

# Ecology and morphology of mouse lemurs (Microcebus spp.) in a hotspot of microendemism in northeastern Madagascar, with the description of a new species

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# Ecology and morphology of mouse lemurs (Microcebus spp.) in a hotspot of microendemism in northeastern Madagascar, with the description of a new species

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- 1 Ecology and morphology of mouse lemurs (*Microcebus* spp.) in
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#### Abstract

Delimitation of cryptic species is increasingly based on genetic analyses but the integration of distributional, morphological, behavioral and ecological data offers unique complementary insights into species diversification. We surveyed communities of nocturnal mouse lemurs (*Microcebus* spp.) in five different sites of northeastern Madagascar, measuring a variety of morphological parameters and assessing reproductive states for 123 individuals belonging to five different lineages. We documented two different non-sister lineages occurring in sympatry in two areas. In both cases, sympatric species pairs consisted of a locally restricted (*M. macarthurii* or *M.* sp. #3) and a more widespread lineage (M. mittermeieri or M. lehilahytsara). Estimated Extents of Occurrence (EOO) of these lineages differed remarkably with 560 and 1,500 km<sup>2</sup> versus 9,250 and 50,700 km<sup>2</sup>, respectively. Morphometric analyses distinguished unambiguously between sympatric species and detected more subtle but significant differences among sister lineages. Tail length and body size were most informative in this regard. Reproductive schedules were highly variable among lineages, most likely impacted by phylogenetic relatedness and environmental variables. While sympatric species pairs differed in their reproductive timing (M. sp. #3 / M. *lehilahytsara* and *M. macarthurii / M. mittermeieri*), warmer lowland rainforests were associated with a less seasonal reproductive schedule for *M. mittermeieri* and M. lehilahytsara compared to populations occurring in montane forests. Distributional, morphological and ecological data gathered in this study support the results of genomic species delimitation analyses conducted in a companion study, which identified one lineage, M. sp. #3, as meriting formal description as a new species. Consequently, a formal species description is included.

Worryingly, our data also show that geographically restricted populations of *M*.

sp. #3 and its sister species (*M. macarthurii*) are at high risk of local and

perhaps permanent extinction from both deforestation and habitat

#### Research highlights

fragmentation.

- Two pairs of *Microcebus* species occur in partial sympatry
- Morphological distinctiveness supports genomic species delimitation in
   cryptic lemurs
- High plasticity in reproductive schedules in a lineage of habitat
   generalists detected

- 79 Keywords: evolution, cryptic species, phenotype, habitat use, sympatry,
- 80 conservation

#### 1. Introduction

Madagascar is one of the world's prime biodiversity hotspots and its endemic
group of primates, the lemurs (*Primates*; *Lemuriformes*), are flagships for
species conservation (Myers, Mittermeier, Mittermeier, Da Fonseca & Kent,
2000). More than 100 species of lemurs are recognized today making up about
one fifth of all living primate species on earth (Estrada et al., 2017). However,
the full extent of lemur species diversity is not yet fully known as several regions

in Madagascar are still poorly studied. Intensified biological inventories during recent years have indeed resulted in a considerable rise in lemur species numbers. One example of increased taxonomic recognition is the genus of mouse lemurs (Microcebus). These small-bodied and nocturnal primates can be found in all regions of Madagascar that offer forested habitats, while partially deforested areas appear to offer at least dispersal opportunities (Knoop, Chikhi & Salmona, 2017; Miller et al., 2018; Schüßler, Radespiel, Ratsimbazafy & Mantilla-Contreras, 2018). Although rather widespread across the island, mouse lemurs suffer from habitat loss due to ongoing deforestation (Vieilledent et al., 2018). According to the IUCN, eleven species are listed as Endangered, three species are Critically Endangered, while four are Vulnerable and only two species are categorized as of Least Concern. The remaining four species have not yet been assessed due to their recent discovery (Andriaholinirina et al., 2014; Hotaling et al., 2016; Rasoloarison et al., 2013). Integrating ecological and distributional data with molecular analyses in mouse lemurs is often difficult, largely because of their cryptic morphology and life history and lack of detailed metadata (Zimmermann & Radespiel, 2014). Analyses of mtDNA datasets have identified divergent lineages despite similar phenotypes and roughly similar ecological niches, and have led to the description of twelve new species over the past 20 years from the western part (Louis et al. 2008; Olivieri et al. 2007; Rasoloarison, Goodman & Ganzhorn, 2000; Yoder et al. 2000; Zimmermann, Cepok, Rakotoarison, Zietemann & Radespiel, 1998) and a further eleven species from the eastern part of Madagascar (Hotaling et al. 2016; Kappeler, Rasoloarison, Razafimanantsoa, Walter & Roos, 2005; Louis et al. 2006; Radespiel et al. 

2008, 2012; Rasoloarison, Weisrock, Yoder, Rakotondravony & Kappeler,

115 2013).

Recent studies indicate that some regions appear to be hotspots of microendemism. One of these is located in northeastern Madagascar where *M. lehilahytsara* (Kappeler et al., 2005), *M. mittermeieri* and *M. simmonsi* (Louis et al., 2006) are known to occur. Radespiel et al. (2008) surveyed the forests of the Makira region (Anjiahely, Figure 1) and found evidence for three divergent lineages occurring in sympatry, a phenomenon previously undocumented for mouse lemurs. One of these was identified as *M. mittermeieri*, while the second was newly described as *M. macarthurii*. The third lineage, named *M.* sp. #3, was hypothesized to be a new species based on mitochondrial sequence data but could not be formally described given that only a single individual was found.

We conducted additional sampling in northeastern Madagascar to fill the gap between the known distribution of *M. simmonsi* (Zahamena NP, Betampona SNR, Tampolo; Louis et al., 2006) and the sympatric species pair *M. macarthurii* and *M. mittermeieri* at Anjiahely (Radespiel et al., 2008; Figure 1). The presence of the *M.* sp. #3 lineage was indeed confirmed but only for three study sites south of Anjiahely by genomic data in a companion study (Poelstra et al., 2020). Based on a comprehensive dataset generated from restriction-site associated DNA sequencing (RADseq) using a total of 63 mouse lemurs from the entire region (Marojejy NP to Betampona SNR, excluding Ile St. Marie, Figure 1), these analyses unambiguously supported four different lineages: *M*.

sp. #3, M. macarthurii, M. lehilahytsara/M. mittermeieri and M. simmonsi. While

the two lineages M. sp. #3 and M. macarthurii unambiguously passed all species delimitation tests (i.e., mitochondrial and nuclear monophyly in RAxML and SVDquartets, clear nuclear clustering in NGSadmix, rejection of a simple isolation-by-distance pattern, formal species delimitation using SNAPP Bayes factors, BPP and gdi), M. mittermeieri and M. lehilahytsara did not fall into two separate monophyletic clades (Poelstra et al., 2020; Figure 2). Instead, these two latter species exhibited a single isolation-by-distance pattern and high levels of interspecific gene flow, suggesting that separate species status may not be justified (Figure 2; discussed in detail in Poelstra et al., 2020). For the purpose of this study, however, we will still treat these two lineages as separate taxa in order to be able to test their distinctiveness in other domains. Besides using molecular data, species delimitation under an integrative taxonomic approach (e.g., Padial, Miralles, de la Riva & Vences, 2010) requires incorporating morphological and ecological information. While phenotypic differences between lineages could, for instance, indicate dietary preferences (e.g., Viguier, 2004), environmental and reproductive data can help to understand the role of habitat selection (Dammhahn & Kappeler, 2008; Rakotondravony & Radespiel, 2009) and reproductive schedules (Evasoa et al. 2018) during speciation. Here, we complement the molecular results presented by Poelstra et al. (2020) by (1) providing morphological, ecological and distributional data for the M. sp. #3 lineage in comparison to all other species from the same region and (2) by formally describing this new species.

#### 2. Methods

#### Study region

Northeastern Madagascar is characterized by a humid climate with abundant precipitation (2,086 ± SD 530 mm SD; Fick & Hijmans, 2017) and tropical rainforests as primary vegetation (Kottek, Grieser, Beck, Rudolf & Rubel, 2006). Forest cover has been steadily declining for decades, with lowland rainforests being particularly prone to deforestation (Schüßler, Mantilla-Contreras, Stadtmann, Ratsimbazafy & Radespiel, 2020; Vieilledent et al., 2018). By 2018, about half of the remaining forested areas were under protection by governmental institutions or non-governmental organizations (Schüßler et al., 2020). The study region is subdivided by more than seven large rivers that flow from the highlands of the central plateau (west of the study region; Figure 1) eastwards into the Indian Ocean. Large rivers have been considered potential biogeographic boundaries for mouse lemurs (e.g., Olivieri et al., 2007; Martin, 1972).

#### Microcebus sampling

Mouse lemurs were sampled between 2008 and 2017 at five lowland rainforest sites ranging in altitude between 42 and 462 m a.s.l. (Figure 1). In particular, animals were captured around the village of Anjiahely (Makira region; where the holotype of *M. macarthurii* was obtained; Radespiel et al., 2008), in the fragmented forests around the village of Ambavala (Schüßler et al., 2018), within Mananara-Nord NP (Ivontaka-Sud section), around Antanambe village in

the vicinity of Mananara-Nord NP, as well as in the Ambodiriana community protected area (Miller et al., 2018). All study sites comprise habitats ranging from undisturbed near-primary rainforest to heavily degraded secondary shrub-, grass- and fernlands (Radespiel et al., 2008; Miller et al., 2018; Schüßler et al., 2018). Mouse lemurs were captured using Sherman Live traps (H. B. Sherman Traps ®) or by hand during nocturnal surveys (e.g., Radespiel et al., 2008). Morphometric measurements were taken for each individual (see below) and additional descriptors such as fur coloration were noted and photographed. Ear biopsies (~2 mm²) were collected to provide DNA samples, and all animals were released unharmed within 24 hours at their exact location of capture. GPS coordinates and the altitude of capture locations were collected to estimate the altitudinal range and Extent of Occurrence of mouse lemur species included in this study. The latter measure follows the definition of the IUCN (2012) in which the "shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon" is used to derive the possible distribution of a certain species. All procedures adhered to the standards of the International Primatological Society (Riley, MacKinnon, Fernandez-Duque, Setchell & Garber, 2014) and the Principles for the Ethical Treatment of Non-Human Primates of the American Society of Primatologists (2001). This research was conducted with permission from institutional and governmental agencies that regulate animal research in Madagascar, Germany, France, Portugal, and the United States. 

#### Morphometric characterization and reproduction

Captured mouse lemurs were measured for 13 different morphometric variables (ear length, ear width, head length, head width, snout length, inter- and intraorbital distance, lower leg length, hind foot length, third toe length, tail length, body length and body mass) following Hafen, Neveu, Rumpler, Wilden and Zimmermann (1998) and Zimmermann et al. (1998). Mouse lemurs were assigned to two age categories based on their body mass and reproductive state: (1) adult in contrast to (2) young mouse lemurs (<1 year old) that had a relatively low body mass (Table 1) and showed no visible nipples (females) and undeveloped, or barely developed testes (males). Young mouse lemurs were excluded from all morphometric comparisons and only values for adult *Microcebus* spp. are used for further analyses. Very light young mouse lemurs of about half of the adult body mass were termed juveniles. To supplement the comparative dataset, we also included published morphometric data from 42 M. lehilahytsara individuals from Mantadia NP (holotype locality, Randrianambinina, 2001) and data from 22 *M. mittermeieri* individuals that had previously been caught near Anjiahely (Radespiel et al., 2008). The morphometric dataset is provided in the supplementary material (Table S1). Mouse lemurs are seasonal breeders and can already reproduce during their first year of life (Evasoa et al., 2018; Kraus, Eberle & Kappeler, 2008; Schmelting, Zimmermann, Berke, Bruford & Radespiel, 2007). Reproductive states were assessed using several morphological indicators (i.e., vaginal morphology and testis size) frequently used in the literature (e.g., Blanco, 2008;

Randrianambinina, Rakotondravony, Radespiel & Zimmermann, 2003; Wrogemann & Zimmermann, 2001). The reproductive state of females was defined as anestrous (closed vagina, non-reproductive), pre-estrous (swollen vagina), estrous (open vagina), pregnant (enlarged belly) or lactating (palpable and enlarged nipples that release milk under soft pressure). Male reproduction was assessed based on testes state: while being completely regressed in the non-breeding season, testes increase considerably in size starting about one to three months prior to female estrus (Evasoa et al., 2018). However, testes size was measured slightly differently across our dataset (i.e., left and right testes separately or only total width) and measures may also differ slightly between different researchers. Therefore, we defined a unified and realistic threshold for classifying total testes width by defining a binary variable for a regressed (< 10.0 mm) or enlarged (> 10.0 mm) width. Total testes width for the regressed category ranged from 0.0 to 5.3 mm and from 10.2 to 26.2 mm for the enlarged category across all species. One limitation to the morphometric analyses is that measurements across the five different lineages were taken by five researchers, thus potentially introducing inter-observer error. It is worth reporting, however, that two researchers contributed data points to more than one species (DS, DWR), and that DS was trained by DWR. Furthermore, there was a strict selection of measurements that fully agreed with collection standards before assembling the dataset. Finally, the dataset was carefully scanned for outliers and inconsistencies within and across species, and a total of 21 measurements was excluded for this reason prior to data analyses. Reproductive data can also be found in supplementary Table S1.

