforestation in the region (Schüßler et al., 2020). As we did not find this species in the areas from which anecdotal reports were present, and few local community members could indicate that it occurs in low population density around their villages, the theory of the vanishing of *P. fuscifer* seems most likely for these places. As a species that occupies the upper canopy niche with a high dependence on specific tree gums (Forbanka, 2018a, 2018b), *P. fuscifer* may be disproportionately impacted by selective logging, the decrease in overall forest area and forest fragmentation, leading to a rapid vanishing of this species as soon as people start extracting wood and converting forests into agricultural fields (i.e., shifting cultivation, Styger et al., 2007). However, this does not explain the complete absence of observations and local community knowledge in the areas between Makira/Masoala and Zahamena NP, which roughly equal about 200 km of aerial distance. Our findings here may rather point towards a disjunctive distribution and an actual absence of *P. fuscifer* from this region, which may in turn raise questions about the possibility of representing two distinct lineages, as also hypothesized for *P. electromontis* in northern Madagascar (Hending, 2021; Salmons et al., 2018). The singular observation of *P. fuscifer* in the Mananara region, however, does not accommodate any of these hypotheses, as the region is highly fragmented, has been long-term isolated from larger and continuous forests of the higher elevations (Schüßler et al., 2018, 2020), and is in the middle of previous reports on this species (Fig. 1).

Taken together, the absence of *Phaner* at all sites investigated in this study, even from some locations where it was historically reported, is worrying and suggests a significant decline in the population size and area of occupancy of this species. The forests of eastern Madagascar remain threatened by ongoing deforestation and unmitigated climate change (Hending et al., 2022; Vieilledent et al., 2018; Schüßler et al., 2020), and lemurs are still routinely hunted within this region (Golden, 2009; Borgerson et al., 2016). Urgent conservation action alongside increased taxonomic efforts and molecular studies are required to safeguard the future of *P. fuscifer*, and the other lemur species with which it occurs sympatrically.

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Population size of nocturnal lemur species and morphological measurements of Cheirogaleidae in Bemanevika Protected Area

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Abstract

We assessed the population sizes of nocturnal lemur species within Bemanevika Protected Area (PA) in the northern highlands of Madagascar from October to December 2019. We used the Transect Distance Sampling method for counting nocturnal lemur species along six permanent transects in the three largest forest blocks of Andriakanala, Matsaborimaitso and Matsaborimena. We surveyed each transect line during three consecutive nights from 18:00 to 22:00. We also carried out capture-releases in order to verify species of the Cheirogaleidae family through morphological parameters. Our findings showed that the three forest blocks had at least 117 individuals belonging to five threatened nocturnal species of lemurs: *Allocebus trichotis* (EN), *Cheirogaleus major* (VU), *Microcebus sambiranensis* (EN), *Lepilemur dorsalis* (EN) and *Avahi unicolor* (CR). The Cheirogaleidae family was represented by *A. trichotis*, *C. major* and *M. sambiranensis* based on morphological measurement. Relative lemur abundance was highest in *C. major* with 39.68 %, whilst *M. sambiranensis* and *A. trichotis* were 33.98 % and 5.28 %, respectively. The estimated population density range of *C. major* was 68 - 131 ind/km², 144 - 202 ind/km² for *M. sambiranensis* and 13 - 23 ind/km² for *A. trichotis*. Only the density of *M. sambiranensis* and *C. major* showed a statistically significant variation between forest blocks. This study provides information on the current population size

of nocturnal lemur species and their distribution throughout three forest blocks in Bemanevika PA, especially for the Cheirogaleidae. *Daubentonia madagascariensis* was not observed, although signs of its presence were reported.

Introduction

Madagascar's primate diversity is striking, with five families (Cheirogaleidae, Lemuridae, Lepilemuridae, Indriidae and Daubentoniidae) and 15 genera found nowhere else in the world (Mittermeier *et al.*, 2010; Schwitzer *et al.*, 2013). The island currently hosts 113 lemur species following the discovery of *Microcebus jonahi*, which is a relatively large-bodied and short-eared mouse lemur located in northeastern Madagascar (Schübler *et al.*, 2020).

Unfortunately, Madagascar's biological heritage of the Strepsirrhine primates, a suborder including its endemic lemurs alongside the lorises and galagos of Asia and Africa, is particularly susceptible to extinction due to anthropogenic activities (Jernvall and Wright, 1998). Whilst some lemur species are adaptable and resilient to habitat degradation and deforestation (Hending, 2021), most species are threatened by habitat destruction such as deforestation (Harper *et al.*, 2007), the expansion of rice cultivation, mining extraction, illicit trafficking, hunting and poaching activities (for food, as pets and selling) and climate change (Raxworthy *et al.*, 2008). Facing this alarming situation, the Malagasy government is aware of the habitat loss from year-to-year and the decline of the lemur populations, and has already established and implemented a conservation plan based on habitat protection and eco-tourism.

The family Cheirogaleidae is represented by five genera and 41 species: *Microcebus*, the mouse lemurs (25 species); *Allocebus*, the hairy-eared dwarf lemur (one species); *Mirza*, the giant mouse lemurs (two species); *Cheirogaleus*, the dwarf lemurs (nine species); and *Phaner*, the fork-marked lemurs (four species) (Hotaling *et al.*, 2016; McLain *et al.*, 2017; Mittermeier *et al.*, 2008). All members of this family are nocturnal, roost during the day in small nests of dead leaves, in tree holes, or holes in the ground, move quadrupedally, have elongated bodies with short legs, and some Cheirogaleidae undergo prolonged periods of seasonal torpor (Mittermeier *et al.*, 2010).

Many studies of different taxa (birds, reptiles and amphibians) have already been conducted in Bemanevika Protected Area (PA) in order to enrich available information on biodiversity and to increase site visibility and awareness at national and international levels. Previous research confirmed the presence of six species of lemur in Bemanevika PA through direct and indirect observations (Goodman *et al.*, 2018; Bezandry *et al.*, 2021): *Cheirogaleus* sp., *Microcebus* sp., *A. trichotis*, *Lepilemur dorsalis*, *Avahi unicolor* and *Daubentonia madagascariensis*. However, information about their population size and morphological data, particularly for the Cheirogaleidae family, remains insufficient. This study aimed to fill this gap with a view to their conservation.

Methods

Study site

The Bemanevika PA covers a total area of 35,605 ha

and is located in the Bealanana District, Sofia Region in the northern highlands of Madagascar, between 14°10' and 14°35' S, and 48°25' and 48°50' E. It is classified as a Protected Harmonious Landscape equivalent to IUCN category V, and co-managed by The Peregrine Fund (TPF) with four community-based local associations. The habitat is composed of a mosaic of ecosystems: rain forests, savannas, lakes and marshes. The climate is characterized by two distinct seasons: hot and humid between September and May, and a cold and dry season from June to August. The annual rainfall and the mean average temperature are 2,595.1 mm and 17.7°C, respectively (Rakotoson, 2018). During the two-month study period (29th October to 28th December 2019), we visited three evergreen rainforest blocks: Matsaborimena, Matsaborimaitso and Andriakanala (Fig. 1), each of which has a permanent volcanic lake.

Nocturnal lemur census

Prior to our census, we investigated each forest block before establishing the transects. We applied the linear transect method (Whitesides *et al.*, 1988) for the nocturnal census. We used six permanent transects (two transects per site) of 1,000 m length each from the edge to the interior of the forest (Tab. 1). Three consecutive nights of observations were spent at each transect from 18:00 to 22:00, using headlamps and with a relatively low walking speed of about 1 km/h. We recorded all lemur individuals seen, and the density of each species was calculated based on the number of individuals observed. Density was calculated by multiplying the total length of the transects by two times the average perpendicular distances to the transect of each individual observed. The relative abundance was obtained by the ratio of the total number of individuals of each species to the total number of all species observed at the site, multiplied by 100.

Capture and measurements

We trapped individuals using 20 Sherman Live Traps (Hafen *et al.*, 1998; Evasoa *et al.*, 2019; Hasiniaina *et al.*, 2020). We set traps every 25 m along the transects, placed them on horizontal branches 1 to 2 m above the ground, and baited them with a small banana slice. We opened traps around 18:00 and checked them the next morning around 05:00. Three consecutive nights of capture were conducted for each transect. A total

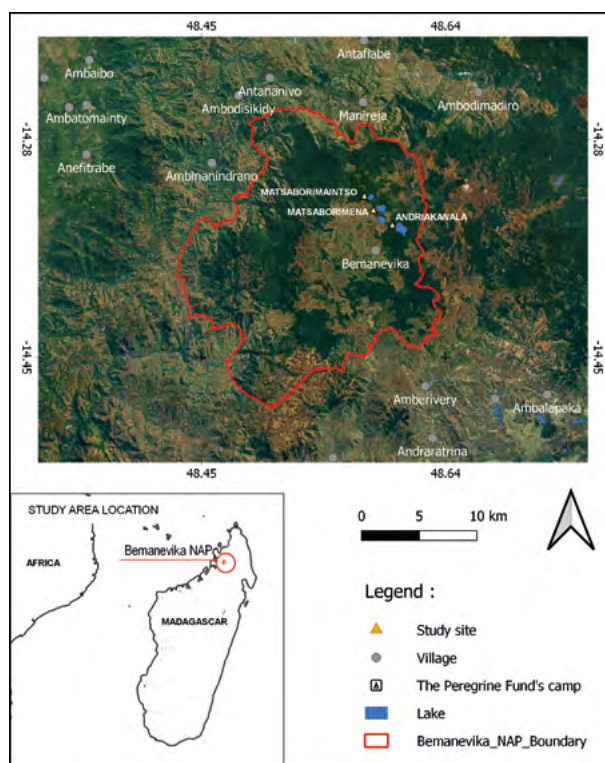


Fig. 1: Location of study sites in the Bemanevika Protected Area.

of 120 night-traps were set during the capture sessions in the two transects for each forest block. All captured animals were anesthetized with 50 mg/ml ketamine to enable proper handling of the animals, and we took measurements by applying the techniques described by Louis *et al.* (2006). After processing, we released the lemurs at the site where they were captured. We identified directly all observed species from their size, the colour of their coat, their vocalization, and their local name. We also used field guides (Mittermeier *et al.*, 2010) for facilitating the identification.

Data analysis

The relative abundance of each species per site was calculated from the relationship of the number of observed individuals of that species to the total number

Tab. 1: Characteristics of transects placed in the study sites.

Site	Forest area	Transect	Length	Geographic Coordinates	
				Start point	Ending point
Matsaborimena	423 ha	A	1 000 m	S 14°20'25" E 048°35'12"	S 14°20'16" E 048°35'10"
		B	1 000 m	S 14°20'32" E 048°35'06"	S 14°20'15" E 048°35'13"
Matsaborimaitso	306 ha	C	1 000 m	S 14°19'41" E 048°34'55"	S 14°21'32" E 048°35'30"
		D	1 000 m	S 14°21'36" E 048°35'42"	S 14°21'29" E 048°35'33 "
Andriakanala	1 050 ha	E	1 000 m	S 14°21'32" E 048°35'30"	S 14°19'39" E 048°34'55"
		F	1 000 m	S 14°21'34" E 048°35'48"	S 14°19'41" E 048°34'53"

of observed individuals of all species. The perpendicular distance between an observed individual and the transect was estimated. The sampled area can be determined by considering the average detection distance and the length of the transect traveled. Density was then calculated by ratio of the number of individual lemurs within our sampling area, based on the derived detection function developed by Whitesides *et al.* (1988).

We also calculated the Jaccard index (J) to evaluate the similarity of composition of nocturnal lemurs in Bemanevika PA with other PAs localized in the northern part of Madagascar. For this, the following formula was used:

$$J = \frac{C}{(N_1 + N_2) - C}$$

Here, C = the number of species in common between two sites, N_1 = the number of distinct species at site 1, and N_2 = the number of distinct species at site 2.