# Statistical analyses of morphometrics

We performed a principal component analysis (PCA) and linear discriminant analysis (LDA) as well as Analyses of Variance (ANOVA) with Tukey post-hoc tests for pair-wise comparisons for all 13 morphometric variables. Assumptions of the respective tests were examined beforehand using Shapiro-Wilk and Levene's tests in R (R Core Team 2019; RStudio Team, 2016) using the car v3.0-2 package (Fox & Weisberg 2011). M. lehilahytsara individuals from Ambavala were excluded from the ANOVA due to small sample size. For LDA and ANOVA, mouse lemurs were a priori assigned to their respective taxon based on the results of the parallel phylogenomic study (Figure 2; Poelstra et al., 2020). For PCA, species assignment was done a posteriori to investigate clustering under naïve conditions in which the distance between sample points reflects their distance along the major axes of variation in the dataset. Accordingly, points that cluster closely together are more similar to each other than points that do not (Abdi & Williams, 2010). In contrast to that, the LDA aims to minimize distances within pre-defined clusters while maximizing distances among clusters (Balakrishnama & Ganapathiraju, 1998). The PCA was followed by a permutational multivariate analysis of variances (PERMANOVA) as implemented in the "vegan" R package (Oksanen et al., 2019), which tests the null hypothesis of no differences in the position of cluster centroids (Anderson, 2017). For both PCA and LDA, we used all measurements except third-toe length, as this measurement was not available for *M. simmonsi*. We further only used a

subset of eleven *M*. sp. #3 individuals for which we had all 13 measurements. The PCA was performed using the "prcomp" command in R (scaled and centered), while the LDA was calculated using the "MASS" package (v7.3-51.3; Venables & Ripley, 2002). Model fit of the latter was evaluated by a jackknife cross-validation and calculated as misclassification error. We also computed Wilks' Lambda and the P-value to evaluate the ability of the LDA model to distinguish between the five lineages.

#### 3. Results

Distribution of *Microcebus* spp. in northeastern Madagascar

First, we confirmed the presence of mouse lemurs at four locations previously not surveyed in our study region (Figure 1 & 2; species delimitation based on genomic data in Poelstra et al., 2020). At two locations, two different mouse lemur species were found in sympatry. These are *M. macarthuriilM. mittermeieri* in Anjiahely and *M.* sp. #3/M. lehilahytsara in Ambavala (Figure 1). In Mananara-Nord NP and around Antanambe village (south of the Mananara River), extensive surveys revealed only the presence of *M.* sp. #3. At Ambodiriana (one major river further south from Antanambe; Figure 1), we only found *M. simmonsi*. Altitudinal ranges vary among the lineages, with *M. macarthurii* and its sister species *M.* sp. #3 being only found in lowland rainforests. The other three lineages, *M. mittermeieri*, *M. lehilahytsara* and *M. simmonsi*, were found in lowland as well as montane rainforests (Table 2). The estimated Extent of Occurrence (EOO) is much smaller for the two lowland species (*M. macarthurii* [560 km²] and *M.* sp. #3 [1,500 km²]) compared to *M.* 

mittermeieri (9,250 km²) and *M. lehilahytsara* (50,700 km²; Table 2). Combined EOO for *M. lehilahytsara* and *M. mittermeieri*, if considered as a single species, is estimated with 66,800 km².

# Morphometric distinction between lineages

All morphometric parameters differed significantly among lineages (ANOVA; P < 0.001; Table S3) and Tukey post-hoc tests revealed many pairwise differences (Figure 3; Table 3; Figure S1). M. sp. #3 can be statistically differentiated from its closest relative, M. macarthurii, by 5 out of 13 parameters. M. macarthurii has smaller body size and longer tail length, and subtle differences were found in head-associated parameters (i.e., ear width, head length and width). By comparison, M. lehilahytsara (from Mantadia NP) and M. mittermeieri (from Anjiahely) differed in 7 out of 13 variables. Major differences were found in snout and tail length, while other differences were more subtle but statistically significant (Figure 3; Figure S1; Table 3). Both M. lehilahytsara and M. mittermeieri were significantly smaller than M. sp. #3 and M. macarthurii, which was mainly reflected in the parameters body mass and length, tail length, lower leg, hind foot and third toe length (Figure 3, Figure S1; Table 3). M. simmonsi took an intermediate position in most comparisons. M. lehilahytsara from Ambavala was not compared by ANOVA due to the small number of adults (N = 3). However, the individuals from this population showed remarkably different measures compared to conspecifics from Mantadia NP or M. mittermeieri from Anjiahely (i.e., body length, tail length; Table 3).

These patterns are also illustrated in the multivariate analyses: the PCA (a posteriori assignment of species clusters) distinguished two clusters along PC1 and PC2 (Figure 4). The two larger species, M. sp. #3 and M. macarthurii, clustered with negative values along PC1 and the smaller M. mittermeieri and M. lehilahytsara had positive values along PC1. Both sister-species pairs were split in two clusters along PC2, while *M. lehilahytsara* from Ambavala clustered with *M. mittermeieri* from Anjiahely. Again, *M. simmonsi* occupied a position in between these two major clusters. PC3 mainly separated M. sp. #3 and M. macarthurii, while all other species clustered together along PC3 and PC4. These first four principal components (PCs) together explained 84.7% of the variance in our dataset. These five clusters corresponding to the five lineages were significantly different from each other as indicated by the PERMANOVA (F = 36.88, df = 77, P < 0.001). The LDA model (a priori assignment of species) could also statistically distinguish between the five lineages (Wilk's Lambda = 0.005, F = 10.338, P < 0.001). Four distinct clusters that included M. lehilahytsara, M. macarthurii, M. mittermeieri and M. sp. #3 are illustrated in Figure 5. M. simmonsi fell again between these major clusters, while M. lehilahytsara and M. mittermeieri exhibited some minor overlap. M. lehilahytsara from Ambavala again showed more affinity to *M. mittermeieri* than to conspecifics from Mantadia NP. Misclassification error after cross-validation was 12.8% and misclassification occurred mainly with *M. simmonsi* (Table S4). The first two discriminant functions explained together 86.9% of the variation between the groups. 

#### Reproductive status

At Anjiahely, all male *M. macarthurii* that were captured from late October to December had enlarged testes (N = 8), while the four female *M. macarthurii* showed no signs of reproduction from September to November (Figure 6). Only one out of five females was in pre-estrus (swollen vagina) in early November. No young or juvenile individuals were found. Sympatric *M. mittermeieri* individuals (N = 22 adults) were captured across three months: in September, all males already had well developed testes (N = 11), while females showed no signals of reproduction (N = 5). In November, testes were still well developed (N = 2), and 2 out of 3 females were in estrus. Juveniles weighing 20-24 g were captured in the population in mid-December (Figure 6). During our surveys at three locations between August 13th and September 17th. none of the M. sp. #3 females (N = 7) showed indications of estrus, pregnancy or lactation. However, all adult males had well developed testes (N = 15) and no juveniles were found. In contrast, at Ambavala between September 8th to 19th, all sympatric M. lehilahytsara females were anestrous (N = 2), while all adult males had regressed testes (N = 6). At the same time, two juvenile males were captured that were still very light with only 19 and 20 g. In contrast, M. lehilahytsara females at Mantadia NP were anestrous from May until late October (N = 5), in estrus in November (N = 1) and pregnant in December (N = 1)3; Figure 6). Males had regressed testes in April and May (N = 8) and enlarged testes from August to November (N = 13). Although young individuals were identifiable between March and August, juvenile individuals (20 g body mass, N = 1) were only found in March (no other captures at that time, Figure 6).

Eight *M. simmonsi* were caught in Ambodiriana in June and July. All males (N = 5) had enlarged testes, while females (N = 3) were not reproductively active (Figure 6).

#### 4. Discussion

We studied the distribution, morphology and reproductive state of five mouse lemur lineages occurring in a complex spatial pattern across a small region in northeastern Madagascar. Comparative phenotypic and ecological data was previously sparse for four of these taxa, and this study therefore represents an important step towards deepening our understanding of mouse lemur diversity in this understudied hotspot of microendemism.

# <u>Distribution of Microcebus spp. in northeastern Madagascar</u>

Our study, in conjunction with the companion study by Poelstra et al. (2020), confirmed the presence of five *Microcebus* spp. lineages, including two pairs of closely related sister lineages, *M. macarthurii | M.* sp. #3 and *M. mittermeieri | M. lehilahytsara* in northeastern Madagascar, with two cases of local sympatry. Besides the case of *M. macarthurii* and *M. mittermeieri* at Anjiahely (Radespiel et al., 2008), sympatry of two mouse lemur species is so far only known from five cases from western Madagascar and one case from the northern part of the island (Sgarlata et al., 2019). In the five western cases, geographically restricted species co-exist with the widely distributed congener *M. murinus* (Radespiel, 2016) which probably expanded northwards rather recently

(Schneider, Chikhi, Currat & Radespiel, 2010). Here, we confirm a new case with *M.* sp. #3 being found in sympatry with *M. lehilahytsara* in Ambavala (Figure 1).

Ecologically, two sister species, *M. macarthurii* and *M.* sp. #3, appear to be restricted to lowland forests, whereas M. mittermeieri and M. lehilahytsara are present in lowland as well as montane forests (Table 2). Thus, M. macarthurii and M. sp. #3 both have geographically restricted distributions and possess a limited Extend of Occurrence, suggesting that they are microendemic, while M. lehilahytsara and M. mittermeieri are more widely distributed. Consequently, the cases of sympatry between M. sp. #3/M. lehilahytsara and M. macarthurii/M. mittermeieri, respectively, may to some extent be similar to the cases of sympatry from western Madagascar, where locally restricted species co-occur with the habitat generalist *M. murinus* (Kamilar, Blanco & Muldoon, 2016; Radespiel, 2016). However, the recent expansion of *M. murinus* seems to have been a unique event that has no clear equivalent in eastern Madagascar. M. simmonsi was previously reported from Zahamena NP, Betampona SNR and Tampolo (Hotaling et al., 2016; Louis et al., 2006). We can now confirm its occurrence 75 km and four inter-river systems (IRSs) further north (Figure 1 & 2) which expands its EOO by almost fivefold. The northern range limit for M. simmonsi appears to be the Anove River, which separates it from M. sp. #3. These two species have (so far) only been found in allopatry (despite intensive sampling north of the river), and we consider two alternative hypotheses

sampling north of the river), and we consider two alternative hypotheses responsible for this pattern: (1) competitive exclusion at the geographic limits of the respective species ranges (Beaudrot et al., 2013; Hardin, 1960) or (2) an

altitudinal range limit of both species below 640-700 m a.s.l corresponding to the source region of the Anove River (DS, unpubl. data). The latter hypothesis appears to be unlikely, as both species are distributed over two or more IRSs that are separated by rivers with much higher headwaters (DS, unpubl. data). Moreover, M. simmonsi has been found at an elevation of around 956 m a.s.l. (in Zahamena NP, Louis et al., 2006), contradicting the altitudinal limitation hypothesis. A further expansion of *M. simmonsi* northwards across the Anove River, however, may have been precluded by the presence of the larger M. sp. #3 that may have a higher competitive potential than the smaller *M. simmonsi* (Table 3; Thorén, Linnenbrink & Radespiel, 2011). In the case of M. sp. #3, the subpopulations on both sides of the large Mananara River (Figure 1) were shown to belong to two separate population clusters evolving largely independently from each other (Figure 2; Poelstra et al., 2020). This suggests that the Mananara River poses a significant barrier to gene flow within this species (Poelstra et al., 2020). This moderate sensitivity to altitude may have limited the colonization potential of *M.* sp. #3 southwards. These complex patterns demonstrate that the biogeography and phylogeography of mouse lemurs in this region of Madagascar are still not completely understood and should be re-evaluated. Biogeographic patterns in the region are further complicated by our unexpected finding that the previously regarded "highland specialist" M. lehilahytsara (Radespiel et al., 2012) also occurs in the lowland rainforests around the village of Ambavala (233-462 m a.s.l). Prior to our study, this species had never been observed at altitudes below 800 m a.s.l., although it is known to occur in an extensive stretch of highland forests in central and northeastern Madagascar

(between Riamalandy; Figure 1; (Weisrock et al., 2010) and Tsinjoarivo (430 km further south; (Yoder et al., 2016)). Besides in the IRS of Ambavala, the other lowland regions are always inhabited by different mouse lemur species (from north to south: *M. simmonsi* (Louis et al., 2006), *M. gerpi* (Radespiel et al., 2012), *M. marohita* (Rasoloarison et al., 2013)). Phylogenomic analyses indicated, that *M. lehilahytsara* and *M. mittermeieri* should rather be considered a single widely distributed species with extensive population structure, which is most likely driven by isolation-by-distance between subpopulations (Figure 2; Poelstra et al., 2020). Under these circumstances, allopatry of southern *M. lehilahytsara* populations with lowland taxa, but sympatry of more northern populations with lowland species (i.e., *M.* sp. #3 (at Ambavala) and *M. macarthurii* (at Anjiahely)) requires further investigation concerning the relative importance of competitive exclusion, different habitat preferences or distributional barriers, all of which have remained unexplored so far.

#### Morphometric differences among mouse lemurs

Mouse lemurs are typically regarded as cryptic species exhibiting only subtle interspecific morphological differences (Zimmermann & Radespiel 2014).

Although our measurements of 13 external body parameters generally confirm their cryptic nature, some differences could be detected that can help to distinguish different species.

All analyses confirmed a noticeable divide between the two larger taxa *M*. sp. #3/*M*. *macarthurii* and the two smaller-bodied lineages *M*. *lehilahytsara* and *M*. *mittermeieri* (along PC1, Figure 4, Table 3). Even sister taxa could be

differentiated by some morphological measurements. Specifically, M. sp. #3 could be distinguished from *M. macarthurii* by body size, tail length and three head-associated parameters (ear width, head length, and head width). Tail length has been previously emphasized as a feature distinguishing mouse lemur species (e.g., Radespiel et al. 2012) and can be measured with high accuracy. The more subtle differences in head-associated parameters must be interpreted more carefully, particularly because measurements were not always made by the same person. Nevertheless, it has been suggested that skull parameters may also vary with feeding habits for lemurs and strepsirrhine primates in general (e.g., omnivorous, folivorous or frugivorous etc.; Fabre et al., 2018; Meloro et al., 2015; Viguier, 2004). If validated by future studies, such differences may indicate dietary or even cognitive differentiation between closely related taxa (Zimmermann & Radespiel 2014). Conversely, M. lehilahytsara and M. mittermeieri differed in tail length, body length, third toe length and four head-associated parameters (Figure 3; Table 3). This comparison was, however, based on two populations that are over 400 km away from each other. Genomic analyses on samples obtained for M. lehilahytsara at two intermediate locations (Riamalandy and Ambavala, Figure 1) and *M. mittermeieri* samples from Anjiahely, Anjanaharibe-Sud SR and Marojejy NP revealed only moderate genomic differentiation along a geographic gradient (Figure 2; Poelstra et al., 2020). It was concluded that these results do not justify separate species status of these two taxa. Unfortunately, we only caught three adult *M. lehilahytsara* at Ambavala making it difficult to assess whether the individuals from this intermediate geographic location also took an intermediate morphometric position. Measurements from these three

individuals, however, suggest that *M. lehilahytsara* from Ambavala was more similar to *M. mittermeieri* from Anjiahely than to *M. lehilahytsara* from Mantadia NP (Table 3). If considered as one species, these differences could indicate morphological adaptations to different environmental conditions (highland versus lowland rainforest) or a morphological gradient across its entire range. These hypotheses, however, will require further testing. M. simmonsi individuals collected at Ambodiriana fell in between the clusters of larger and smaller-bodied species in all analyses. However, when comparing these individuals to *M. simmonsi* sampled further south (Zahamena NP and Betampona SNR; Louis et al., 2006), our individuals were smaller (9.2 vs. 8.9 cm body size), had lower body mass (65 vs. 52 g) and had shorter tails (14.2 vs. 13.1 cm). These differences are even more pronounced when comparing our dataset to the holotype specimen for M. simmonsi (9.8 cm, 77 g and 14.9 cm, respectively; Louis et al. 2006). On the other hand, the holotype specimen of M. boraha, occurring on Ile St. Marie (an island less than 20 km off the coast of Ambodiriana, Figure 1) had about the same average body mass (56.5 g; Hotaling et al., 2016) as the population in Ambodiriana. While these comparisons should be interpreted with caution due to small sample sizes and different collection details, they suggest that M. simmonsi from Ambodiriana and M. boraha from Ile St. Marie may be more closely related than previously thought. Genomic analyses revealed only slight differentiation between southern *M. simmonsi* and the population at Ambodiriana (Poelstra et al., 2020). However, future analyses should also include samples from *M. boraha* from Ile

St. Marie to clarify relationships among these populations and lineages.

Reproductive patterns of *Microcebus* spp. in northeastern Madagascar Differences in reproductive schedules among mouse lemur species depend on phylogenetic relatedness, although environmental parameters (i.e., rainfall and temperature) likely play a role in fine tuning reproductive function (Evasoa et al., 2018). Although photoperiod is generally considered the main trigger of reproductive physiological function in mouse lemurs and is a relatively good predictor of food availability in seasonal habitats, there is substantial variation in the timing and duration of reproduction within and across mouse lemur species, as evident in our study populations. Reproductive observations from this study and those from published sources (Evasoa et al., 2018) suggest that M. sp. #3 may start their mating season in October-November, because males showed developed testes by August/September, while females were still anestrous and not lactating (Figure 6), and juvenile individuals were not found. This timing of reproduction is comparable to that of *M. lehilahytsara* from other sites but interestingly not from Ambavala, where this species is sympatric with *M.* sp. #3. In September, the two adult male *M. lehilahytsara* from Ambavala did not have enlarged testes and we also captured juvenile M. lehilahytsara with less than half of the adult body mass (19-23 g). A body mass of about 20 g was found around the time of weaning in juvenile captive M. lehilahytsara of about seven weeks of age (Radespiel, Zimmermann & Wittkowski, unpubl. data). Adding these seven weeks (49 days) to about 57 days of gestation (for *M. lehilahytsara*, Wrogemann & Zimmermann, 2001; for *M. rufus*, Blanco, 2008), this could point

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towards a mating season of the *M. lehilahytsara* in Ambavala potentially lasting until May.

These findings contrast strikingly with those from *M. lehilahytsara* inhabiting montane and high elevation rainforests. For instance, at Mantadia NP (300 km further south of Ambavala; Figure 1) all adult males had enlarged testes in September, and some adult females were in estrus in November. Juveniles at this site (20 g body mass) were only found in late March (Randrianambinina et al., 2003; this study). Similar observations were made at Ambatovy, a montane forest (near Mantadia NP) where MBB (unpubl. data) captured two juveniles in late February (~2 months old), suggesting a distinct birth season in mid-late December. An adult male captured in early March showed evidence of tail fattening. At Tsinjoarivo (Table S2), another high-altitude forest, M. lehilahytsara females were observed gestating or lactating in late November, December and early January (Blanco, 2010). From these sites there was also evidence of rebound polyestry, i.e., females undergo renewed estrus after the loss of offspring or early abortions. The capture of juvenile mouse lemurs (2-3 months old) in early February, however, suggested a main birth season at this site in early-mid December. In sum, observations of tail fattening at Tsinjoarivo and Ambatovy in early March suggest that, at least for a portion of the mouse lemur population, reproductive season is over by this time of the year.

Ambavala, unlike Mantadia NP, Ambatovy and Tsinjoarivo, is a low elevation rainforest site (250 m vs. >800 m a.s.l., respectively). Seasonal climatic fluctuations are more pronounced in montane rainforests than in the lowland rainforests of eastern Madagascar. For example, Mantadia NP has a lower

mean annual temperature (19°C compared to 23°C), lower minimum temperature (9°C compared to 15°C) and a higher annual temperature range (19°C compared to 15°C; Fick & Hijmans, 2017) than Ambavala. Climatic conditions have already been suggested as major determinants of reproductive schedules for small-bodied mouse lemurs (Evasoa et al., 2018) with higher mean ambient temperatures and smaller temperature fluctuations allowing a less seasonal reproduction compared to the harsh conditions of the montane rainforests (Evasoa et al., 2018; Randrianambinina et al., 2003). Taken together, the findings of this study and previous work suggest a considerable degree of intraspecific variation concerning reproductive timing in M. lehilahytsara. Another pair of sympatric mouse lemur species from lowland rainforests (Anjiahely: about 350-400 m a.s.l.) were characterized with regard to reproductive activities in the northern part of our study region: *M. macarthurii* and M. mittermeieri. The enlarged testes of M. macarthurii males from October onwards and the presence of pre-estrous females in November indicate that the mating season in these forests probably begins at that time (Figure 6). Furthermore, the absence of juvenile and young mouse lemurs during our sampling period may indicate one short mating season probably limited to November-December. Sympatric *M. mittermeieri* females were also found in estrus in November and the respective males had enlarged testes in September. Moreover, juvenile M. mittermeieri of about 20 g (~2 months old) were also found in November and December. In analogy to the case of *M. lehilahytsara* (see above), we therefore

also predict some mating of *M. mittermeieri* to occur as early as in July - August in Anjiahely. Reproductive observations of two M. mittermeieri females from another low elevation forest (Marojejy NP east site, ~200 m a.s.l.; MBB, unpubl. data) captured in mid-late March, also suggest an extended reproductive period and evidence of polyestry in this species. One of the females showed vaginal swelling (pre-estrus) and 3 pairs of developed nipples, suggesting she had given birth earlier in the season and was getting ready to mate again. The second female showed a vaginal opening (estrus) and well-developed nipples, also suggesting she had given birth earlier in the season and could, if mating were successful, have another birth at the end of May or early June. Interestingly, reproductive observations of *M. mittermeieri* from a montane rainforest at Anjanaharibe Sud SR (980 m a.s.l; MBB, unpubl. data), were more similar to those of *M. lehilahytsara* from other montane/high elevation forests than to conspecifics from nearby low elevation forests: for instance, one adult female captured in early May showed visible nipples but no signs of recent lactation and evidence of tail fattening, and one adult male showed regressed testes and tail fattening during the same capture period. Five captured young mouse lemurs (~2-3 months old) showed no signs of reproductive activity and no evidence of tail fattening. That a portion of the mouse lemur population is displaying tail fattening in early May is indicative of a shorter reproductive season, likely over by March. In conclusion, and if supported by future studies, the *M. lehilahytsara/M.* mittermeieri lineage in the warmer lowland rainforests of eastern Madagascar seem to have more flexible and extended reproductive schedules compared to

populations living in the harsher montane humid forest sites or to species inhabiting the western dry deciduous forests (see Evasoa et al., 2018). In this respect, these mouse lemurs show similarities to *M. mamiratra* and *M. margotmarshae* that live in the lowland humid forests of northwestern Madagascar (Sambirano region) and that are also reproductively active in the first half of the dry season (Evasoa et al. 2018). Reproductive timing of sympatric non-sister species was different, since the two microendemic species (*M. macarthurii* and *M.* sp. #3) did not show extended reproductive schedules, while allopatric sister linages showed highly similar schedules in both cases.