In this study, we compared the similarity of the Bemanevika PA in terms of species composition with the surrounding Protected Areas such as Mahimborondro PA, COMATSA Nord PA, Manongarivo Special Reserve and Tsaratanana Strict Nature Reserve (Mittermeier *et al.*, 2010; Goodman *et al.*, 2018). We used an analysis of variance test (ANOVA) to compare lemur species density between forest blocks in R version 3.6.0 (R Core Team, 2019). For the test, we used $\alpha = 0.05$ to investigate the statistical significance of results.

Results

We surveyed for 18 nights along the six transects inside the three large forest blocks (Matsaborimena, Matsaborimaitso and Andriakanala) within Bemanevika PA. We recorded 117 individual lemurs belonging to five species and three families (Cheirogaleidae, Indriidae and Lepilemuridae), all threatened according to the IUCN Red List (Tab. 2).

We identified through morphometric measurements the taxonomic names of the three species in the family Cheirogaleidae. A total of 360 trap-nights yielded 10 adult individuals, comprising six *Cheirogaleus major*, three *Microcebus sambiranensis* and one *Allocebus trichotis* (Tab. 3). The mean mass of *C. major* was 282.5 ± 1.86 g ($N = 6$), with a mean tail length of 28.6 ± 1.03 cm (Tab. 3). *M. sambiranensis* had a mean mass of 32.33 ± 2.08 g ($N = 3$) and mean tail length of 12.2 ± 0.26 cm. The single individual of *A. trichotis* had a mass of 70 g and a tail length of 16 cm.

The relative abundance values ranged from 3.51% to 44.44% for the five species recorded (Tab. 2). For the Cheirogaleidae species, *C. major* had the highest relative abundance at 39.68% (36.00 - 44.44%), and *M. sambiranensis* and *A. trichotis* were 33.98% (29.82 - 36.11%) and 5.28% (3.51 - 8.33%), respectively. These results suggest that *C. major* and *M. sambiranensis* were more abundant in comparison to the rarer *A. trichotis*. The Matsaborimena site hosted all five nocturnal lemur species observed in Bemanevika PA.

For Cheirogaleidae, the highest number of individuals were recorded at the Matsaborimena site, followed by Matsaborimaitso and Andriakanala. The calculated density was also highest within Matsaborimena compared to the other sites: 202 ind/km² for *M. sambiranensis*, 131 ind/km² for *C. major* and 23 ind/km² for *A. trichotis* (Tab. 4). However, only the densities of *M. sambiranensis* ($P < 0.001$) and *C. major* ($P < 0.001$) showed a statistically significant variation between the three forest blocks. Density remains homogeneous and does not indicate significant variation between sites for other species.

When comparing nocturnal lemur species composition within Bemanevika PA with the four other surrounding protected areas, all were nearly equal in the number of species, ranging from five to seven species. *Daubentonia madagascariensis* has been reported from each of the PAs, while *Lepilemur seali* has only been found at COMATSA

Tab. 2: Number of individuals (n) and relative abundance (%) of each species recorded at the three study sites in Bemanevika PA. (EN: Endangered; VU: Vulnerable)

Species	Conservation status (IUCN 2022-2)	Andriakanala		Matsaborimaitso		Matsaborimena	
		n	%	n	%	n	%
<i>Allocebus trichotis</i>	EN	1	4	3	8.33	2	3.51
<i>Cheirogaleus major</i>	VU	9	36	16	44.44	22	38.6
<i>Microcebus sambiranensis</i>	EN	9	36	13	36.11	17	29.82
<i>Lepilemur dorsalis</i>	EN	0	-	4	11.11	7	12.28
<i>Avahi unicolor</i>	CR	6	24	0	-	9	15.79

Tab. 3: Morphometric parameters of recorded individuals in the family Cheirogaleidae.

Parameters	<i>Cheirogaleus major</i> (N = 6)	<i>Microcebus sambiranensis</i> (N = 3)	<i>Allocebus trichotis</i> (N = 1)
Weight (g)	282.5 ± 1.86	32.33 ± 2.08	70
Head length (cm)	6.67 ± 0.13	5.07 ± 0.12	5.1
Body length (cm)	19.8 ± 1.39	7 ± 0	10
Tail length (cm)	28.6 ± 1.02	12.2 ± 0.26	16

PA. *Avahi unicolor* was recorded at two contiguous PAs: Bemanevika and Mahimborondro. Across all the regional PAs, the family Cheirogaleidae is represented by eight species, of which six are threatened (Tab. 5). Among them, *A. trichotis* and *C. major* were the most represented. The PAs host almost the same number of Cheirogaleidae species, which varies from three to four species, respectively.

In terms of total lemur species richness, there was some variation between the northern protected areas (Tab. 5). Bemanevika and Mahimborondro PAs are very similar to each other in composition and in proximity. They recorded the highest value of similarity (Tab. 6), reflecting the number of species in common that are shared between these two sites. Whereas in comparing Bemanevika and Tsaratanana, Bemanevika and COMATSA, and Mahimborondro and COMATSA, similarity values were lower (Fig. 2).

Discussion

Our results broadly mirror previous research from Bemanevika PA. Bemanevika was known to host six nocturnal lemur species: *Allocebus trichotis*, *Microcebus* sp., *Cheirogaleus* sp., *Lepilemur dorsalis*, *Avahi unicolor* and *Daubentonia madagascariensis* (Rabearivony et al., 2010; Bezandry et al., 2021). During the two-month study period, we encountered five nocturnal lemur species

but did not confirm the presence of *D. madagascariensis*. However, we established the taxonomic identity of two species previously unidentified, from morphometric measurements of samples developed by Louis et al. (2006). These two taxa were *Cheirogaleus major* and *Microcebus sambiranensis*.

Groves (2000, 2001) divided *Cheirogaleus* into two species groups: the *C. major* group is composed of six species (*C. major*, *C. andysabini*, *C. crossleyi*, *C. grovesi*, *C. lavasoensis* and *C. sibreei*), and the *C. medius* group of three species (*C. medius*, *C. shethi* and *C. thomasi*). Our morphometric measurements allowed us to confirm only *C. major* in Bemanevika PA. *Microcebus* can be distinguished from *Cheirogaleus* by their much smaller size and more active movement (Mittermeier et al., 2010). However, a genetic analysis is needed to support these results.

The mouse lemurs, the smallest of all living primates in the world, are widespread throughout Madagascar and occupy both primary and secondary forests and even disturbed habitats (Mittermeier et al., 2010). Our study showed the same findings, with *M. sambiranensis* occurring at both primary and secondary forest habitats. Its known distribution is Manongarivo Special Reserve (Rasoloarison et al., 2000; Goodman and Soarimalala, 2002), northern Andranomalaza River and southern Sambirano River (Louis et al., 2006), and Sahamalaza-Iles Radama National Park, where a conservation action plan is in place to

Tab. 4: Densities (ind/km²) of nocturnal lemurs in Bemanevika PA.

Species	SITES		
	Andriakanala	Matsaborimaitso	Matsaborimena
<i>Allocebus trichotis</i>	13	23	23
<i>Cheirogaleus major</i>	68	130	131
<i>Microcebus sambiranensis</i>	144	164	202
<i>Lepilemur dorsalis</i>	-	18	28
<i>Avahi unicolor</i>	34	-	39

Tab. 5: Species composition for protected area sites in northern Madagascar: * = family of Cheirogaleidae; CR: Critically Endangered, EN: Endangered, VU: Vulnerable, NT: Near Threatened (IUCN 2022).

Species	Manongarivo	Bemanevika	Mahimborondro	Tsaratanana	COMATSA
* <i>Allocebus trichotis</i> (EN)	-	+	+	-	+
* <i>Microcebus sambiranensis</i> (EN)	+	+	-	-	-
* <i>Microcebus mittermeieri</i> (NT)	-	-	-	-	+
* <i>Microcebus</i> sp.	-	-	+	+	-
* <i>Cheirogaleus crossleyi</i> (VU)	-	-	-	-	+
* <i>Cheirogaleus major</i> (VU)	+	+	+	+	-
<i>Daubentonia madagascariensis</i> (EN)	+	+	+	+	+
<i>Lepilemur dorsalis</i> (EN)	+	+	+	-	-
<i>Lepilemur mustelinus</i> (VU)	-	-	-	+	-
<i>Lepilemur seali</i> (VU)	-	-	-	-	+
<i>Avahi occidentalis</i> (VU)	+	-	-	-	+
<i>Avahi unicolor</i> (CR)	-	+	+	-	-
* <i>Phaner parienti</i> (EN)	+	-	-	-	-
* <i>Phaner pallescens</i> (EN)	-	-	-	+	+

Tab. 6: Proximity matrix between Bemanevika PA and the other protected area sites in northern Madagascar in terms of nocturnal lemurs.

PA	Bemanevika	Mahimborondro	Manongarivo	Tsaratanana	COMATSA
Bemanevika	-				
Mahimborondro	0.67	-			
Manongarivo	0.38	0.22	-		
Tsaratanana	0.11	0.25	0.22	-	
COMATSA	0.10	0.10	0.20	0.10	-

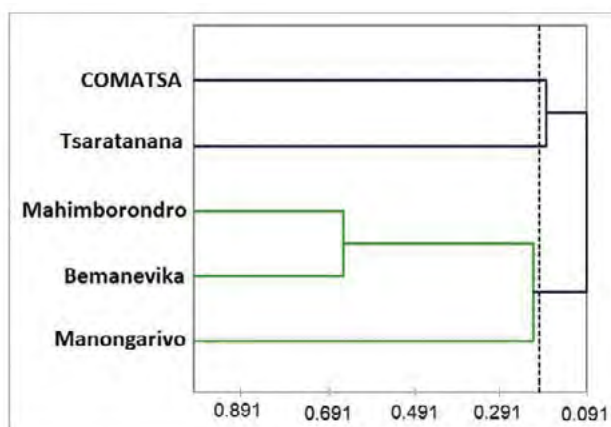


Fig. 2: Diagram of similarity among the compared protected areas of northern Madagascar.

protect this species (Hending *et al.*, 2017a; Hending *et al.*, 2017b). We confirmed its presence inside Bemanevika PA. The possibility of finding isolated populations is also reported on the Ampasindava Peninsula and in the Tsaratanana Massif (Randrianambinina *et al.*, 2003; Louis *et al.*, 2008).

A. trichotis is a tiny nocturnal lemur from the rainforests of eastern Madagascar. This species is superficially very similar to the mouse lemurs, except for the long-tufted hair around the ears (Mittermeier *et al.*, 2010). According to Bezandry *et al.* (2021), Bemanevika PA was a range extension for *A. trichotis*, but its population size was still unknown. Our study provided this information, although we only recorded six individuals at the study sites. This finding reflects its rarity; as Coppeto and Harcourt (2005) stated, *A. trichotis* remains a rare species. At least, four localities were confirmed to provide a range extension of this species within the PA; it currently occurs in the three moist evergreen forest blocks (Andriakanala, Matsaborimaitso and Matsaborimena) and on the forest edge of Marotaolana marsh (Bezandry *et al.*, 2021).

For Cheirogaleidae abundances, we estimated that they were relatively low within the Bemanevika PA considering the species' small sizes. Caldecott (1980) hypothesized that small lemur species would show their maxima of abundance in lowland rainforests, since the ratio between energy expenditure and nutrient intake is disadvantageous for them at high elevations due to the increased costs of thermoregulation and locomotion in cool and harsh habitats.

Some types of threats were observed, including a cyclone, selective logging for house construction,

and honey harvesting. Nevertheless, threat levels still seem low until now, even if slash-and-burn agriculture, firewood collection and charcoal production are cited as the main threats to lemurs within the PAs surrounding Bemanevika (Mittermeier *et al.*, 2010). Human presence and resource use are still low due to the isolation of the sites (TPF, 2019).