# Conclusion and implications for conservation

A total of five different *Microcebus* lineages were demonstrated to occur in a geographically restricted region of northeastern Madagascar. All of these taxa inhabit a 130 km wide stretch of lowland rainforest making this region one of the most species-rich areas so far identified for mouse lemurs. These lineages can be distinguished genetically (Poelstra et al., 2020) and morphologically as shown in this study. The genomic and phenotypic differentiation between *M. macarthurii* and *M.* sp. #3 provides sufficient support for the recognition of *M.* sp. #3 as a distinct species which we describe below (see *Species Description*). The studied taxa were found in a variety of habitat types, ranging from nearly undisturbed to selectively logged forest, from shrubby secondary re-growth vegetation to areas dominated by perennial plants (i.e., *Aframomum* spp.; Miller et al., 2018; Radespiel et al., 2008; Schüßler et al., 2018). However, species differed most substantially in their altitudinal range and the inferred Extent of

Occurrence. M. lehilahytsara and M. mittermeieri were found both in montane and lowland forests, but M. sp. #3 and M. macarthurii occurred only in lowland forests. Locally restricted so-called "lowland specialists" have been found in at least three other cases along the Malagasy east coast, i.e., M. gerpi (Radespiel et al., 2012), M. marohita (Rasoloarison et al., 2013) and M. jollyae (Louis et al., 2006). These taxa share a narrow altitudinal range and a small estimated Extent of Occurrence. Alarmingly, lowland rainforest habitats have disappeared from most of the east coast and our study region is no exception (Schüßler et al., 2020; Vieilledent et al., 2018). Under these circumstances, population declines are unavoidable, and ongoing anthropogenic land use change and forest cover loss (Schüßler et al., 2020) will probably accelerate and increase this threat to the newly described species. M. sp. #3 occurs in one National Park, Mananara-Nord NP, which is already isolated from surrounding forests. Anticipated environmental disruptions due to future climatic changes and the need for species to flexibly adapt to altered environments may be severely compromised, if conservation planning does not generate and maintain possible dispersal pathways for migrating species (Brown & Yoder, 2015; Schüßler et al., 2020).

#### **5. Species Description**

#### Systematics

Order: Primates (Linnaeus 1758)

665 Suborder: Strepshirrini (É. Geoffroy 1812)

666 Family: Cheirogaleidae (Gray 1873)

| 667 | Genus:  | Microcebus (É. Geoffroy 1828)   |
|-----|---|---|
| 668 | Species:  | Microcebus jonahi species nova  |
| 669 |   |   |
| 670 | Holo  | <u>otype</u>  |
| 671 | B34, adult  | male, captured on 06 September 2017 by DS. Tissue samples, hair         |
| 672 | samples as  | s well as e-voucher photos of the animal are stored at the Institute of |
| 673 | Zoology, University of Veterinary Medicine Hanover, Germany. The animal itse  |   |
| 674 | was released after field handling, sampling, and photographing, since its     |   |
| 675 | taxonomic distinctiveness was not recognized at the time of capture. Field    |   |
| 676 | measurements (all lengths measured in mm): ear length: 17.6, ear width: 13.7, |   |
| 677 | head lengt  | h: 37.7, head width: 23.0, snout length: 10.0, intra-orbital distance:  |
| 678 | 8.2, inter-o  | rbital distance: 26.0, lower leg length: 41.7, hind foot length: 24.5,  |
| 679 | third toe le  | ngth: 10.6, body length: 95.6, tail length: 130.0, body mass: 66 g. The |
| 680 | population  | around Ambavala is designated as the source population for physical     |
| 681 | specimens   | in support of the holotype.   |
| 682 |   |   |
| 683 | Тур   | e locality  |
| 684 | Forest nea  | r the rural village of Ambavala (S 16° 12.307', E 49° 35.371'), in a    |
| 685 | community   | protected forest at about 342 m a.s.l. approx. 20 km west of            |

688 <u>Paratypes</u>

Mananara Avaratra (Mananara-Nord), Province of Analanjirofo, Madagascar.

(a) BD1, adult female, captured in the community protected forest of Antsiradrano (near Ambavala) on 04 September 2017. Tissue and hair samples as well as photographs and morphometric measurements are stored at the Institute of Zoology, University of Veterinary Medicine Hanover, Germany. (b) B13, adult male, captured in the community protected forest near Ambavala on 11 September 2017. Tissue and hair samples as well as photographs and morphometric measurements are stored at the Institute of Zoology of the University of Veterinary Medicine Hanover in Germany. It is planned that one physical specimen will be obtained as a further paratype soon and that this specimen will then be deposited in the Museum of the Zoology Department of the University of Antananarivo, Madagascar. Although not being a standard procedure, this method is most appropriate for endangered primates that should not be prematurely sacrificed if the taxonomic assignment is not yet clear. The same procedure was used for the scientific description of *M. gerpi* (Radespiel et al., 2012) for which a paratype individual had been collected during a subsequent field mission and was then deposited at the University of Antananarivo.

#### **Description**

*Microcebus jonahi* is a large-bodied, reddish-brown and small-eared mouse lemur (Figure 7). This species has short and dense fur. The head is rufous colored with a darker brownish area around the eyes which can slightly vary among individuals. A distinct white stripe lies between the eyes ending at the

forehead (Figure 7C). The ears are of the same rufous color as the head. The cheeks are lighter brownish and less rufous than the head becoming even lighter and almost white towards the throat. The ventrum is white with slightly yellowish nuances (Figure 7D) which can vary in appearance among individuals. The dorsum is rather uniformly brown than reddish (Figure 7E). A darker dorsal stripe can be either present or absent. The ventrum and dorsum are separated by a significant change in coloration with only marginal transition. The coloration of the limbs shows the same pattern with a brownish dorsal and a white to slightly yellowish ventral side. The tail is densely furred and of the same coloration as the dorsum. Hands and feet show only sparse but whitishgray hair. The skin on the palmar and plantar surfaces of hands and feet is brownish pink. Males and females do not show any sexual dimorphism.

#### Habitat information

M. jonahi individuals were captured at altitudes between 42 and 356 m a.s.l.

Out of the 25 captured individuals, six were caught in near-primary forest (= low degradation) with a rather continuous canopy and five were captured in highly degraded forests with discontinuous canopy cover and strong regrowth of early successional trees. The majority of individuals (N = 14) were captured in 2 - 4 m high stands of the perennial Madagascar cardamom (Aframomum angustifolium), sometimes intermixed with trees along the forest edges. At Antanambe (Figure 1), a total of 39 individuals were sighted of which 35 were found in forest habitats of different degradation stages. No M. jonahi were sighted in treeless secondary vegetation except for dense Aframomum

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angustifolium habitats. It currently inhabits one protected area (Mananara-Nord NP) and a community managed forest area around the village of Ambavala (Schüßler et al., 2018).

#### Diagnosis

M. jonahi can be distinguished from other taxa in northeastern Madagascar by morphometric features and genomic distinctiveness. Compared to its closest relative, M. macarthurii, M. jonahi is longer, has a shorter tail, wider ears, a larger head width and a shorter head length. In addition, M. jonahi can be differentiated from M. macarthurii by its ventral coloration which is rather whitish (Figure 6), but distinctly yellowish orange in M. macarthurii (Radespiel et al., 2008; Radespiel & Raveloson, unpubl. data).

Moreover, it can be easily distinguished from the sympatric, small-bodied M. lehilahytsara (at Ambavala) by its higher body mass, larger body size and longer tail length. Finally, M. jonahi can be differentiated from its southern geographical neighbor, M. simmonsi, by its shorter ear length and its larger inter- and intra-orbital distances. M. jonahi could be unambiguously

inter- and intra-orbital distances. *M. jonahi* could be unambiguously distinguished from the other four taxa in this study across all analyses of nuclear RADseq data (Poelstra et al., 2020). However, it may not be reliably distinguished from *M. macarthurii* based solely on mitochondrial sequences, likely due to some introgression from *M. jonahi* into *M. macarthurii* in the past

757 (Poelstra et al., 2020).

# <u>Etymology</u>

M. jonahi is named in honor of Malagasy primatologist Professor Jonah Ratsimbazafy. He has dedicated his life's work to the conservation of Malagasy lemurs. With both national and international outreach to the scientific community (e.g., GERP, IPS, LemursPortal), to the public of Madagascar (e.g., by initiating the World Lemur Festival), and to the political leaders of Madagascar, he serves as an inspirational role model for young Malagasy students and scientists. He provides hope for the future of Madagascar and for its iconic lemurs during very challenging times. 

#### Vernacular name

- English name: Jonah's mouse lemur, French name: Microcèbe de Jonah,
- 771 German name: Jonah's Mausmaki.

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- Data availability statement:
- The data that support the findings of this study are added in the supplementary files.

### 7. References

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Tables:

**Table 1:** Age classes of *Microcebus* spp. based on their mean body mass in g (± standard deviation). Intraspecific differences between age classes were highly significant in all cases (two-tailed t-tests: P < 0.001). For M. *macarthurii* and *M. simmonsi* only adult individuals were caught.

| Species      | M. sp. #3  | M. lehilahytsara | M. lehilahytsara | M. mittermeieri |  |  |  |  |
|--------------|------------|------------------|------------------|-----------------|--|--|--|--|
|              | (Ambavala- | (Ambavala)       | (Mantadia NP)    | (Anjiahely)     |  |  |  |  |
|              | Antanambe) |                  |                  |                 |  |  |  |  |
| Capture time | AugSept.   | Sept.            | May-Nov.         | SeptDec.        |  |  |  |  |
| Adults       | 57.4 ± 5.6 | 43.3 ± 5.5       | $43.8 \pm 4.7$   | 45.1 ± 6.2      |  |  |  |  |
|              | (N = 18)   | (N = 3)          | (N = 30)         | (N = 22)        |  |  |  |  |
| Young        | 45.9 ± 2.5 | $24.4 \pm 5.3$   | 31.2 ± 4.0       | 21.5 ± 1.9      |  |  |  |  |
|              | (N = 7)    | (N = 5)          | (N = 12)         | (N = 4)         |  |  |  |  |
|              |            |                  |                  |                 |  |  |  |  |

**Table 2:** Occurrence locations, altitudinal range (m a.s.l.) and estimated Extent of Occurrence (EOO in km² as defined by the IUCN, 2012; see Figure 1) of *Microcebus* spp. in northeastern Madagascar. Combined EOO for *M. lehilahytsara* and *M. mittermeieri* is estimated with 66,800 km². Coordinates of the locations are given in Supplementary Table S2.

| Taxon            | Locations             | Altitude  | E00    | References                        |
|------------------|-----------------------|-----------|--------|-----------------------------------|
| M. mittermeieri  | Marojejy NP,          | 350-1,056 | 9,250  | Louis et al., 2006; Radespiel et  |
|                  | Anjanaharibe-Sud SR,  |           |        | al., 2008; Weisrock et al., 2010; |
|                  | Anjiahely             |           |        | this study                        |
| M. macarthurii   | Anjiahely             | 350-400   | 560    | Radespiel et al., 2008; this      |
|                  |                       |           |        | study                             |
| M. lehilahytsara | Ambavala, Riamalandy, | 233-1,552 | 50,700 | Kappeler et al., 2005; Weisrock   |
|                  | Mantadia NP,          |           |        | et al., 2010; Yoder et al., 2016; |
|                  | Ambohitantely,        |           |        | this study                        |
|                  | Ankofabe, Tsinjoarivo |           |        |                                   |
| M. sp. #3        | Ambavala, Mananara-   | 42-356    | 1,500  | This study                        |
|                  | Nord NP, Antanambe    |           |        |                                   |
| M. simmonsi      | Ambodiriana, Tampolo, | 19-956    | 13,250 | Louis et al., 2006; this study    |
|                  | Zahamena NP,          |           |        |                                   |
|                  | Betampona SNR         |           |        |                                   |
|                  |                       |           |        |                                   |
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**Table 3:** Morphometric measurements of *Microcebus* spp. in northeastern Madagascar (mean ± standard deviation). Comparisons are based on one-way ANOVA (P < 0.001 for all parameters) and grouping (letters after values) according to Tukey *post-hoc* tests. Sample sizes per site for *M*. sp. #3 are N = 5 at Ambavala, N = 7 at Mananara-Nord NP, N = 6 at Antanambe. §: N = 11 for *M*. sp. #3.