For the biogeographic affinity, Bemanevika and Mahimborondro PAs have the same species composition. The main reason for this is that these sites are contiguous and have the same habitat. Conversely there is an obvious dissimilarity between Bemanevika and Tsaratanana, between Bemanevika and COMATSA Nord, and between Mahimborondro and COMATSA Nord. This can be explained by the following: (1) there is an ecological barrier (large river) which prevents gene flow exchange between Bemanevika and Tsaratanana; (2) Bemanevika and COMATSA are separated by Mahimborondro, the two sites are therefore quite far apart, a situation which probably increases the number of distinct species for each site; and (3) the altitudinal variation may also affect species richness and species composition. The altitude value ranges from 700 to 1,800 m in Bemanevika, from 1,000 to 2,256 m in Mahimborondro, between 1,600 and 2,100 m for COMATSA and up to 2,200 m for Tsaratanana.

Conclusion

We have provided new information on the current population size of nocturnal lemur species, especially the family Cheirogaleidae, in Bemanevika PA, and have identified the species names for two taxa known only to genus level previously: *Cheirogaleus major* and *Microcebus sambiranensis*. This highlights the distribution range of these two species. Our study did not provide any evidence of the presence of *D. madagascariensis*, but many authors have reported the probability of its occurrence inside the PA. Therefore, Bemanevika PA may currently host six nocturnal lemur species, and all are threatened. Four localities (Andriakanala, Matsaborimaitso, Matsaborimena and Marotaolana) were identified as occurrence areas for *M. sambiranensis*, *C. major* and *A. trichotis* inside the PA. However, we estimate that their distribution may extend towards other localities. The findings of our study serve as baseline information and are an important resource for the Bemanevika PA managers to improve the status of nocturnal lemur populations. Currently, Bemanevika PA can be considered as a refuge for several nocturnal threatened lemur species, including the rare *A. trichotis*, and the Critically Endangered *Avahi unicolor*, reflecting the urgent need to improve the conservation of the site and its nocturnal lemur populations.

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Testing semi-captive settings to study mouse lemur behaviour

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Abstract

Mouse lemurs (*Microcebus* spp.) are one of the most diverse lineages of lemurs. They are difficult to study under field conditions, and there is a lack of basic behavioural data for many species. Recently, semi-captive conditions, i.e., when individuals are housed in temporary enclosures in proximity to their capture sites, have emerged as an alternative method to study a range of topics in challenging species. In this study, we use this setting to compare the activity budgets in three species of mouse lemur, namely *M. ravelobensis*, *M. bongolavensis*, and *M. myoxinus*, in northwest Madagascar. The objective of this work was to understand how semi-captivity might influence behaviour. We housed 24 wild mouse lemurs (with 12 male and 12 female adults) under semi-captive conditions for six consecutive nights in mixed-sex dyads with a similar body mass and collected scan sampling and behavioural states every 15 seconds from 18:00 to 21:00. We found no evidence of stereotypic behaviour, including pacing or over self-grooming. On average, mouse lemurs spent 83% of their time resting inside shelter boxes, 14% of their time moving, and 2% of their time self-grooming. None of these daily behaviours changed in frequency across the one-week study period. We found moderate differences between species, with *M. myoxinus* resting more and self-grooming less than either *M. ravelobensis* or *M. bongolavensis*. While recognizing the limitations of our study and of semi-captivity more generally, we highlight

the potential comparative information to be gained from semi-captive experiments across species, conditions, and fields of study.

Introduction

Mouse lemurs (*Microcebus* spp.) have emerged in recent years as one of the most diverse groups of lemurs. We currently recognize 25 species (Hotaling et al., 2016; Schübler et al., 2020) that live in virtually every habitat type in Madagascar, from rainforests to spiny deserts, and from primary habitats to agroforestry plots (Hending, 2021; Hending et al., 2018). In some places, multiple species can be sympatric and show strong signals of niche differentiation by diet, local habitat, and metabolic strategies (Radespiel, 2006). Mouse lemurs are thus a useful system for comparative research of primate behaviour, speciation, and ecology (Zimmermann and Radespiel, 2014). Nevertheless, because mouse lemurs are nocturnal, elusive, and fast, behavioural and ecological data are challenging to collect under field conditions. Most of the available behavioural data are limited to a handful of species from well-established sites with easier field work. To help close this gap, we ask about the utility of semi-captive settings for researching the behaviour of diverse mouse lemurs.

Despite the great diversity of mouse lemur species, only two are currently kept in captivity – the grey mouse lemur (*M. murinus*) from the western dry deciduous forests (Zehr et al., 2014) and Goodman's mouse lemur (*M. lehilahytsara*) from the eastern rainforests and central highlands (Karanewsky et al., 2015). In captivity, mouse lemurs are much easier to see and study, and it is possible to collect behavioural data with great resolution under controlled conditions (*M. Blanco*, personal communication). Significant research attention has focused on conducting experiments of mouse lemur cognition (Teichroeb and Vinnig, 2019), semiochemical signalling (Kollikowski et al., 2020), and metabolic flexibility (Terrien et al., 2018) in captivity. Such studies even highlight differences between the behaviour of *M. murinus* and *M. lehilahytsara* under identical conditions (Kollikowski et al., 2020). Nevertheless, the lack of mouse lemur species diversity under human care misses the full range of ecological and behavioural repertoires that characterize the genus.

More recently, research teams have used an intermediate approach where wild mouse lemurs are temporarily brought into semi-captive enclosures set in proximity to capture sites (Hasiniaina et al., 2020; Henke-von der Malsburg et al., 2021). Semi-captivity consists of placing an animal temporarily in a cage under the condition relevant for the environment of the target animal, that housing required several criteria such as: enough space for locomotion, food availability, shelter if needed etc. In general, the animals kept in the cage have no interaction with people except the observer during the time of the study. So, we put the animals in semi captivity to record mouse-lemur vocalizations linked to behavioural context (Hasiniaina et al., 2018, 2020) and in cognitive experiments that find differences across sympatric species that match differences in their ecologies (Henke-von der Malsburg et al., 2020). These studies highlight the use of semi-captive enclosures to compare behaviour, communication, and cognition across mouse lemur

species living in diverse habitats. However, we lack understanding of how semi-captivity itself, particularly for naïve individuals, might influence behaviour or how their behaviours change over the circumstance; the purpose of this study is to observe the behaviour of the mouse lemurs in semi-captive conditions.

Here, three species of mouse lemur have been studied, all classified as Endangered by the International Union for Conservation of Nature (IUCN), namely *M. ravelobensis*, *M. bongolavensis* and *M. myoxinus* (Baden et al., 2014; Blanco et al., 2020a, 2020b). We brought field-collected individuals into semi-captivity for one week and investigated (1) if we see stereotypies (i.e., repetitive behaviours) in wild mouse lemurs brought into semi-captive settings; (2) if we can detect behavioural patterns indicative of biological differences in our study subjects; and (3) if the behaviour of mouse lemurs in semi-captive settings changes over a week.

Methods

Ethical Statement

This study was conducted with the authorization of the Ministère de l'Environnement, de l'Ecologie et des Forêts (MEEF) (Permission No:130/16/ MEEF/SG/ DGF/DAPT/SCBT.Re) and adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Non-Human Primates (<https://www.asp.org/2021/04/20/principles-for-the-ethical-treatment-of-non-human-primates/>). Data for this study were collected opportunistically during ongoing projects (Hasiniaina et al., 2018, 2020; Evasoa et al., 2019).

Study sites and study species

The study took place from May to October 2015 at three dry deciduous forests and focused on three different species of *Microcebus*. We studied *M. ravelobensis* in Ankarafantsika National Park (Ampijoroa: 16°06'57.70"S, 47°05'49.82"E) (April-June), *M. bongolavensis* in the Bongolava forest (Marosely: 15°39'55.12"S, 47°34'40.08"E) (July-August), and *M. myoxinus* in the Bombetoka forest (Mataitromby: 15°51'05.43"S, 46°15'37"E) (September-October).

These sites are all situated in northwestern Madagascar (Fig. 1). At each study site, mouse lemurs were trapped using live Sherman traps or caught by hand using established methods (Hafen et al., 1998; Evasoa et al., 2019; Hasiniaina et al., 2020). We set traps every 25 m along 1 km transects, placed them in pairs on horizontal branches 1 to 2 m above the ground, and baited them with a small banana slice. We opened traps around 18:00 and checked them the next morning around 05:30. All captured mouse lemurs were brought to the campsite and individuals were selected for the semi-captive experiments.

Experimental setup and subject selection

We installed cages of 1 m³ (0.5 m × 0.5 m × 1 m) on the forest ground in vicinity

to the research camp. Within the cages, we categorized eight areas (A–H) and four extra locations: roof (Ro), ground (T), shelter (S) and feeding station (FS) (Fig. 2). The upper and lower areas were equipped with two pairs of wooden bars each that crossed the entire length of the enclosure. Two boxes for shelter were attached to the left and right side of each cage, and a small plastic dish for food was placed in the middle of the cage. Water was provided *ad libitum* during the experiments, and animals were fed with bananas every evening before starting observations. Insects were available to the subjects when they naturally entered the cage. The enclosures were spot-cleaned as necessary.

For each species, we selected one mixed-sex dyad for each semi-captive experiment. Dyads were matched based on similar body size and mass and on their capture locale. We selected animals for dyads that came from different capture sites, to minimize the chance that dyads were already familiar (Hasiniaina et al., 2020). In each dyad, one animal was marked by trimming the fur on the tail. Using this setup, we studied three pairs of *M. bongolavensis*, six pairs of *M. ravelobensis*, and three pairs of *M. myoxinus*. The mouse lemur pairs were placed into the enclosure for six consecutive nights (with two exceptions for *M. ravelobensis* – one pair was housed for five nights and one pair was housed for seven nights). Mouse lemurs were released at their respective capture point at dusk after experimentation. But before we started the experiment, we had a habituation day, which meant we did not start observing the dyads the day of the capture, but we instead left them for one or two days before observing them. During the experiment, the shelter box was always open in case the animals were afraid. For more details on the setting and subjects see Evasoa et al. (2019).

Behavioural data and statistics

This setting was originally designed to collect acoustic communication data (Hasiniaina et al., 2018, 2020) and social interactions between the dyads (Evasoa et al., 2019), but also allowed opportunity for us to collect activity budgets. The observer stayed 2–4 m in front of the cage

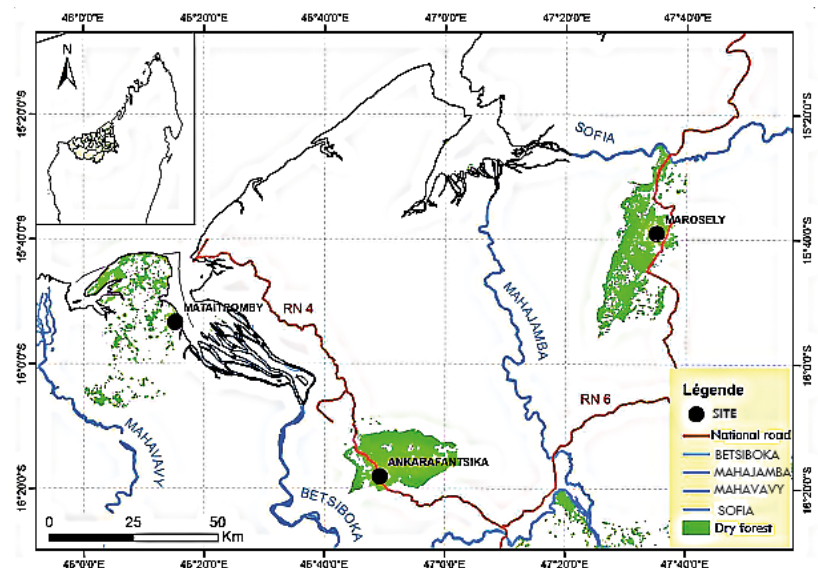


Fig. 1: Map of northwestern Madagascar highlighting the three study sites in black dots (map created in QGIS (version 2.18.4).

and used a dimmed head lamp to observe the animals to avoid any disturbance, as our presence might affect the behaviour. We collected the behaviour of the male and female per pair concurrently each night between 6pm and 7pm for six consecutive nights. Behaviour was recorded using the scan sampling method (15 second scans) according to Altmann (1974), resulting in 720 scans per animal per night. For each scan, behaviour was noted if the animals were resting, moving, self-grooming (moving the toothcomb or tongue through fur), or engaged in other behaviours (e.g., feeding, scent marking, etc.). The “other” behaviours were very low occurrences, and we focused our analysis on resting, moving, and self-grooming. Importantly, “resting” behaviour includes scans when the animal was inside a shelter box.

To analyse the data, we calculated the percentage of scans that each mouse lemur spent resting, moving, or self-grooming per night. To compare species differences in behaviours, an average value for each mouse lemur was computed across all study nights. The averages

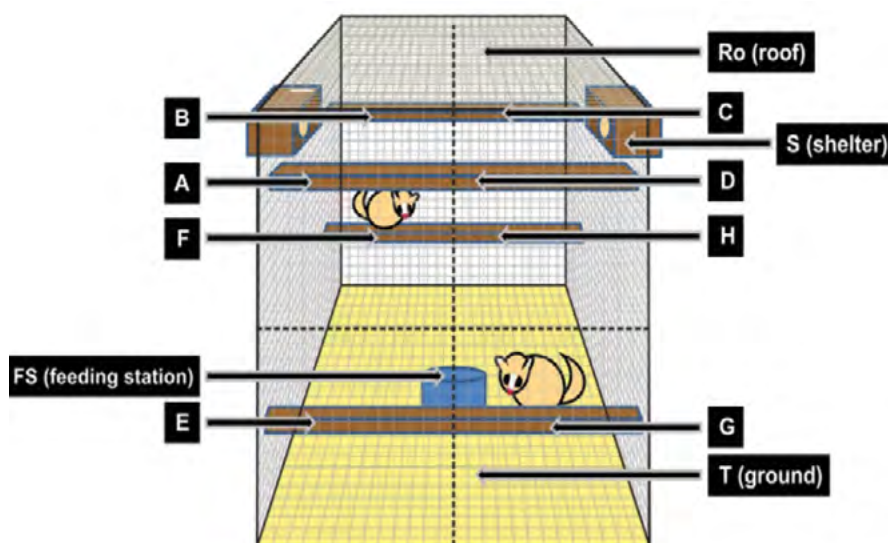


Fig. 2: Schematic of the captive enclosures, highlighting the different areas of the cage (A-H) and other features. Copied with permission from Hasiniaina et al. (2018) and Rina Evasoa et al. (2019).

were analysed by using non-parametric Kruskal-Wallis tests, with Dunn’s Multiple Comparisons, implemented in GraphPad Prism. Next, we used linear regressions to compare study night (1-6) against the proportion of time spent moving or resting separately for each species.

Results

We saw no signs of repetitive, stereotypic behaviours in the wild mouse lemurs brought into semi-captive enclosures. We noted no signs of pacing or over-grooming. In fact, most of the mouse lemurs spent most of their time resting. On average, resting accounted for 82.7% of the scans. Moving accounted for 14.2% of the scans and self-grooming accounted for 1.9% of scans, on average across individuals. We found a difference trending towards significance in resting between the three species ($H = 5.300$, $P = 0.070$); *post-hoc* pairwise comparisons confirmed the biggest difference was between *M. ravelobensis* and *M. myoxinus* ($P = 0.063$; Fig. 3). In contrast,

we found no differences in the time spent moving across species ($H = 4.200$, $P = 0.120$). We did find a significant difference across species in the time spent self-grooming ($H = 6.400$, $P = 0.040$), with *M. myoxinus* spending less time grooming than either *M. ravelobensis* or *M. bongolavensis* ($P = 0.070$, for both pairwise comparisons).

We found no evidence that the *Microcebus* individuals changed their behaviour during the span of the experiment (Fig. 4). We note that *M. bongolavensis* individuals trended towards resting more ($R^2 = 0.076$, $P = 0.100$) and moving less ($R^2 = 0.075$, $P = 0.100$) as they spent more days in semi-captivity, but the same trend was absent for both *M. ravelobensis* ($R^2 < 0.030$, $P > 0.180$, for both behaviours) and *M. myoxinus* ($R^2 < 0.014$, $P > 0.500$, for both behaviours) individuals.

Discussion

We compared the activity budgets of wild mouse lemurs temporarily housed in semi-captive settings to ask if the setting can be used for comparative behavioural research, as has been shown for vocalization (Hasiniaina et al., 2020), social (Evasoa et al., 2019), and cognitive research (Henke-von der Malsburg et al., 2021). In answering our three major questions, we found (1) no evidence that the mouse lemurs showed stereotypic, repetitive behaviours when housed under semi-captive conditions, including pacing and over grooming: the mouse lemurs spent most of their time resting inside shelter boxes. We did find (2) species differences in resting and self-grooming, with *M. myoxinus* spending more time resting and less time self-grooming than the other two species; and we found (3) that the percentage of time spent resting, moving, and self-grooming did not change over six days of semi-captivity for any species, indicating that experiments conducted under these conditions might be comparable across an entire week.

Although our sample size was small, *M. myoxinus* individuals spent more time resting inside their shelter boxes. While this could reflect the different seasons under which we studied the three species, this is unlikely, as we studied *M. myoxinus* during the onset of the mating season when mouse lemurs are typically most active (Radespiel, 2000). More likely, our results highlight biological differences between species in neophobia or neophilia, as has been shown for different mouse lemurs under fully captive conditions (Kollikowski et al., 2020). One important distinction is between resting and hiding: we considered mouse lemurs to be resting when inside shelter boxes, but an alternate interpretation is that individuals were hiding from conspecifics or because of the novelty of the setting.

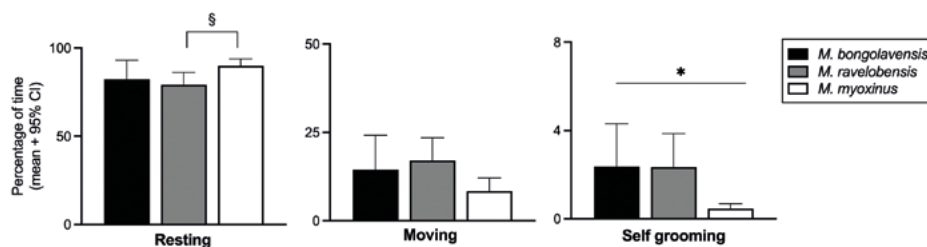


Fig. 3: Species comparisons in measured behaviors, including resting (left), moving (center), and self-grooming (right) for *M. bongolavensis* (black), *M. ravelobensis* (grey), and *M. myoxinus* (white) individuals. * $P = 0.040$; § $P = 0.060$.

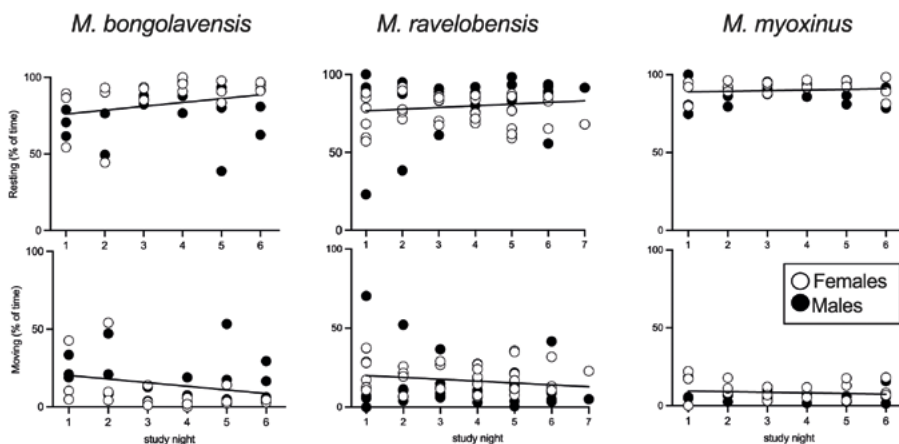


Fig. 4: Linear regressions comparing consecutive study nights to the percentage of scans spent resting (top row) and moving (bottom row) for female (white) and male (black) *M. bongolavensis* (left), *M. ravelobensis* (center), and *M. myoxinus* (right).

We are also careful in the interpretation of our results due to the limitations of our study. First, we studied three mouse lemur species in different seasons, and seasonality is a strong predictor of mouse lemur behaviour and ecology (Thorén *et al.*, 2011). Second, we only collected data for the first three hours of the night phase, and our results are not representative of the total active phase for mouse lemurs. Third, we offered mouse lemurs a limited diet of bananas and the occasional insect, which is not representative of their foraged diets (Radespiel *et al.*, 2006). Last, the social context of our experiments likely influenced our results (Evasoa *et al.*, 2019). The design of our study, involving co-housing male-female dyads, was established for vocalization and social research (Hasiniana *et al.*, 2018, 2020; Evasoa *et al.*, 2019). Likely, housing animals singly versus socially influences activity budgets and behaviours. Moreover, different mouse lemur species have different social systems and differ in the normal interactions between males and females (Radespiel *et al.*, 2003). While housing species under identical conditions does create comparable settings for experimental rigor, this setting may bias results towards species that naturally live under similar social conditions and against those that naturally live under different social conditions (Evasoa *et al.*, 2019). Understanding how differences in social housing under semi-captivity can influence behavioural data or activity budgets requires further testing.

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Densité de la population des lémuriens (*Eulemur albifrons* et *Varecia variegata subcincta*) et transformation d'occupation du sol du Nosy Mangabe, nord-est de Madagascar

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Keywords: Nosy Mangabe, *Varecia variegata subcincta*, *Eulemur albifrons*, density, forest, remote sensing

Résumé

L'objectif de cette étude est de comprendre la nécessité de la préservation des lémuriens (*V. v. subcincta* et *E. albifrons*) et de faire l'état des lieux actualisés sur la situation et l'évolution de la forêt dense du Nosy Mangabe de 1997 à 2017. Les données obtenues serviront à renforcer les stratégies de conservation de la population de lémuriens. L'étude a été réalisée du 27 janvier au 19 septembre 2017 et du 28 janvier au 22 septembre 2017 dans le noyau dur et dans la zone de service du Nosy Mangabe. Pour l'estimation de la densité et l'abondance des deux espèces, la méthode transect linéaire a été utilisée. Les résultats obtenus dans la zone de service montrent une densité de 5,62 ind/ha pour *E. albifrons* et une densité de 2,87 ind/ha pour les *Varecia variegata subcincta*. Dans la partie du noyau dur, les résultats montrent une densité de 3,62 ind/ha pour *E. albifrons* et une densité de 1,25 ind/ha pour les *V. v. subcincta*. La conversion d'occupation du sol sur une période de 20 ans a été cartographiée à partir des images multitemps du satellite Landsat. La méthode de la classification non supervisée a été utilisée à l'aide du Logiciel ArcGis 10.4.1. Quelques points GPS ont été relevés pour chaque type d'occupation du sol pour valider les résultats cartographiques. Les résultats obtenus indiquent que la forêt dense a perdu une superficie de 1,47 km² (26%) entre l'année 1997 et l'année 2017. Les cyclones et la politique touristique sont les principales causes naturelles menaçant la conservation. Le paysage du site est en pleine transformation et dominé par la forêt dense dégradée.