| Variables           |       |   |     | M. macarthurii       |       |   | M. simmonsi   |     |       |                                     | M. mittermeieri |     |       |   | M. lehilahytsara |     |       |  | M. lehilahytsara |   |       |                                     |      |
|---------------------|-------|---|-----|----------------------|-------|---|---|-----|-------|-------------------------------------|-----------------|-----|-------|---|------------------|-----|-------|--|------------------|---|-------|-------------------------------------|------|
| (in mm)             |       |   |     | Mananara-Nord NP and |       |   | (N = 14, at Anjiahely, this<br>study and Radespiel et al.,<br>2008) |     |       | (N = 8, at Ambodiriana, this study) |                 |     |       | (N = 22, at Anjiahely,<br>Radespiel et al., 2008) |                  |     |       | (N = 29, at Mantadia<br>NP,<br>Randrinambinina,<br>2001) |                  |   |       | (N = 3, at Ambavala,<br>this study) |      |
| Ear length          | 17.2  | ± | 0.8 | а                    | 18.0  | ± | 0.8   | a,c | 19.5  | ±                                   | 2.7             | b,c | 18.3  | ±   | 1.4              | a,c | 20.0  | ±  | 1.1              | b | 17.9  | ±                                   | 0.2  |
| Ear width§          | 12.7  | ± | 1.0 | а                    | 10.6  | ± | 1.3   | b   | 12.6  | ±                                   | 0.9             | а   | 12.1  | ±   | 0.8              | а   | 12.3  | ±  | 0.9              | а | 11.8  | ±                                   | 1.1  |
| Head length         | 36.2  | ± | 1.4 | а                    | 37.5  | ± | 1.3   | b   | 35.3  | ±                                   | 0.9             | a,c | 34.3  | ±   | 0.8              | С   | 33.2  | ±  | 1.0              | d | 35.2  | ±                                   | 1.3  |
| Head width          | 21.5  | ± | 0.9 | а                    | 20.0  | ± | 1.5   | b   | 20.4  | ±                                   | 0.2             | a,c | 19.3  | ±   | 0.7              | b,c | 18.6  | ±  | 1.0              | С | 20.0  | ±                                   | 1.2  |
| Snout length        | 10.7  | ± | 1.2 | а                    | 9.6   | ± | 1.4   | а   | 10.0  | ±                                   | 1.8             | а   | 7.8   | ±   | 0.9              | b   | 4.9   | ±  | 0.6              | С | 9.6   | ±                                   | 0.7  |
| Interorbital dist.§ | 24.7  | ± | 1.1 | а                    | 23.6  | ± | 1.5   | a,b | 22.6  | ±                                   | 0.7             | b   | 20.6  | ±   | 1.1              | С   | 20.1  | ±  | 0.6              | С | 21.6  | ±                                   | 2.0  |
| Intraorbital dist.§ | 7.7   | ± | 0.5 | а                    | 7.1   | ± | 0.6   | a,b | 6.5   | ±                                   | 0.6             | b   | 6.6   | ±   | 0.7              | b   | 5.8   | ±  | 0.5              | С | 7.1   | ±                                   | 0.6  |
| Lower leg length§   | 39.9  | ± | 1.9 | а                    | 39.9  | ± | 1.3   | а   | 38.7  | ±                                   | 3.0             | а   | 35.4  | ±   | 1.5              | b   | 35.7  | ±  | 1.3              | b | 37.5  | ±                                   | 0.9  |
| Hind foot length§   | 22.7  | ± | 1.1 | а                    | 23.3  | ± | 1.5   | а   | 23.4  | ±                                   | 2.7             | а   | 20.2  | ±   | 1.3              | b   | 20.3  | ±  | 1.0              | b | 20.7  | ±                                   | 0.5  |
| Third toe length§   | 9.8   | ± | 1.2 | а                    | 9.5   | ± | 0.9   | а   | NA    | ±                                   | NA              | NA  | 7.9   | ±   | 0.5              | b   | 7.1   | ±  | 0.6              | С | 8.0   | ±                                   | 0.2  |
| Tail length         | 132.7 | ± | 9.0 | а                    | 142.6 | ± | 5.5   | b   | 130.6 | ±                                   | 9.6             | а   | 121.5 | ±   | 8.3              | С   | 115.2 | ±  | 5.1              | d | 108.7 | ±                                   | 19.7 |
| Body length§        | 93.3  | ± | 6.3 | а                    | 89.9  | ± | 7.0   | b   | 89.2  | ±                                   | 6.1             | a,c | 70.9  | ±   | 4.5              | С   | 71.3  | ±  | 4.5              | d | 80.6  | ±                                   | 6.4  |
| Body mass (g)       | 57.4  | ± | 5.6 | а                    | 61.1  | ± | 7.8   | а   | 51.8  | ±                                   | 9.1             | a,b | 45.1  | ±   | 6.2              | b   | 43.8  | ±  | 4.7              | b | 43.3  | ±                                   | 5.5  |

Figure legends:

**Figure 1:** Map depicting the study region with confirmed species occurrences (Hotaling et al., 2016; Kappeler et al., 2005; Louis et al., 2006; Radespiel et al., 2008, 2012; Weisrock et al., 2010). New sampling locations for this study are indicated with "\*" and forest cover in 2017/2018 was derived from Vieilledent et al. (2018) and Schüßler et al. (2020). NP = National Park; SNR = Special Nature Reserve; SR = Special Reserve.

**Figure 2**: Maximum likelihood tree illustrating the phylogenetic relationships between *Microcebus* spp. in northeastern Madagascar as inferred by RAxML (based on nuclear sequence data). Sampling locations are indicated at the tips of the branches. Illustration adapted from Poelstra et al. (2020). NP = National Park; SNR = Special Nature Reserve; SR = Special Reserve.

**Figure 3**: Selected morphometric measurements of *Microcebus* spp. in northeastern Madagascar. Comparison based on one-way ANOVA (P < 0.001 for all parameters) and grouping (letters above values) according to Tukey *post-hoc* tests. Plots for all parameters in supplementary Figure S1. Abbreviations: sp.3 = *M.* sp. #3 (at Ambavala and Antanambe); mac = *M. macarthurii* (at Anjiahely); sim = *M. simmonsi* (at Ambodiriana); mit = *M. mittermeieri* (at Anjiahely); leh = *M. lehilahytsara* (at Mantadia NP).

**Figure 4:** Principal component analysis including all morphometric parameters (except third toe length) showing PC1/PC2 (left) and PC3/PC4 (right). Small (*M. mittermeieri* and *M. lehilahytsara*) and large (*M.* sp. #3 and *M. macarthurii*) lineages differ along PC1, with some differentiation of *M. mittermeieri* and *M. lehilahytsara* along both PC1 and PC2, whereas *M.* sp. #3 and *M. macarthurii* split along PC3. Clusters corresponding to the five lineages were significantly different from each other (PERMANOVA: F = 36.88, df = 77, P < 0.001). Abbreviations: dia: Mantadia NP, vala: Ambavala

**Figure 5:** Linear discriminant analysis including all morphometric parameters (except third toe length). All five linages can be distinguished statistically (Wilk's Lambda = 0.005, F = 10.338, P < 0.001) with a misclassification rate of 12.8%. Abbreviations: dia: Mantadia NP, vala: Ambavala

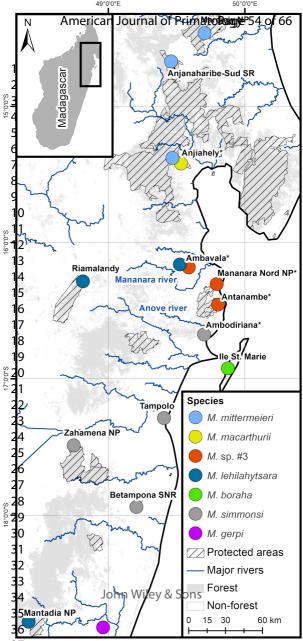
**Figure 6**: Reproductive records for adult males (A) and females (B) of *Microcebus* spp. in northeastern Madagascar and presence of juvenile individuals (C) in the population.

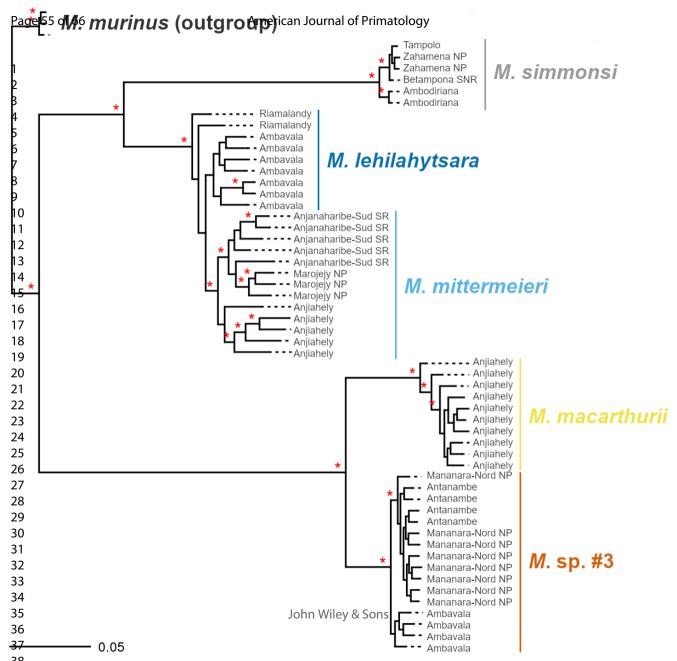
**Figure 7:** Outer morphology of *Microcebus jonahi*. (A) Drawing of an adult individual; (B) Habitus of adult female (paratype individual BD1); (C-E) Closeups of adult male (holotype B34). Illustration copyright by Stephen D. Nash / IUCN SSC Primate Specialist Group; used with permission. Photos by D. Schüßler.

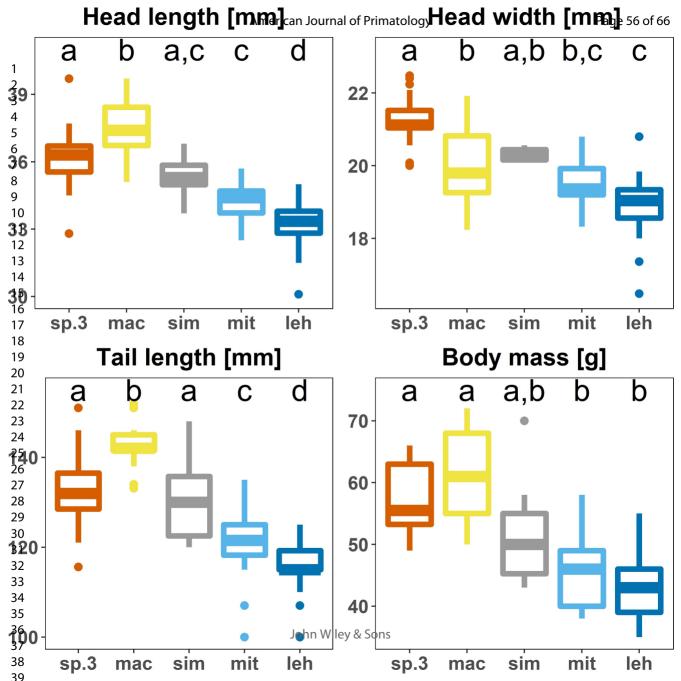
# Research highlights

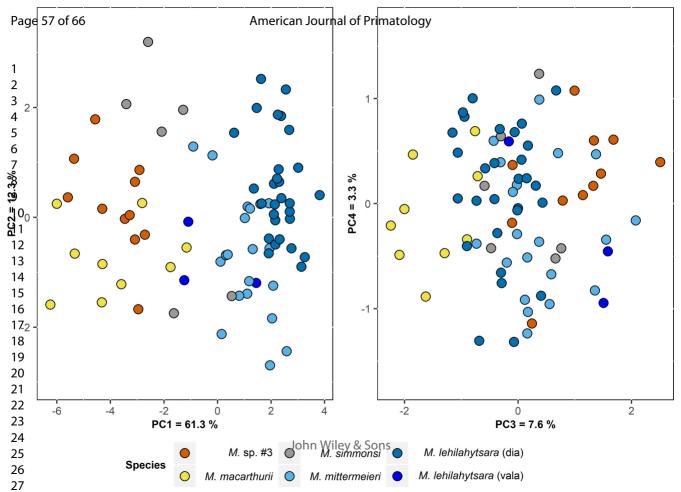
- Two pairs of *Microcebus* species occur in partial sympatry
- Morphological distinctiveness supports genomic species delimitation in cryptic lemurs
- High plasticity in reproductive schedules in a lineage of habitat generalists detected