Abstract

The objective of this study was to understand the need for the preservation of lemurs (*V. v. subcincta* and *E. albifrons*) and to provide an updated inventory of the situation and evolution of the dense forest of Nosy Mangabe from 1997 to 2017. The data obtained will be used to strengthen conservation strategies for the lemur population. The study was carried out from January 27th to September 19th 2017 and from January 28th to September 22nd 2017 in the Nosy Mangabe service area. For estimation of the density and abundance of the two species, the line transect method was used. The results obtained in the

service area show a density of 5.62 ind/ha for *Eulemur albifrons* and a density of 2.87 ind/ha for *V. v. subcincta*. In the core part, the results show a density of 3.62 ind/ha for *E. albifrons* and a density of 1.25 ind/ha for *V. v. subcincta*. Land cover conversion over a period of 20 years was mapped using multi-date images from the Landsat satellite. The unsupervised classification method was used using ArcGis 10.4.1 software. A few GPS points were recorded for each type of land use to validate the cartographic results. The results obtained indicate that the dense forest lost an area of 1.47 km² (26%) between the year 1997 and the year 2017. Cyclones and tourism policy are the main natural causes threatening conservation. The landscape of the site is in full transformation and dominated by dense degraded forest.

Introduction

Madagascar fait partie des centres de biodiversité les plus importants du monde (Moat et Smith, 2007) où les forêts tropicales humides couvraient 11,5 millions d'hectares dans les années 1950 (Harper *et al.*, 2007). L'endémisme est extrêmement élevé, allant de 55 à 100% au niveau de l'espèce (Mittermeier *et al.*, 2013). Cette richesse est pourtant menacée par des perturbations importantes de l'habitat naturel, dues aux différentes pressions anthropiques ainsi qu'aux catastrophes naturelles (Ravaloharimanitra, 2017). Le taux de dégradation et de destruction des forêts tropicales a beaucoup augmenté ces derniers temps (Harper *et al.*, 2007). La dégradation spectaculaire de la forêt Malgache déclencherà probablement des nouvelles cascades d'extinction en particulier pour les lémuriens. Plus de 90 % de la couverture forestière originale de Madagascar est détruite à cause de l'agriculture, de l'élevage, de l'exploitation minière, de l'extraction des bois précieux, de la collecte de bois de chauffe et d'autres produits à divers usages (Mittermeier *et al.*, 2014). La perte d'habitat et le changement climatique sont les principaux facteurs d'extinctions des lémuriens (Borgerson *et al.*, 2021) et les autres formes de vie qui leurs sont associées. La destruction et la dégradation de l'habitat forestier tropical étaient classées comme les premières menaces à travers le monde, alors que la plupart des lémuriens vivent dans cet habitat (plus de 90 %) (Sahondraninjaka, 2017). En raison de la destruction forestière humide, il est important de recenser les restes des lémuriens qui y vivent, les comptages des primates sont essentielles dans la gestion et dans la conservation de la biodiversité. Il est basé sur la surveillance du milieu et consiste à recueillir systématiquement dans le temps des informations visant à répondre à une ou plusieurs questions spécifiques. Les primates du Nosy Mangabe (*V. v. subcincta* et *E. albifrons*) ont été comme cibles lors de la recherche. L'objectif est de fournir des informations de base d'ordre quantitatif sur les populations des primates, de définir les alternatives en termes de protection durable et de produire des cartes de la végétation actualisée du site entre 1997 et 2017.

Methodes

Site d'étude

L'étude a été effectuée dans le district de Maroantsetra, à Nosy Mangabe, dans le noyau dur (15°28' S, 49°46' E) et dans la zone de service ou zone tampon (15°30' S, 49°45' E) (Fig. 1 et Fig. 2). Le site s'étend sur une superficie de

520 ha (données issues du traitement d'image satellitaire Landsat datant de 2022) et l'altitude varie de 0 à 750 m. Du fait de sa situation géographique, située sur la partie est de l'île, elle est soumise à un climat humide pluvial apportant une forte précipitation (Raherilalao *et al.*, 2016). Le site est caractérisé par une topographie accidentée. La végétation est constituée uniquement par la forêt dense humide (Goodman and Raherilalao, 2013) soumise à des catastrophes naturelles telles que les cyclones et notamment aux environs de Maroantsetra. Les vestiges forestiers abritent une diversité considérable en matière de faune et de flore et servent de refuges pour de nombreuses espèces ainsi que de zones tampon aux activités de l'homme (Moat et Smith, 2007). Sur le plan touristique le site ne reste pas dépourvu d'un panorama attirant de son originalité et sa beauté. Les potentialités en termes de biodiversités et certaines particularités distinguent le site des autres aires protégées. Nosy Mangabe, géré par Madagascar National Parks, est une destination ayant contribué davantage à l'augmentation du nombre de touristes à Madagascar. D'après les informations fournies par le service touristique du Parc Masoala-Nosy Mangabe, le nombre des touristes qui ont visité l'île entre l'année 2010 et l'année 2016 est de 20.736 dont 2341 (11.28%) en 2010, 3020 (14.56%) en 2011, 3506 (16.9%) en 2012, 2480 (11.95%) en 2013, 2731 (13.17%) en 2014, 3136 (15.12%) en 2015 et 3522 (16.98%) en 2016. La fréquentation a connu une forte progression grâce à l'amélioration des capacités d'hébergement, de la restauration et de la traçabilité des circuits.

Mode de recensement

Les lémuriens ont été estimés par l'utilisation de la méthode transect linéaire (Whitesides *et al.*, 1988). Dans une forêt dense humide comme celle de Nosy Mangabe, la méthode la plus adéquate et efficace pour étudier les populations de lémuriens est le recensement direct utilisant des transects ou des pistes. Deux transects de 2000 m chacun, parmi les 16 déjà mis en place par les gestionnaires du site pour les suivis des espèces de lémuriens, ont été utilisés. Les observations ont été réalisées au rythme d'une par jour pendant neuf mois que ce soit pour la zone de service (MSL_Transect 5a) ou celle du noyau dur (MSL_Transect 5b) (Fig. 3), et ont démarré à la même heure. Les transects ont été menés par l'équipe Masoala-Nosy Mangabe, composée d'un spécialiste en suivi et de deux (02) écogardes du site. Tous les membres de l'équipe étaient des observateurs durant les recensements. Ces derniers ont été parcourus entre 05:30 et 08:30 du matin avec une vitesse de déplacement de 700 m/h. Puisque Nosy Mangabe présente un habitat naturel non perturbé parmi les habitats de l'aire protégée Masoala, nous avons dû adopter ce déplacement lent, car la canopée est fermée, ce qui rend assez difficile l'observation visuelle des lémuriens. Les espèces ont été découvertes dans un rayon de 40 m de part et d'autre du transect, soit par leurs mouvements, soit par leurs cris, soit à l'œil nu. Les outils utilisés pour le bon déroulement des inventaires sont: des paires de jumelles, un carnet de notes, un crayon, une gomme, un GPS, une montre et un appareil photo. Les observations sur le noyau dur et la zone de service du site portent principalement sur le *V. v. subcincta* et l'*E. albifrons*. A chaque rencontre lors du transect, les informations suivantes sont notées: la date d'observation, les heures du début et de la fin du

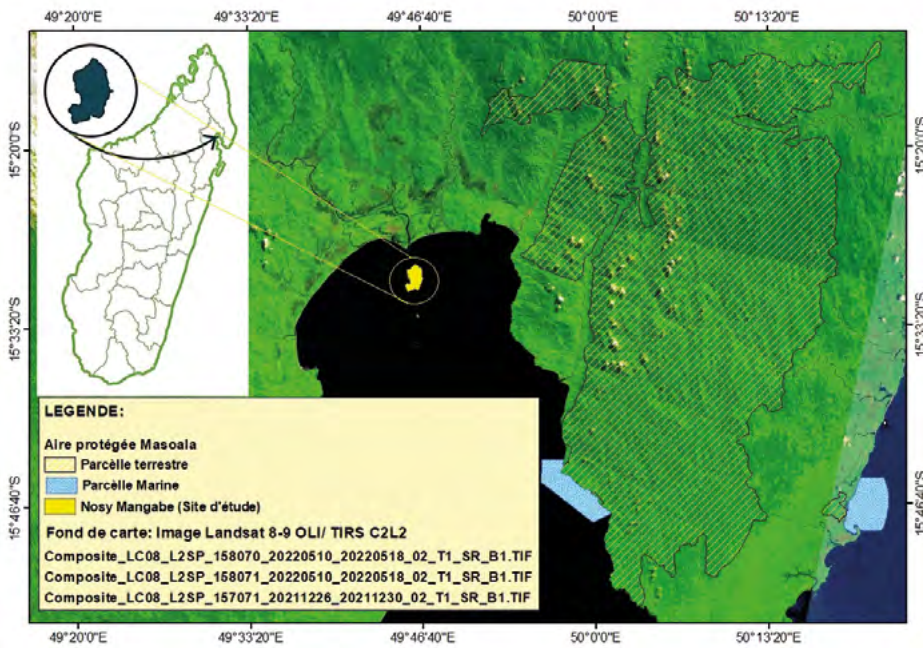


Fig. 1: Localisation du site d'étude.



Fig. 2: Vu général du Nosy Mangabe (Maroantsetra).

transect, le point métrique du transect, l'heure à laquelle nous avons vu ou entendu l'animal ou le groupe, les espèces rencontrées par âge et par sexe, le nombre total d'individus observés, le comportement de l'animal pendant l'observation et les points GPS de l'endroit de localisation de l'animal.

Calcul de la densité, surface recensée et sex-ratio

La densité de la population des lémuriens recensés est calculée sur le nombre d'individus observés divisé par la surface recensée ($D = N / S$). Les deux espèces ont

été découvertes dans un rayon de 40 m de part et d'autre du transect de 2 km. La surface recensée est calculée sur la longueur du transect multipliée par la largeur du rayon ($S_r = L_t \times l_r$) avec L_t : Longueur du transect, l_r : largeur du rayon (2 x 40 m x 2000 m). Le sex-ratio est défini comme le rapport numérique entre le nombre des mâles et celui des femelles dans une population donnée, c'est-à-dire le nombre des mâles au numérateur et le nombre des femelles au dénominateur ($SR = Nb_{m\grave{a}le} / Nb_{femelle}$).

Apport de la télédétection

Le recours à une approche de détection de changements est nécessaire afin de réaliser de façon optimale la caractérisation et la détection des changements d'occupation et d'utilisation du sol. Les images satellitaires utilisées (Tab. 1) dans ce travail couvrent l'ensemble du Nosy Mangabe dans une résolution suffisante (30 mètres) pour voir l'évolution de la couverture végétale.

Après la correction radiométrique et la composition colorée, la classification a été faite. Nous avons utilisé la classification non supervisée à l'aide du logiciel ArcGis 10.4.1. Il s'agit de la classification automatique de l'occupation du sol recouvrant l'ensemble

de la zone d'étude. L'algorithme de ces classifications non dirigées s'appuie sur la détermination des pics de fréquence de l'histogramme de l'image à classifier (Collet, 1992). Il a été obtenu trois classes (03) d'occupation du sol à savoir: forêt dense, forêt dégradée, sable et sol nu. Les classes d'occupation du sol définitive ont été validées grâce à la vérité du terrain lors du recensement des lémuriens. La performance globale de la classification a été évaluée par le coefficient Kappa dont la valeur est comprise entre 0 et 1 (Congalton et al., 1991) et le résultat de classification satisfaisant est caractérisé par un taux de fiabilité moyen de l'ordre de 0.87 ou 87%.

Tab. 1: Références des images Landsat utilisées.