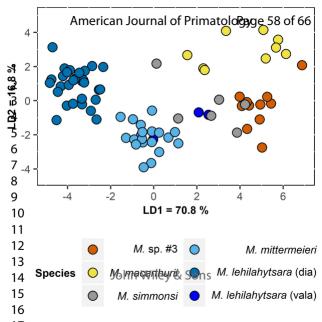




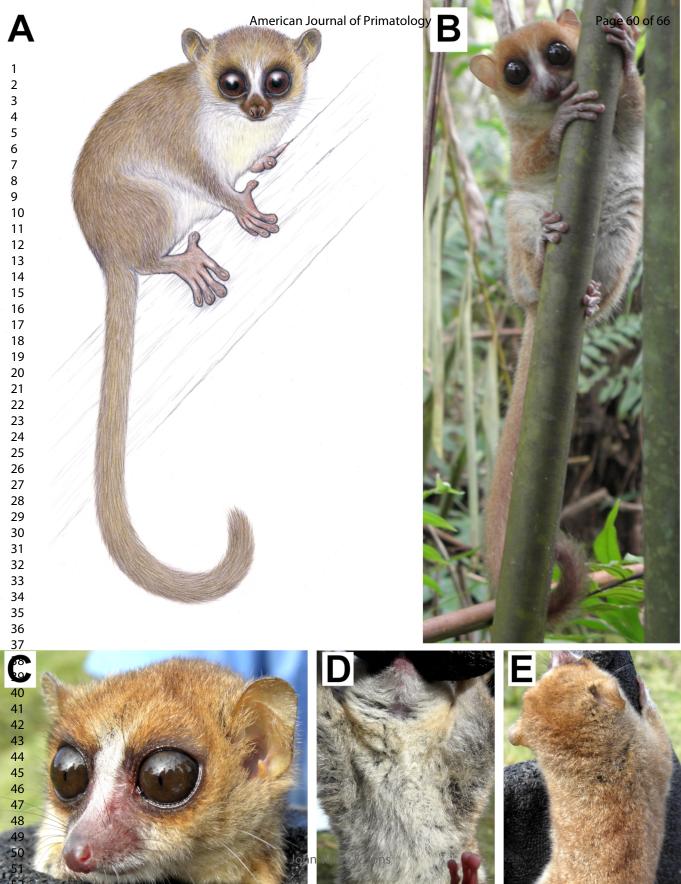








| A: Males              | ;              |         |           |              |               |                                       |          |            |            |   |
|-----------------------|----------------|---------|-----------|--------------|---------------|---------------------------------------|----------|------------|------------|---|
| Page 59               | of 66          |         |           | _ A          | merican J     | ournal of P                           | rimatele | av         |            | M. macarthurii (Anjiahely)                                |
|                       |                |         |           |              |               |                                       |          |            |            | M. mittermeieri (Anjiahely)                               |
|                       |                |         |           |              |               |                                       |          |            |            | M. lehilahytsara (Mantadia NP)                            |
| 1                     |                |         |           |              |               |                                       |          |            |            | M. lehilahytsara (Ambavala)                               |
| <u>'</u>              |                |         |           |              |               |                                       |          |            |            | M. sp. #3 (Ambavala-Antanam.)                             |
| 2                     |                |         |           |              |               |                                       | 0        |            |            | M. simmonsi (Ambodiriana)                                 |
| 3March                | April          | May     | June      | July         | August        | September                             | October  | November   | December   |   |
| 4                     |                |         |           |              |               |                                       |          |            |            |   |
| B5 Fema               | les            |         |           |              |               |                                       |          |            |            |   |
| 6                     |                |         |           |              |               |                                       |          | §          |            | M. macarthurii (Anjiahely)                                |
| 7                     |                |         |           |              |               |                                       |          | §          |            | M. mittermeieri (Anjiahely)                               |
| 8                     |                |         |           |              |               |                                       |          |            |            | M. lehilahytsara (Mantadia NP)                            |
| 9                     |                |         |           |              |               |                                       |          |            |            | M. lehilahytsara (Ambavala)                               |
| 10                    |                |         |           |              |               |                                       |          |            |            | M. sp. #3 (Ambavala-Antanam.)                             |
| 1March                | April          | May     | June      | July         | August        | September                             | October  | November   | December   | M. simmonsi (Ambodiriana)                                 |
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| . •                   | g individu     | iais    |           |              |               |                                       |          |            |            |   |
| 16                    |                |         |           |              |               |                                       |          |            |            | M. macarthurii (Anjiahely)                                |
| 17                    |                |         |           |              |               |                                       |          |            |            | M. mittermeieri (Anjiahely)                               |
| 18                    |                |         |           |              |               |                                       |          |            |            | M. lehilahytsara (Mantadia NP)                            |
| 19                    |                |         |           |              |               | · · · · · · · · · · · · · · · · · · · |          |            |            | M. lehilahytsara (Ambavala) M. sp. #3 (Ambavala-Antanam.) |
| 20                    |                |         |           |              | lohi          | N/ilov 9 C                            | 000      |            |            | M. simmonsi (Ambodiriana)                                 |
| 2 <sup>March</sup>    | April          | May     | June      | July         | August        | n Wiley & S<br>September              | October  | November   | December   | (   |
| 22                    |                | _       |           |              |               | _                                     |          |            |            | las importing as a second                                 |
| = pres                | sent           |         | = not pre | sent in capt | ure populatio | 111                                   |          | = no captu | re j=ai    | so juveniles captured                                     |



#### Jonah's mouse lemur Microcebus jonahi



© Stephan Nash

The newly described Jonah's mouse lemur (Microcebus jonahi) is distributed in northeastern Madagascar with an estimated Extent of Occurrence of about 1,500 km². This species has a mean head-body length of 13.0 cm, a mean tail length of 13.3 cm and weighs on average 57.4 g.

50x67mm (150 x 150 DPI)

## Supplementary material for:

Ecology and morphology of mouse lemurs (Microcebus spp.)

in a hotspot of microendemism in northeastern Madagascar,

with the description of a new species

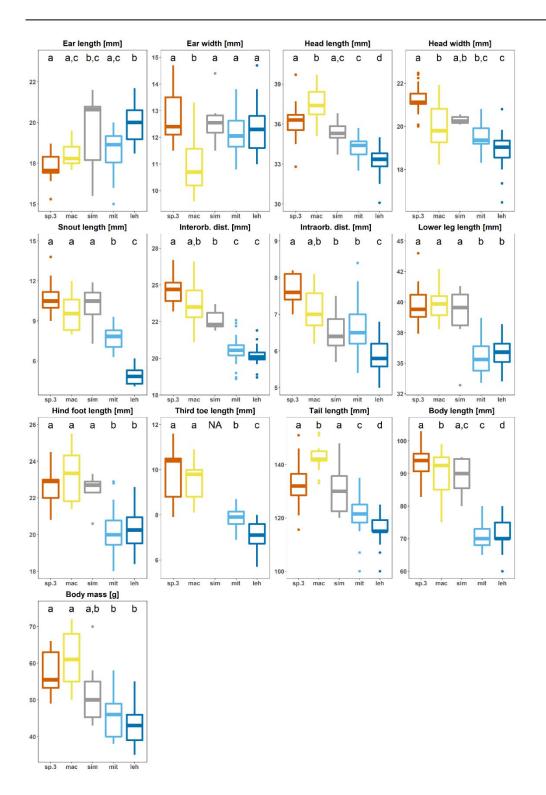
Dominik Schüßler, Marina B. Blanco,

Jordi Salmona, Jelmer Poelstra, Jean B. Andriambeloson, Alex Miller, Blanchard Randrianambinina, David W. Rasolofoson, Jasmin Mantilla-Contreras, Lounès Chikhi, Edward E. Louis Jr., Anne D. Yoder

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**Supplementary Figure S1**: Morphometric measurements of *Microcebus* spp. in northeastern Madagascar. Comparisons are based on one-way ANOVA (P < 0.001 for all parameters) and grouping (letters after values) according to Tukey *post-hoc* tests. Abbreviations: sp.3 = M. sp. #3 (at Ambavala and Antanambe); mac = M. *macarthurii* (at Anjiahely); sim = M. *simmonsi* (at Ambodiriana); mit = M. *mittermeieri* (at Anjiahely); leh = M. *lehilahytsara* (at Mantadia NP).

**Supplementary Table S1:** Morphometric and reproductive dataset provided as supplementary xlsx-file.

**Supplementary Table S2:** Coordinates and altitude of sampling locations of *Microcebus* spp. used in this study.

| Location      | Longitude     | Latitude      | Altitude   | Reference             |
|---------------|---------------|---------------|------------|-----------------------|
|               | J             |               | [m a.s.l.] |                       |
| Marojejy NP   | +49° 50' 21"  | -14° 28' 02'' | 344        | Weisrock et al., 2010 |
| Anjanaharibe- | +49° 27' 53"  | -14° 47' 27'' | 1056       | Louis et al., 2006    |
| Sud SR        |               |               |            |                       |
| Anjiahely     | +49° 29' 38"  | -15° 24' 45'' | 350-400    | Radespiel et al.,     |
|               |               |               |            | 2008, this study      |
| Ambavala      | +49° 34' 42'' | -16° 11' 03'' | 233-462    | This study            |
| Mananara-Nord | +49° 47' 41'' | -16° 18' 18'' | 277-377    | This study            |
| NP            |               |               |            |                       |
| Antanambe     | +49° 48' 10'' | -16° 27' 32'' | 42-273     | This study            |
| Riamalandy    | +48° 48' 54"  | -16° 17' 06'' | 833        | Weisrock et al., 2010 |
| Ambodiriana   | +49° 42' 05'' | -16° 40' 27'' | 42-222     | This study            |
| Tampolo       | +49° 25' 00'' | -17° 16' 60'' | 19         | Louis et al., 2006    |
| Zahamena NP   | +48° 44' 30'' | -17° 29' 13"  | 956        | Louis et al., 2006    |
| Betampona     | +49° 12' 12'' | -17° 55' 52"  | 300        | Louis et al., 2006    |
| SNR           |               |               |            |                       |
| Mantadia NP   | +48° 25' 29"  | -18° 48' 29'' | 969        | Kappeler et al., 2005 |
| Ankofabe      | +47° 11' 15'' | -18° 05' 27"  | 1459       | Yoder et al., 2016    |
| Ambohitantely | +47° 16' 26'' | -18° 28' 33'' | 1271       | Weisrock et al., 2010 |
| Tsinjoarivo   | +47° 41′ 43′′ | -19° 40' 22'' | 1552       | Yoder et al., 2016    |

**Supplementary Table S3:** Test statistics from parameter-wise comparisons of morphometric measurements using Analyses of Variance. For third toe length, comparison excluding *M. simmonsi* individuals.

| Morphometric          | F     | Р       |
|-----------------------|-------|---------|
| parameter             |       |         |
| Ear length            | 13.80 | < 0.001 |
| Ear width             | 8.14  | < 0.001 |
| Head length           | 35.09 | < 0.001 |
| Head width            | 20.73 | < 0.001 |
| Snout length          | 91.84 | < 0.001 |
| Interorbital distance | 48.20 | < 0.001 |
| Intraorbital distance | 21.36 | < 0.001 |
| Lower leg length      | 26.70 | < 0.001 |
| Hind foot length      | 16.03 | < 0.001 |
| Third toe length      | 42.65 | < 0.001 |
| Body length           | 53.08 | < 0.001 |
| Tail length           | 30.29 | < 0.001 |
| Body mass             | 23.89 | < 0.001 |
|                       |       |         |
|                       |       |         |

**Supplementary Table S4:** Classification matrix of the Linear Discriminant Analysis (LDA). Misclassification rate is 12.8%. Correct classifications on diagonal.

|   | M. lehilahytsara<br>(at Mantadia NP) | M. lehilahytsara<br>(at Ambavala) | M. macarthurii<br>(at Anjiahely) | M. mittermeieri<br>(at Anjiahely) | M. simmonsi<br>(at Ambodiriana) | M. sp. #3<br>(at Ambavala and<br>Antanambe) |
|---|--------------------------------------|-----------------------------------|----------------------------------|-----------------------------------|---------------------------------|---|
| M. lehilahytsara<br>(at Mantadia NP)                            | 29                                   | 0                                 | 0                                | 0                                 | 0                               | 0   |
| M. lehilahytsara (at Ambavala)                                  | 0                                    | 1                                 | 0                                | 0                                 | 2                               | 0   |
| <i>M. macarthurii</i> (at Anjiahely)                            | 0                                    | 0                                 | 7                                | 0                                 | 0                               | 2   |
| M. mittermeieri<br>(at Anjiahely)                               | 1                                    | 0                                 | 0                                | 19                                | 0                               | 0   |
| <ul><li>M. simmonsi</li><li>(at Ambodiriana)</li></ul>          | 1                                    | 0                                 | 0                                | 1                                 | 3                               | 1   |
| <ul><li>M. sp. #3</li><li>(at Ambavala and Antanambe)</li></ul> | 0                                    | 0                                 | 1                                | 0                                 | 1                               | 9   |

# Supplementary Table S1 for: Ecology and morphology of mouse lemurs (*Microcebus* spp.) in a hotspot of microendemism in northeastern Madagascar, with the description of a new species

Dominik Schüßler, Marina B. Blanco, Jordi Salmona, Jelmer Poelstra, Jean B. Andriambeloson, Alex Miller, Blanchard Randrianambinina, David W. Rasolofoson, Jasmin Mantilla-Contreras, Lounès Chikhi, Edward E. Louis Jr., Anne D. Yoder & Ute Radespiel

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Remarks: all values in mm except weight, this parameter is in g, NA: not available all measurements are according to Hafen et al. 1998 (Folia Primatologica 69:342-356) and Zimmermann et al. 1998 (Folia Primatologia 69:106-114)