Type d'image	Scènes	(Path et Row)	Dates
Landsat 4-5 TM C2 L2	LT05_L2SP_158071_19970926_20200909_02_T2	158-071	1997/09/26
Landsat 8-9 OLI/TIRS C2 L2	LC08_L2SP_158071_20170205_20200905_02_T1	158-071	2017/02/05

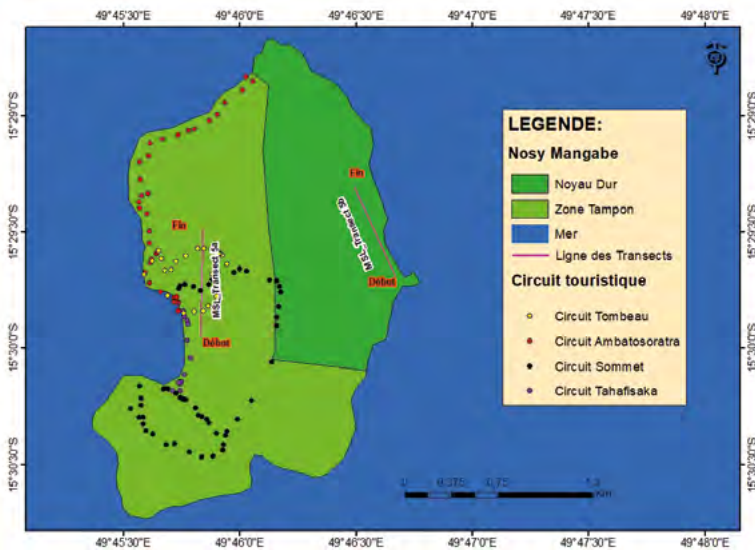


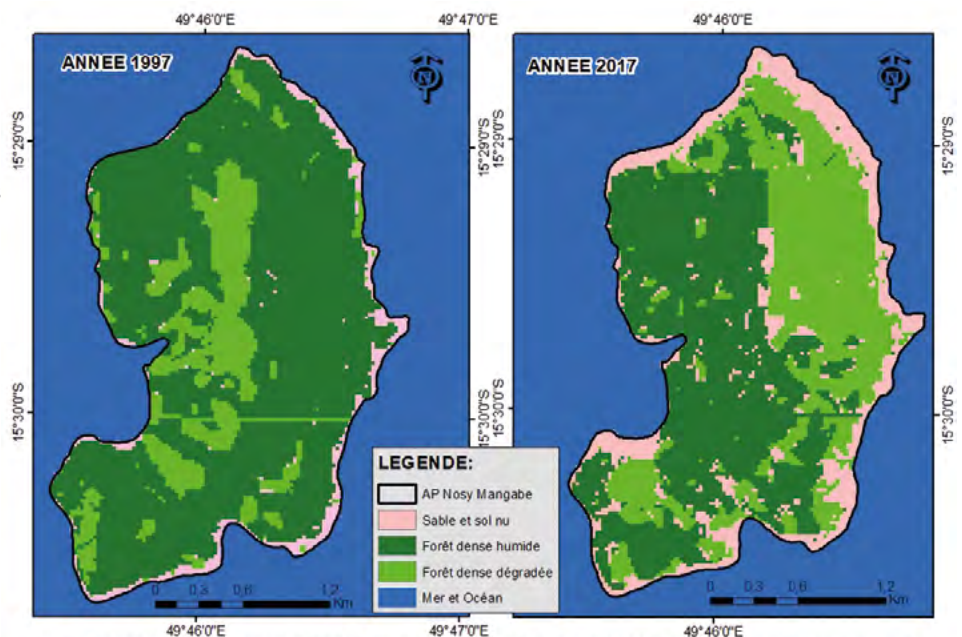
Fig. 3: Zone de service (Zone dégradée) et Noyau dur (Zone intacte) de Nosy Mangabe.

Résultats

Au total, 18 trajets des deux transects ont été réalisés et enregistrés dans le Nosy Mangabe sur les 36 km parcourus par l'équipe Masoala-Nosy Mangabe, dont neuf pour le noyau dur et neuf pour la zone de service en 2017. Nous avons recensé 09 fois sur le même transect 214 individus. Au total, 136 lémuriens diurnes ont été recensés dans la zone de service (forêt dégradée), dont 46 *Varecia v. subcincta* (25 mâles-19 femelles-01 jeune) et 90 *Eulemur albifrons* (38 mâles-46 femelles-06 jeunes) et 78 lémuriens diurnes recensés dans le noyau dur (forêt intacte), dont 58 *E. albifrons* (24 mâles-31 femelles-01 jeune) et 20 *V. v. subcincta* (11 mâles-09 femelles). En général, 63% des lémuriens ont été trouvés dans la ZS tandis que 36.44% dans le ND. Les individus recensés directement (lié au comportement de l'animal: en mouvement, repos ou se nourrir) représentent 83.87% et les individus rencontrés indirectement (cri) représentent 16.12% pour la zone intacte (ND). Dans la zone dégradée (ZS), par contre, 42% des individus ont été observés directement et 22.22% observés indirectement. Théoriquement, la surface recensée par transect est de $2 \times 40 \text{ m} \times 2000 \text{ m} = 160000 \text{ m}^2$, soit 16 ha. Il est à noter que la largeur de de détection était la même que ce soit pour la zone intacte que pour la zone dégradée. Une inégale répartition des lémuriens a été constatée dans le site. Pour les jeunes lémuriens, leurs sexes n'ont pas été reconnus lors du transect d'observations et de dénombrements. Les

adultes mâles et femelles sont plus nombreux que les jeunes. Concernant la structure d'âge, la population a été subdivisée en 02 classes à savoir: adulte et jeune. Les adultes sont dominants dans les deux sites dont 96% adultes et 4% jeune pour le ND et 94.81% adultes et 5.18% jeune pour la ZS. Nous avons vu entre 2 et 16 individus (médian: 4.0) de *E. albifrons* et entre 0 et 10 individus (médian: 2.0) de *V. v. subcincta* sur le transect dans la forêt intacte et entre 0 et 23 individus (médian: 6.0) de *E. albifrons* et entre 0 et 16 individus (médian: 4.0) de *V. v. subcincta* sur le transect dans la forêt dégradée. Ni pour *E. albifrons*, ni pour *V. v. subcincta* la différence entre les nombres des individus vus par transect étaient significative (Mann-Whitney-U: $P > 0.050$). Pour les deux transects ensemble, les médianes des animaux vus était 4.5 pour *E. albifrons* et 2.0 pour *V. v. subcincta*. La différence entre les espèces est significative (Mann-Whitney-U: $z = 2.460$; $P = 0.014$). Si on estime un layon de 40 m à chaque côté du transect dans lequel tous les lémuriens étaient vus, la surface recensée par transect est de $2 \times 40 \text{ m} \times 2000 \text{ m} = 160000 \text{ m}^2$, soit 16 ha ou 0.16 km^2 . Puis, la densité d'*E. albifrons* est de $4.5 \text{ individus} / 0.16 \text{ km}^2 = 28.1 \text{ individus} / \text{km}^2$. La densité de *V. v. subcincta* est de $2.0 \text{ individus} / 0.16 \text{ km}^2 = 12.5 \text{ individus} / \text{km}^2$. La variation de sex-ratio entre les deux sites n'est pas très grande: 1.22 pour *Varecia v. subcincta* et 0.77 pour *Eulemur albifrons* pour le ND, et 1.36 pour *V. v. subcincta* et 0.82 pour *E. albifrons* pour la ZS.

La cartographie de l'occupation du sol (1997 – 2017) fait ressortir que la forêt dense a perdu une superficie de 1.47 km^2 (26%) (Fig. 4). En l'espace de 20 ans, la forêt dégradée a perdu 0.81 km^2 (14.49%) (Fig. 4) et 0.67 km^2 (12.09%) des sols nus ont été recouverts par la végétation.



Sources: BD 500 FTM, 2005, Image Landsat 4-5 TM C2 L2 datant de 1997 et Image Landsat 8-9 OLI/TIRS C2 L2 datant de 2017 (<https://earthexplorer.usgs.gov>)
Système de projection cartographique: Laborde Madagascar

Fig. 4: Occupation du sol de Nosy Mangabe (1997 et 2017).

Tab. 2: Chiffres sur les lémuriens dénombrés dans le ND (Zone intacte) de Nosy Manage (2017). Code: EUL_ALB: *Eulemur albifrons*, VAR_SUB: *Varecia v. subcincta*, POINT_METR: Point Métrique, RPS: Repos, MVT: Mouvement, ALIM: Alimentation, COMP: Comportement, NB: Nombre.

DATE	ESPECE	POINT_METR	GPS X	GPS Y	NB INDIV	NB MALE	NB FEM	NB JEUN	COMP	OBS Début
27/01/2017		0	49,76795	-15,4809						
27/01/2017	EUL_ALB	250	49,76987	-15,48156	2	1	1		MVT	
27/01/2017	EUL_ALB	350	49,77079	-15,48228	5	2	2	1	MVT	
27/01/2017	VAR_SUB	500	49,77175	-15,48302	1	1			CRI	
27/01/2017	VAR_SUB	650	49,77317	-15,48387	2	1	1		MVT	
27/01/2017	EUL_ALB	750	49,77365	-15,48413	5	2	3		MVT	
27/01/2017	EUL_ALB	1150	49,77425	-15,48809	2	2			CRI	
27/01/2017	EUL_ALB	1950	49,77715	-15,49486	7	2	3	2	MVT	
27/01/2017		2000	49,77726	-15,49533						fin
27/02/2017		0	49,7681	-15,48062						début
27/02/2017	VAR_SUB	200	49,76942	-15,48124	2	1	1		CRI	
27/02/2017	EUL_ALB	350	49,77093	-15,48242	1		1		CRI	
27/02/2017	EUL_ALB	400	49,77269	-15,4837	3	1	2		ALIM	
27/02/2017	EUL_ALB	700	49,77355	-15,48415	1		1		MVT	
27/02/2017	VAR_SUB	700	49,77355	-15,48415	3	2	1		CRI	
27/02/2017	VAR_SUB	750	49,77436	-15,48563	2	1	1		RPS	
27/02/2017	EUL_ALB	1500	49,77486	-15,49149	3	1	2		MVT	
27/02/2017	VAR_SUB	1600	49,77495	-15,49181	2	1	1		RPS	
27/02/2017		2000	49,77725	-15,49535						Fin
25/03/2017		0	49,76809	-15,48061						début
25/03/2017	EUL_ALB	700	49,7732	-15,48395	2	1	1		MVT	
25/03/2017	EUL_ALB	1650	49,77511	-15,49281	2	1	1		MVT	
25/03/2017		2000	49,77726	-15,49538						Fin
26/04/2017		0	49,76795	-15,48066						début
26/04/2017	EUL_ALB	9000	49,77449	-15,48518	3	1	2		RPS	
26/04/2017		2000	49,77729	-15,49541						Fin
26/05/2017		0	49,76835	-15,48092						début
26/05/2017	EUL_ALB	500	49,7719	-15,48312	3	1	2		RPS	
26/05/2017		2000	49,77721	-15,49541						Fin
17/06/2017		0	49,76822	-15,48071						début
17/06/2017	EUL_ALB	1400	49,7749	-15,49029	5	2	3		MVT	
17/06/2017	VAR_SUB	1450	49,77489	-15,49115	2	1	1		MVT	
17/06/2017	EUL_ALB	1800	49,77642	-15,49377	2	1	1		MVT	
17/06/2017	EUL_ALB	2000	49,77726	-15,49542	3	1	2		MVT	Fin
25/07/2017		0	49,76795	-15,48059						début
25/07/2017	EUL_ALB	200	49,76964	-15,4813	2	1	1		MVT	
25/07/2017		2000	49,77726	-15,4954						Fin
21/08/2017	EUL_ALB	0	49,77807	-15,48059	3	1	2		MVT	Début
21/08/2017	EUL_ALB	1450	49,77497	-15,49104	1	1			MVT	VU
21/08/2017	VAR_SUB	1550	49,77523	-15,49287	2	1	1		CRIE	
21/08/2017		2000	49,77729	-15,4954						Fin
19/09/2017		0	49,76814	-15,48063						Début
19/09/2017	EUL_ALB	150	49,76973	-15,48143	2	1	1		MVT	
19/09/2017	EUL_ALB	300	49,77028	-15,48195	1	1			MVT	
19/09/2017	VAR_SUB	500	49,77164	-15,48293	2	1	1		RPS	
19/09/2017	VAR_SUB	900	49,77448	-15,48518	2	1	1		RPS	
19/09/2017		2000	49,77726	-15,49535						Fin
					78	35	40	3		

Tab. 3: Chiffres sur les lémuriens dénombrés dans la ZS (Zone dégradée) de Nosy Mangabe (2017). Code: EUL_ALB: *Eulemur albifrons*, VAR_SUB: *Varecia v. subcincta*, POINT_METR: Point Métrique, RPS: Repos, MVT: Mouvement, ALIM: Alimentation, COMP: Comportement, NB: Nombre.

DATE	ESPECE	POINT_METR	GPS X	GPS Y	NB_INDIV	NB_MALE	NB_FEM	NB_JEUN	COMP	OBS
28/01/2017		0	49,76292	-15,50243						
28/01/2017	VAR_SUB	50	49,76336	-15,50179	2	1	1		RPS	Début
28/01/2017	EUL_ALB	550	49,76551	-15,49492	7	3	3	1	RPS	
28/01/2017	VAR_SUB	550	49,76551	-15,49492	2	1	1		MVT	
28/01/2017	EUL_ALB	1000	49,76742	-15,49407	3	1	2		MVT	
28/01/2017	VAR_SUB	1250	49,76801	-15,49163	3	1	1	1	RPS	
28/01/2017	EUL_ALB	1250	49,76801	-15,49163	6	3	3		MVT	
28/01/2017	VAR_SUB	1400	49,76888	-15,49029	1				ALIM	
28/01/2017	EUL_ALB	1400	49,76888	-15,49029	2	1	1		ALIM	
28/01/2017	EUL_ALB	1550	49,76952	-15,48925	3	1	2		ALIM	
28/01/2017	EUL_ALB	1800	49,76918	-15,48667	2	1	1		MVT	
28/01/2017	VAR_SUB	1850	49,7691	-15,48614	2	1	1		CRI	
28/01/2017		2000	49,7693	-15,48513						Fin
28/02/2017		0	49,76294	-15,50237						Début
28/02/2017	EUL_ALB	250	49,7642	-15,50007	2	1	1		MVT	
28/02/2017	VAR_SUB	600	49,7659	-15,4974	1		1		RPS	
28/02/2017	VAR_SUB	650	49,76624	-15,49697	1		1		RPS	
28/02/2017	EUL_ALB	750	49,7667	-15,49605	2	1	1		MVT	
28/02/2017	EUL_ALB	1350	49,76858	-15,49076	1	1			MVT	
28/02/2017	EUL_ALB	1450	49,76926	-15,49012	1		1		MVT	
28/02/2017	VAR_SUB	1700	49,76915	-15,48751	3	2	1		CRI	
28/02/2017	EUL_ALB	2000	49,76914	-15,48488	2	1	1		CRI	fin
24/03/2017		0	49,76271	-15,50251						Début
24/03/2017	VAR_SUB	250	49,76432	-15,50049	2	1	1		CRIS	2groupes
24/03/2017	VAR_SUB	350	49,76455	-15,49948	1	1			CRIS	
24/03/2017	EUL_ALB	600	49,76593	-15,49746	5	2	3		ALIM	
24/03/2017	VAR_SUB	700	49,76641	-15,49669	2	2			CRIS	
24/03/2017	EUL_ALB	750	49,76678	-15,4961	5	2	3		ALIM	
24/03/2017	VAR_SUB	1100	49,76874	-15,4932	2	1	1		RPS	
24/03/2017	VAR_SUB	1150	49,76782	-15,49265	2	1	1		RPS	
24/03/2017	EUL_ALB	1150	49,76782	-15,49265	6	2	3	1	MVT	
24/03/2017	VAR_SUB	1250	49,76812	-15,49156	1	1			RPS	
24/03/2017	VAR_SUB	1350	49,76842	-15,4908	1	1			ALIM	
24/03/2017	VAR_SUB	1400	49,76878	-15,49031	2	1	1		CRI	
24/03/2017	VAR_SUB	1700	49,76924	-15,48778	2	1	1		CRI	
24/03/2017	VAR_SUB	1900	49,76908	-15,48584	2	1	1		CRIS	
24/03/2017		2000	49,76912	-15,48495						Fin
24/04/2017		0	49,763	-15,50239						Début
24/04/2017	VAR_SUB	750	49,76665	-15,4961					MVT	
24/04/2017	EUL_ALB	1000	49,76744	-15,49407	3	1	2		RPS	
24/04/2017	VAR_SUB	1150	49,76789	-15,4925	2	1	1		RPS	
24/04/2017	EUL_ALB	1150	49,76789	-15,4925	7	2	3	2	MVT	
24/04/2017	EUL_ALB	1350	49,76852	-15,49083	3	1	2		MVT	
24/04/2017	EUL_ALB	1400	49,76919	-15,49021	3	1	1	1	MVT	
24/04/2017	VAR_SUB	1400	49,76919	-15,49021	2	1	1		RPS	
24/04/2017	EUL_ALB	1700	49,76927	-15,48779	5	2	2	1	RPS	
24/04/2017	VAR_SUB	1900	49,76914	-15,48578	2	1	1		CRIS	
24/04/2017		2000	49,76916	-15,48489						Fin
27/05/2017		0	49,76194	-15,49619						Début
27/05/2017	VAR_SUB	900	49,76704	-15,49488	1	1			CRI	
27/05/2017	VAR_SUB	1550	49,76958	-15,48924	1	1			CRI	

DATE	ESPECE	POINT_METR	GPS X	GPS Y	NB_INDIV	NB_MALE	NB_FEM	NB_JEUN	COMP	OBS Début
27/05/2017		2000	49,76921	-15,48487						Fin
19/06/2017		0	49,76292	-15,50231	5	3	2			Début
19/06/2017	EUL_ALB	650	49,76594	-1 549 735					RPS	
19/06/2017		2000	49,76909	-1 548 490						Fin
23/07/2017		0	49,77075	-15,5084						Début
23/07/2017	VAR_SUB	400	49,76478	-15,4989	2	1	1		MVT	
23/07/2017	EUL_ALB	450	49,76491	-15,49856	1	1			MVT	
23/07/2017	VAR_SUB	850	49,76688	-15,49534	2	1	1		RPS	
23/07/2017	EUL_ALB	1200	49,76793	-15,49212	3	1	2		MVT	
23/07/2017		2000	49,7691	-15,48482						Fin
25/08/2017		0	49,76295	-15,50247						Début
25/08/2017	EUL_ALB	200	49,76419	-15,50098	1	1			MVT	VU
25/08/2017	VAR_VAR	300	49,76436	-15,49995	2	1	1			CRIE
25/08/2017	EUL_ALB	1050	49,76773	-15,49336	3	1	2		RPS	VU
25/08/2017	EUL_ALB	1300	49,76822	-15,49126	5	2	3		MVT	VU
25/08/2017	EUL_ALB	1700	49,76923	-15,48771	4	2	2		RPS	VU
25/08/2017		2000	49,7691	-15,4849						Fin
22/09/2017		0	49,76292	-15,50233						Début
22/09/2017	EUL_ALB	550	49,76557	-15,49797	2	1	1		MVT	
22/09/2017	VAR_SUB	800	49,76675	-15,49581	1	1			MVT	
22/09/2017		2000	49,76912	-15,48499						Fin
					136	63	65	7		

Tab. 4: Superficie des classes d'occupation des sols dans le Nosy Mangabe (1997 et 2017).

OCCUPATION DU SOL	ANNEE 1997		ANNEE 2017	
	Sup(%)	Sup(Km ²)	Sup(%)	Sup(Km ²)
Forêt dense humide	74,99	4,159	48,41	2,685
Forêt dense dégradée	18,86	1,047	33,35	1,85
Sable et sol nu	6,13	0,340	18,22	1,011
TOTAL	100	5,546	100	5,546

Le résultat de l'analyse de fiabilité d'occupation du sol a donné une précision globale de 80.2% et un indice de Kappa 0.36.

Discussion

La forêt humide de Nosy Mangabe est directement liée à l'abondance des lémuriens. Ce genre de paramètre reflète la disponibilité des ressources (nourriture) et détermine la densité des lémuriens. L'exploitation humaine a exercé un impact sur les forêts de Nosy Mangabe depuis plus de 1200 ans, ce qui a probablement contribué à la grande diversité des plantes trouvées aujourd'hui sur l'île (Hatchwell, 2003a), à l'exemple des arbres fruitiers qui sont la nourriture des lémuriens. Actuellement, la présence de ces arbres dans la pointe nord de l'île n'est qu'un témoignage de la présence européenne entre les 17e et 18e siècles (Hatchwell, 2003b). Le recensement effectué en 2017 dans le Nosy Mangabe a révélé une population totale de 216 individus répartis sur une superficie de 32 ha. Il est fortement possible, que nous avons rencontré les mêmes individus plusieurs fois. Le nombre des grands arbres et des arbres fruitiers du site est lié probablement à la composition spécifique et à la biomasse des primates. En général, le pourcentage élevé des observations directes n'est pas dû au hasard, mais

probablement lié à la non-perturbation de l'habitat naturel. Vu les nombres d'individus recensés, le site offre une condition de vie meilleure et viable pour les lémuriens cibles utilisant des supports de locomotion. Les lémuriens, plus particulièrement les *Varecia* sont des disperseurs de grains, après qu'ils ont digéré leur nourriture, les grains, no digestibles, ressortent avec les excréments pour donner naissance à des nouvelles jeunes plantes et ainsi à la reforestation. Les changements et transformations sont à attribuer à un accouplement des facteurs majeurs naturels et politiques (tourisme). Les menaces et pressions pesant sur le site et sur les lémuriens sont les cyclones et les améliorations des circuits touristiques. Des études récentes sur la grande île indiquent aussi que l'intensité des cyclones tropicaux augmente pour le pays, avec des trajectoires qui se déplacent légèrement vers la partie nord. En général, n'importe quel secteur du Nosy Mangabe est susceptible d'être touché par un cyclone et chaque année par des orages tropicaux dont les conséquences sont catastrophiques, surtout sur les habitats naturels des lémuriens et sur les villages de Maroantsetra proches du site. Bien que la télédétection fournisse un apport potentiel en matière de classification du sol et des études diachroniques, cette dernière présente des limites dont il faut tenir compte lors des études semblables, à l'exemple

de l'effet d'ombrage des arbres qui cache la réflectance du sol. L'avènement de la haute résolution spatiale dans les années 1980, et l'existence de photographies aériennes anciennes remontant jusqu'aux années 1960 ont rendu possible une évaluation de la ressource forestière et de son évolution à moyen terme.

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Reproductive flexibility in Goodman's mouse lemurs (*Microcebus lehilahytsara*) at Ankafoabe, central highlands

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Introduction

Mouse lemurs are seasonal breeders and, like in many lemur species, infants are predominantly weaned during the time of "plenty", at the height of the rainy season (Wright, 1999). However, we also know that mouse lemurs are exceptionally flexible in the timing and duration of their reproductive season depending on the individual, species, and site (Evasoa *et al.*, 2018). For instance, female grey mouse lemurs (*Microcebus murinus*) at Kirindy forest have a single litter per season (Eberle and Kappeler, 2004), but in littoral forests or less seasonal dry deciduous habitats, they can have up to three litters per year (Lahann *et al.*, 2006; Schmelting *et al.*, 2000). Moreover, mouse lemurs inhabiting the low-altitude, evergreen humid forests in northern Madagascar display extended reproductive schedules: For example, female Antafondro mouse lemurs (*M. margotmarshae*) were observed in estrous and pregnant in August, in the midst of the dry season, at a time when most mouse lemur species are reproductively inactive (Evasoa *et al.*, 2018). The range of physiological responses across individuals, populations, and species suggests a complex interplay between environmental cues that modulate reproductive activity and species-specific responses that underlie reproductive physiology.

That reproduction is triggered by photoperiod (i.e., daylength) has been demonstrated in mouse lemurs subjected to experimental conditions in captivity (Perret and Aujard, 2001; Wrogemann *et al.*, 2000). For example, when individuals experience "summer" and "winter" at opposite times of the year, which occurs when lemurs are shifted from the southern to the northern hemisphere, they adjust their reproductive cycles to match the concurrent environment. Yet, when subjected to the same environmental conditions in captivity- e.g., daylength, temperature, and food- the timing and number of estrous cycles per year differs between species: Female grey mouse lemurs display estrous cycles between February and September, which is both a month earlier and later than was seen in female Goodman's mouse lemurs (*M. lehilahytsara*) under identical conditions (Wrogemann *et al.*, 2000).

Compared to grey mouse lemurs, one of the most broadly distributed lemurs in Madagascar, Goodman's mouse lemurs were originally described as highland specialists (Radespiel *et al.*, 2012). Nevertheless, additional

and accruing surveys confirm their presence in several eastern sites, including low elevation localities (Schüßler *et al.*, 2020). Moreover, recent taxonomic revisions now recognize Mittermeier's mouse lemurs (*M. mittermeieri*) as Goodman's mouse lemurs (synonymized in Poelstra *et al.*, 2020), considerably expanding this species' range. In fact, Goodman's mouse lemurs are currently the most broadly distributed species in central-eastern and northeastern Madagascar (Dolch *et al.*, 2022). Similar to what was reported for grey mouse lemurs in the West, Goodman's mouse lemurs inhabiting less seasonal, low-elevation humid forests in northern Madagascar (formerly *M. mittermeieri*) display an extended reproductive season: e.g., with estimates of females in estrous as early as July-August, November and March (Schüßler *et al.*, 2020). Goodman's mouse lemurs inhabiting mountainous forests (e.g., Tsinjoarivo, Anjanaharibe-Sud) display a more restricted reproductive season, with a main birth season in December-January and a portion of the population showing fattening in preparation for the dry season as early as February (Blanco, 2010; Schüßler *et al.*, 2020). Unlike grey mouse lemurs, data resolution for reproductive schedules in Goodman's mouse lemurs is spotty and restricted to a few months per year at each study site.

One of the most seasonal and coldest environments inhabited by Goodman's mouse lemurs are the forest fragments in the central highlands. For instance, at Ankafoke we have reported that a portion of Goodman's mouse lemurs hibernate during the cold, dry season (Blanco *et al.*, 2017). If great seasonality and harsh winter conditions are associated with a restricted reproductive season, we might expect a single birth season per year at a site like Ankafoke, with weaning timed to coincide with the rainy season. Moreover, we expect that young mouse lemurs at Ankafoke attain adult size by the beginning of winter, and that only individuals unable to deposit significant fats remain active throughout the lean season. Herein, we combined reproductive observations and reproductive estimates to characterize reproductive schedules in Goodman's mouse lemurs at Ankafoke. Finally, we gather unpublished and published data on reproductive observations in Goodman's mouse lemurs from other localities to characterize the reproductive schedules of this species.

Methods

Ankafoke forest (S18.10643 E47.18701, 1472 m) is a protected area comprising two small forest fragments (12 ha and 30 ha) enclaved in the central highlands and surrounded by grasslands (Andriambeloson *et al.*, 2021). At Ankafoke, the climate is subhumid and seasonal, comprising a wet and relatively hot season between December and April, and a dry and cool season between

May and November. During the coldest months (June-August), temperatures can drop below 6 °C (Goodman *et al.*, 2018).

We used capture/mark/recapture techniques to document reproductive observations during 4 field seasons (Tab. 1). For more information about capture details, see Andriambeloson *et al.* (2021) and Blanco *et al.* (2017). Captured mouse lemurs were brought to the campsite for data collection: Individuals were weighed and mildly sedated (Ketamine, 5-7 mg/kg), and microchipped for permanent identification (Trovan). We observed reproductive condition (e.g., vaginal status, signs of pregnancy or lactation in females, testes development in males), and collected standard morphometrics. We also measured tail-base circumference (in mm) as proxy for tail fattening prior to the dry season.

During captures, we tentatively described individuals as "juveniles" or "adults" based on body mass (g) and reproductive observations (e.g., no visible nipples in females, no testes development in males). Using body mass to estimate age is problematic, however, due to seasonal variation in fat accumulation: A young mouse lemur with tail fattening may weigh more than a skinny adult. We therefore confirmed our field-assigned age classifications using Principal Component Analysis (PCA) of nine morphometric measurements (excluding body mass and tail circumference): head length, head width, snout length, ear length, ear width, tail length, leg length, hind foot length, thumb length. We only included measurements from individuals once, i.e., we excluded morphometrics from recaptures. We retained the top 4 Principal Components (PCs) (i.e., those with eigenvalues > 1 and that accounted for >1% of variation) and used them as covariates in a linear discriminant analysis (LDA). We entered our age classifications as the independent variable. PCA/LDA analyses were conducted in JMP Pro 16.

To assess reproductive schedules, we combined our reproductive observations and estimates from Ankafoke with additional data from published sources: Tsinjoarivo forest (Blanco, 2010), Mantadia (Evasoa *et al.*, 2018; Randrianambinina *et al.*, 2003), Anjanaharibe Sud and Marojeiy (formerly *M. mittermeieri*, Blanco pers. obs. in Schüßler *et al.*, 2020), Anjahely, Riamalandy and Ambavala (Radespiel *et al.*, 2008; Schüßler *et al.*, 2020).

Results

Body mass, tail circumference, and morphometrics

We captured 23 mouse lemurs across seasons. Of these, 18 were unique individuals (10 females, 8 males). We found seasonal variation in body mass and tail girth, with a greater range in summer (Fig. 1). In spring, the heaviest individual was a pregnant female (77 g, with a skinny tail

Tab. 1: Field seasons and animal captures. * No morphometric data were collected on this capture mission.

Season	Year	Dates	Adult females		Adult males		Juveniles	
			Number	Weights (g)	Number	Weights (g)	Number	Weights (g)
Spring	2015	Sept 30-Oct 3	2	42-47	1	47	1	42
	2016	*Nov 2-6	2	71-77	0	NA	0	NA
Summer	2016	Feb 5-13	4	52-73	2	46-49	3	32-39
Winter	2022	Jul 9-15	3	39-43	4	38-45	1	31

of 15 mm); in summer, the heaviest female was post-reproductive for the season and had accumulated fat in her tail (73 g and 27 mm). This individual was found hibernating in late May.

During captures, we tentatively assigned 5 individuals as juveniles, likely to be ≤ 3 months of age. On the PCA plot of 9 morphometric measurements, these 5 individuals scored lower on the first component, which is predominantly a size axis, differentiating larger individuals to the right, from smaller individuals to the left (Fig. 2). LDA revealed a significant correlation between the top 4 PCs and our age classifications (Wilks' $\lambda = 0.22$, $P = 0.003$), and correctly assigned all animals to the correct age classification. Juveniles were thus captured in all three seasons.

Reproductive observations

At Ankafoke, we observed vaginal activity consistent with estrous in early October, pregnant females in November, and lactating females in February. We observed juvenile individuals (estimated ~3-month-old) in October, February, and July (Tab. 2). Because pregnancy is ~60 days in mouse lemurs (Blanco and Zehr, 2015; Wrogemann and Zimmermann, 2001), we therefore estimate the primary birth season to occur between December and January, though additional births may sporadically occur at later times in the year, including in April and July. Reproductive observations from other sites expanded the window for estrous in Goodman's mouse lemur females from October until March. We estimated that births could occur outside of the primary birth season, which is defined between December and April (Tab. 2).

Discussion

Mouse lemurs are known for their ecological flexibility across species and habitats. Even within a single population, individual mouse lemurs can vary in their reproductive strategies. At Ankafoke, some adult females give birth to litters in December, wean their offspring in February, and begin depositing fats in preparation for hibernation. These individuals are reproductively inactive until the Spring (e.g., October). Other individuals, however, show variations to this theme: For instance, some females may suffer early abortions and cycle again a few weeks later. If these pregnancies are successful, they will result in later births, e.g., in April, which would explain our observation of young mouse lemurs in July. Under these conditions, females may be lactating during the lean season, and therefore unable to deposit fats and sustain hibernation. They would thus remain reproductively active later in the dry season. As shown for other mouse lemur species, this reproductive flexibility may be beneficial if individuals can rely on fallback foods to sustain metabolism during the lean season (Blanco *et al.*, 2015).

Our reproductive observations at Ankafoke suggest that births may sporadically occur at different times in a year (and as late as July). This is in contrast to grey mouse lemurs at Kirindy, a seasonal dry deciduous forest, where females are known to give birth to a single litter per year (Eberle and Kappeler, 2004). After weaning their offspring, most females deposit fats and undergo seasonal torpor, whereas other mouse lemurs (mostly males) remain active during the dry season (Schmid, 1999). Perhaps some births occur outside of the December-January window at Kirindy, but infant survival may be poor if high-quality food is scarce.

It is perhaps not a coincidence that Goodman's mouse lemurs persist in seasonal, fragmented, and cold environments like Ankafoke, where opportunistic responses are key to survival. By evolving under seasonal and unpredictable conditions, Goodman's mouse lemurs perhaps developed mechanisms to cope with energetic crises: e.g., by relying on metabolic strategies like torpor to minimize energy expenditure, tolerating the digestion of low-quality fallback foods, and/or having the reproductive flexibility to invest in multiple litters/offspring per year. Mouse lemurs, in general, are one of the most resilient and ecologically flexible groups of lemurs; Goodman's mouse lemurs, in particular, may be one of the most flexible species in Madagascar.

Acknowledgements

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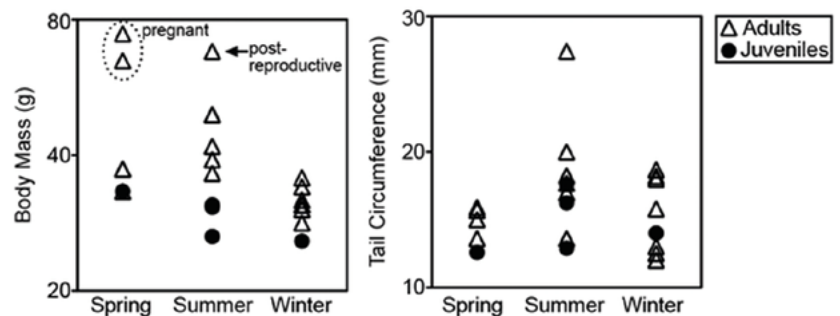


Fig. 1: Body mass (left) and tail circumference (right) of adult (triangle) and juvenile (circle) mouse lemurs captured in three seasons. The dotted circle highlights two pregnant individuals and the arrow highlights the post-reproductive female (i.e., finished reproducing until upcoming breeding season).

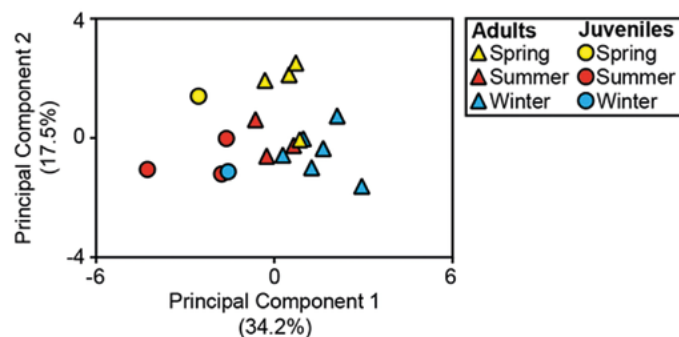


Fig. 2: PCA of morphometrics of juveniles (circles) and adults (triangles) captured in three seasons.

Tab. 2: Reproductive observations and birth estimates of Goodman's mouse lemurs from this study (A) and other published sources.

Observations												
Estrus/Swelling		A										
Pregnancy			A									
Lactation						A						
Juveniles		A				A					A	
Births (Inferred)				A				A			A	
Month	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug

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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 lemur (*Lemur coronatus*) and Sanford's lemur (*Lemur fulvus sanfordi*) of Madagascar. Ph.D. thesis, Washington University, St. Louis, USA.

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IUCN. 2008. IUCN Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 21 April 2009.

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