Reproductive state is provided for first-time capture

| Part   |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                |                        |          |                            |            |
|--|----------------------|---------------|----------|--------|---------------|----------|--------------|------------|--------------|--------------|----------|-----------|--------------|----------|----------|----------|----------|----------------|------------------------|----------|----------------------------|------------|
|  |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                |                        |          |                            |            |
| March   Marc   | B-MM-B23             |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                | regressed<br>regressed |          | 9-Sep-2017<br>9-Sep-2017   |            |
| Mary      | B-MM-B14<br>B-MM-C12 |               |          |        |               |          |              | 11,7       |              |              |          | 8,0       |              |          |          |          | 79,1     |                | regressed<br>regressed |          | 12-Sep-2017                |            |
| March   Marc   | B-MF-BC3             | Ambavala      | adult    | F      | lehilahytsara | 47       | 17,7         | 13,0       | 35,4         | 19,9         | 21,7     | 7,6       | 9,0          | 38,0     | 21,3     | 8,0      | 87,7     | 118,0          | NA                     | closed   | 19-Sep-2017                | DS         |
| Column   | B-MM-C23             | Ambavala      | juvenile |        | lehilahytsara | 23       | 15,3         | 10,7       | 30,7         | 17,4         | 18,1     | 6,5       | 6,6          | 24,4     | 17,8     | 7,5      | 68,3     | 97,0           | regressed              | NA       | 19-Sep-2017                | DS         |
| Mary      | F12-99               | Mantadia      | adult    | F      | lehilahytsara | 41       | 20,2         | 13,6       | 34,7         | 18,8         | 20,4     | 6,8       | 5,3          | 38,2     | 21,9     | 7,6      | 80,0     | 125,0          | NA                     | closed   | 9-May-1999                 | BR         |
| March   Marc   | F32-99               | Mantadia      | adult    |        | lehilahytsara | 45       | 20,0         | 11,9       | 33,8         | 19,2         | 20,1     | 5,0       | 4,3          | 35,1     | 21,2     | 7,3      | 75,0     | 115,0          | NA                     | closed   | 4-Sep-1999                 | BR         |
| Column   | F45-99               | Mantadia      | adult    | F      | lehilahytsara | 46       | 19,8         | 11,6       | 34,1         | 19,1         | 20,3     | 5,8       | 4,3          | 37,2     | 22,6     | 7,4      | 70,0     | 115,0          | NA                     | open     | 9-Nov-1999                 | BR         |
| March   Marc   | F48-99               | Mantadia      | adult    |        | lehilahytsara | 49       | 21,7         | 12,7       | 33,8         | 18,9         | 19,9     | 4,7       | 4,8          | 37,2     | 20,2     | 6,8      | 70,0     | 115,0          | NA                     | pregnant | 7-Dec-1999                 | BR         |
| Column   |                      |               |          |        | lehilahytsara |          |              |            |              |              |          |           |              |          |          |          |          |                | regressed              |          |                            |            |
| March   Marc   |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                | regressed              |          | 5-May-1999                 |            |
| March   Marc   |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                | regressed              |          | 11-Apr-1999                |            |
| Mart   | M08-99               | Mantadia      | adult    | M<br>M | lehilahytsara | 37       | 20,8         | 12,5       | 35,0         | 18,5         | 19,6     | 6,0       | 5,9          | 36,0     | 20,0     | 6,9      | 68,0     | 115,0          | regressed              | NA       | 7-May-1999                 | BR         |
| Column   | M18-99               |               | adult    |        | lehilahytsara | 37       | 18,7         | 11,9       | 32,4         | 18,8         | 18,9     | 6,2       | 4,8          | 34,5     |          | 6,8      |          | 107,0          | regressed              | NA       | 30-May-1999                |            |
| Wester   W   | M33-99               | Mantadia      | adult    | M      | lehilahytsara | 42       | 20,6         | 12,3       | 31,5         | 19,1         | 20,2     | 6,2       | 4,5          | 35,4     | 20,8     | 7,9      | 75,0     | 115,0          | enlarged               | NA       | 7-Sep-1999                 | BR         |
| March   Marc   | M35-99               | Mantadia      | adult    | M      | lehilahytsara | 47       | 20,2         | 12,8       | 34,1         | 18,8         | 20,5     | 6,1       | 4,8          | 35,3     | 19,5     | 7,8      | 70,0     | 110,0          | enlarged               | NA       | 7-Sep-1999                 | BR         |
| March   Marc   | M37-99               | Mantadia      | adult    | M      | lehilahytsara | 42       | 20,0         | 11,3       | 30,1         | 18,6         | 20,0     | 5,7       | 5,2          | 36,4     | 20,5     | 7,0      | 70,0     | 115,0          | enlarged               | NA       | 7-Sep-1999                 | BR         |
| March   Marc   |                      |               |          | M      |               |          |              |            |              |              |          |           |              |          |          |          |          |                |                        |          |                            |            |
| March   Marc   |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                |                        |          |                            |            |
| March   Marc   |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                | enlarged               |          |                            |            |
| The color of the   | M20-99               | Mantadia      | adult    | M      | lehilahytsara | NA       | 21,9         | 13,5       | 33,7         | 21,0         | 20,0     | 5,7       | 4,6          | 35,9     | 19,6     | 7,2      | 80,0     | 120,0          | enlarged               | NA       | 31-May-1999                | BR         |
| Secondary   1968   1969   19   | F11-99               | Mantadia      | young    | F      | lehilahytsara | 33       | NA           | NA         | NA           | NA           | NA       | NA        | NA           | NA       | NA       | NA       | NA       | NA             | NA                     | closed   | 9-May-1999                 | BR         |
| March   Marc   | M05-99               | Mantadia      | young    | M      | lehilahytsara | 30       | NA           | NA         | NA           | NA           | NA       | NA        | NA           | NA       | NA       | NA       | NA       | NA             | regressed              | NA       | 5-May-1999                 | BR         |
| March   Marc   | M13-19               | Mantadia      | young    | M      | lehilahytsara | 30       | NA           | NA         | NA           | NA           | NA       | NA        | NA           | NA       | NA       | NA       | NA       | NA             | regressed              | NA       | 18-May-1999                | BR         |
| March   Marc   | M19-99               |               |          | M      | lehilahytsara | 32       |              |            |              |              |          |           | NA           |          |          |          |          |                | regressed<br>regressed |          | 31-May-1999                |            |
| No.    |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                |                        |          |                            |            |
| West   |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                | regressed<br>regressed |          |                            |            |
| March   Marc   |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                | NA                     |          | 9-Nov-2006                 |            |
| Model   Marches   Marche   | W01-07               | Anjiahely     | adult    |        | macarthurii   |          | 19,5         | 11,1       | 35,1         | 19,7         | 21,6     | 6,4       | 8,3          | 38,7     | 23,5     | 8,2      | 85,0     | NA             | NA                     | closed   | 4-Sep-2007                 |            |
| March   Marc   | M05-08               | Anjiahely     | adult    | M      | macarthurii   | 72       | 17,5         | 8,5        | 39,7         | 22,4         | 24,4     | 8,0       | 11,3         | 40,8     | 25,5     | 10,0     | 95,0     | 143,0          | NA                     | NA       | 12-Dec-2008                | DWR        |
| Fig.   Part      | M07-08               | Anjiahely     | adult    | M      | macarthurii   | 62       | 17,6         | 10,3       | 39,0         | 21,3         | 25,6     | 7,8       | 10,8         | 40,6     | 25,4     | 9,9      | 94,0     | 138,0          | enlarged               | NA       | 13-Dec-2008                | DWR        |
| March   Marc   | F04-11               | Anjiahely     | adult    | F      | macarthurii   | 72       | 19,4         | 10,3       | 38,7         | 22,0         | 23,8     | 8,1       | 12,0         | 42,7     | 24,5     | 10,9     | 99,0     | 146,0          | NA                     | closed   | 22-Nov-2011                | DWR        |
| Fig. 1.2   Associated   Fig.   | M01-13               | Anjiahely     | adult    | M      | macarthurii   | 70       | 17,1         | 11,8       | 37,6         | 17,8         | 26,6     | 7,2       | NA           | 38,4     | NA       | 10,3     | 96,6     | 141,8          | enlarged               | NA       | 25-Oct-2013                | DWR        |
| Fig. 1   |                      |               |          | F      |               |          |              |            |              |              |          |           |              |          |          |          |          |                |                        |          |                            |            |
| Mod-20   |                      | Anjiahely     |          | F      |               |          |              |            |              |              |          |           |              |          |          |          |          |                |                        |          |                            |            |
| Mod-06 A-gleenly and M memory a |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                |                        |          |                            |            |
| McC-07 Applewy end F millerment 49 200 11.8 34.7 18.8 20.8 6.8 6.0 20.2 36.6 7.8 34.4 28.8 7.5 76.0 11.0 enterpol MA 4-59-2007 DVRI MC-07 Applewy end F millerment 49 20.0 13.8 34.5 20.2 32.2 35.8 7.2 34.9 20.0 5.0 6.0 13.0 enterpol MA 5-69-2007 DVRI MC-07 Applewy end F millerment 41 30 11.2 11.8 34.4 20.0 11.8 34.6 20.0 11.8 34.5 20.0 | M07-06               | Anjiahely     | adult    | M      | mittermeieri  | 40       | 17,7         | 12,7       | 32,5         | 18,8         | 22,6     | 6,4       | 6,3          | 33,8     | 20,0     | 7,6      | 72,0     | 107,0          | enlarged               | NA       | 12-Nov-2006                | DWR        |
| Web-Color   Perform    | M02-07               | Anjiahely     | adult    | M      | mittermeieri  | 49       | 20,0         | 11,8       | 34,7         | 18,8         | 20,6     | 6,6       | 8,0          | 36,6     | 19,4     | 7,5      | 70,0     | 119,0          | enlarged               | NA       | 4-Sep-2007                 | DWR        |
| Mod-27   Applicable   Substitution   Mod-27   Applicable   | W04-07               | Anjiahely     | adult    | F      | mittermeieri  | 49       | 18,9         | 11,0       | 34,8         | 20,0         | 20,2     | 6,6       | 7,6          | 36,4     | 20,8     | 8,4      | 70,0     | 135,0          | NA                     | closed   | 5-Sep-2007                 | DWR        |
| Wilson   W   | M06-07               | Anjiahely     | adult    | M      | mittermeieri  | 43       | 19,9         | 12,4       | 34,2         | 18,1         | 19,0     | 6,4       | 8,9          | 35,6     | 20,7     | 7,9      | 72,0     | 115,0          | enlarged               | NA       | 5-Sep-2007                 | DWR        |
| Wilson   W   | W08-07               |               | adult    | F      |               | 39       | 18,7         | 11,9       | 34,5         | 19,9         | 20,9     |           | 7,8          | 34,2     | 21,0     |          | 70,0     | 120,0          | NA                     | closed   | 5-Sep-2007                 | DWR        |
| M1-27 Arginarily add M mitemenics 12 2.0 12.0 33.4 10.0 20.8 6.2 8.0 34.4 10.6 7.8 75.0 12.0 enlarged NA 6-89-2007 DVR M1-27 Arginary add M mitemenics 4 18.8 11.8 34.6 12.5 20.5 20.0 7.7 75.0 125.0 enlarged NA 6-89-2007 DVR M1-27 Arginary add M mitemenics 4 15.5 11.0 35.7 10.0 10.2 7.1 10.0 8.0 60.0 120.0 enlarged NA 6-89-2007 DVR M1-27 Arginary add M mitemenics 4 10.5 11.0 35.7 10.0 10.2 7.1 10.0 8.0 60.0 120.0 enlarged NA 6-89-2007 DVR M1-27 Arginary add M mitemenics 4 10.0 12.1 33.4 10.2 11.5 10.0 10.0 10.0 10.0 10.0 10.0 10.0  |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                |                        |          |                            |            |
| M14-07 Applicable solution millermental 58 19.8 13.8 35.3 21.0 21.6 6.5 8.3 37.7 20.1 7.7 80.0 135.0 enlarged NA \$6.90-2007 DVR M14-07 Applicable solution millermental 4 10.0 12.1 33.4 19.2 18.6 6.8 7.7 20.0 18.0 8.0 12.0 18.0 18.0 18.0 18.0 18.0 18.0 18.0 18   |                      | Anjiahely     |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                |                        |          | 6-Sep-2007                 |            |
| M1-07   Aginthey  abult   M   millermeint   42   15.0   12.1   34.7   10.0   16.7   7.1   8.2   33.7   18.1   8.6   70.0   10.0   millinged   M   cosed   6-Sep-2007   DWR   W1-07   Aginthey  principle   M   cosed   6-Sep-2007   DWR   W1-07   Aginthey  principle   M   cosed   6-Sep-2007   DWR   W1-07   Aginthey  principle   M   cosed   6-Sep-2007   DWR   M   cosed     | M13-07               | Anjiahely     | adult    | M      | mittermeieri  | 58       | 19,8         | 13,8       | 35,3         | 21,0         | 21,6     | 6,5       | 8,3          | 37,9     | 20,1     | 7,7      | 80,0     | 135,0          | enlarged               | NA       | 6-Sep-2007                 |            |
| Wide-Solid Acade   F   | M15-07               | Anjiahely     | adult    | M      | mittermeieri  | 42       | 15,0         | 12,1       | 34,7         | 19,0         | 18,7     | 7,1       | 8,2          | 33,7     | 18,1     | 8,6      | 70,0     | 100,0          | enlarged               | NA       | 6-Sep-2007                 | DWR        |
| Mot    | W17-07               | Anjiahely     | adult    | F      | mittermeieri  | 42       | 17,1         | 11,3       | 33,7         | 20,0         | 19,6     | 5,8       | 6,6          | 33,4     | 18,2     | 8,6      | 73,0     | 118,0          | NA                     | closed   | 6-Sep-2007                 | DWR        |
| W05-08   Anjlishedy   Juvenille   F   millemenient   22   14,9   8,7   32,6   18,0   18,7   7,6   7,9   31,1   20,8   8,2   74,8   93,5   NA   closed   11-De-2008   DWR   AI   Ambodinian   adult   F   simmonial   50   NA   12,9   35,5   20,4   22,2   7,5   11,9   NA   23,3   NA   NA   148,0   NA   closed   18,111-2014   AMI   AI   AI   AI   AI   AI   AI   A  | M01-08               | Anjiahely     | juvenile | М      | mittermeieri  | 20       | 11,3         | 9,8        | 27,3         | 18,0         | 15,4     | 4,0       | 9,0          | 25,9     | 17,2     | 6,3      | 51,0     | 85,0           | regressed              | NA       | 11-Dec-2008                | DWR        |
| A1 Ambodissan abut F simmonsi 50 NA 12,9 35,5 20,4 22,2 7,5 11,9 NA 23,3 NA NA 148,0 NA 148,0 NA closed 15-un-2014 AM A3 Ambodissan abut F simmonsi 46 NA 12,4 33,7 20,7 22,1 6,0 10,5 NA 23,8 NA NA NA 121,0 NA closed 15-un-2014 AM A3 Ambodissan abut F simmonsi 43 15,5 11,5 35,1 20,2 22,2 6,8 11,0 37,8 22,7 NA 80,0 130,0 NA closed 15-un-2014 AM A4 Ambodissan abut F simmonsi 43 15,5 11,5 35,1 20,5 22,0 6,4 11,5 13,5 24,1 32,3 NA 95,0 130,0 esimped NA 2-un-2014 AM A4 Ambodissan abut M simmonsi 70 20,7 12,8 36,8 20,5 23,0 6,4 11,5 13,6 14,1 32,3 NA 85,0 120,0 esimped NA 2-un-2014 AM A4 Ambodissan abut M simmonsi 43 16,7 11,5 34,8 20,7 21,8 35,7 7,3 33,2 20,6 NA 88,0 120,0 esimped NA 2-un-2014 AM A5 Ambodissan abut M simmonsi 50 20,0 12,4 35,8 20,2 23,4 6,4 10,5 40,8 12,3 NA 85,0 130,0 esimped NA 17-un-2014 AM A5 Ambodissan abut M simmonsi 50 20,0 12,4 35,8 20,2 23,4 6,4 10,5 40,8 12,3 NA 87,0 135,0 esimped NA 17-un-2014 AM A5 Ambodissan abut M simmonsi 50 20,0 12,4 35,8 20,2 23,4 6,4 10,5 40,8 12,3 NA 87,0 135,0 esimped NA 17-un-2014 AM A5 Ambodissan abut M sp3 66 17,0 12,4 35,8 20,2 23,4 6,4 10,5 40,8 12,3 NA 87,0 135,0 esimped NA 17-un-2014 AM A5 Ambodissan abut M sp3 66 17,0 12,4 35,8 20,2 20,2 23,4 6,4 10,5 40,8 12,3 NA 87,0 135,0 esimped NA 17-un-2014 AM A5 Ambodissan abut M sp3 66 17,0 12,4 35,8 20,2 20,2 23,4 6,4 10,5 40,8 12,3 NA 87,0 135,0 esimped NA 17-un-2014 AM A5 Ambodissan abut M sp3 66 17,0 12,4 35,8 20,2 20,2 23,4 6,4 10,5 40,8 12,3 NA 87,0 130,0 esimped NA 18-un-2014 AM A5 Ambodissan abut M sp3 63 13,1 NA 8,3 3,8 20,2 20,2 23,4 6,4 10,5 40,8 12,3 NA 87,0 130,0 esimped NA 18-un-2014 AM A5 Ambodissan abut M sp3 63 13,1 NA 8,3 3,8 20,2 20,2 23,4 6,4 10,5 40,8 12,3 NA 87,0 130,0 esimped NA 18-un-2014 AM A5 NA | W03-08               | Anjiahely     | juvenile |        | mittermeieri  | 22       | 14,9         | 8,7        | 32,6         | 18,0         | 18,7     | 7,6       | 7,9          | 31,1     | 20,8     | 8,2      | 74,8     | 93,5           | NA                     | closed   | 11-Dec-2008                | DWR        |
| A3 Ambodiframs adult F simmons 43 15,5 11,5 35,1 20,2 22,2 6,8 11,0 37,8 22,7 NA 80,0 130,0 NA closed 21-lum-2014 AM A4 Ambodiframs adult M simmons 70 20,7 12,8 36,8 20,5 23,0 6,4 11,5 41,3 22,3 NA 85,0 130,0 enlarged NA 2-Jul-2014 AM A6 Ambodifram adult M simmons 43 16,7 11,5 34,6 20,1 21,9 5,7 7,3 33,2 20,6 NA 85,0 120,0 enlarged NA 17-Jul-2014 AM A7 Ambodifram adult M simmons 54 21,0 12,7 35,1 20,7 22,4 6,2 7,4 39,0 22,7 NA 93,0 120,0 enlarged NA 17-Jul-2014 AM A8 Ambodifram adult M simmons 55 20,9 12,4 58,8 20,2 22,4 6,2 7,4 39,0 22,7 NA 93,0 120,0 enlarged NA 17-Jul-2014 AM A8 Ambodifram adult M simmons 50 20,9 12,4 35,8 20,2 22,4 6,4 10,5 40,8 22,3 NA 87,0 135,0 enlarged NA 17-Jul-2014 AM A8 Ambodifram adult M simmons 50 20,9 12,4 35,8 20,2 22,4 6,4 10,5 40,8 22,3 NA 87,0 135,0 enlarged NA 17-Jul-2014 AM A8 Ambodifram adult M sp3 61 77,6 13,7 37,7 20,0 26,0 8,2 10,0 41,1 24,0 10,4 103,0 151,0 NA closed 4-Sep-2017 DS B-MM-B34 Ambodifram adult M sp3 61 77,6 13,7 37,7 20,0 26,0 8,2 10,0 41,1 24,5 10,5 95,6 130,0 enlarged NA 17-Sep-2017 DS B-MM-B34 Ambodifram adult M sp3 65 11,0 11,8 38,8 20,0 24,9 7,0 10,3 39,3 21,5 8,4 94,0 138,0 enlarged NA 15-Sep-2017 DS B-MM-B34 Ambodifram adult M sp3 65 11,0 11,8 38,8 20,0 24,9 7,0 10,3 39,3 21,5 8,4 94,0 138,0 enlarged NA 15-Sep-2017 DS B-MM-B34 Ambodifram adult M sp3 65 11,0 12,1 33,8 21,1 23,8 6 10,0 13,1 39,1 22,0 8,9 9,8 26,1 135,0 MA closed 4 NA 15-Sep-2017 DS B-MM-B34 Ambodifram adult M sp3 65 17,0 12,1 32,8 20,0 24,9 7,0 10,3 39,3 21,5 8,4 94,0 138,0 enlarged NA 15-Sep-2017 DS B-MM-B34 Ambodifram adult M sp3 65 17,0 12,1 32,8 20,0 24,9 7,0 10,3 39,3 21,5 8,4 94,0 138,0 enlarged NA 15-Sep-2017 DS B-MM-B34 Ambodifram adult M sp3 65 17,0 12,1 32,8 20,0 12,1 23,8 4,0 13,1 23,8 34,0 12,1 23,8 4,0 13,1 23,8 34,0 12,1 23,8 4,0 13,1 23,8 34,0 12,1 23,8 34,0 12,1 23,8 4,0 13,1 23,8 34,0 12,1 23,8 34,0 12,1 23,8 34,0 12,1 23,8 34,0 12,1 23,8 34,0 12,1 24,0 12,1 24,0 12,1 24,0 12,1 24,0 12,1 24,0 12,1 24,0 12,1 24,0 12,1 24,0 12,1 24,0 12,1 24,0 12,1 24,0 12,1 24,0 12,1 24 | A1                   | Ambodiriana   | adult    | F      | simmonsi      | 50       | NA           | 12,9       | 35,5         | 20,4         | 22,2     | 7,5       | 11,9         | NA       | 23,3     | NA       | NA       | 148,0          | NA                     | closed   | 18-Jun-2014                | AM         |
| A5 Ambodrians adult M simmonsi 43 16,7 11,5 34,6 20,1 21,9 5,7 7,3 33,2 20,6 NA 85,0 120,0 enlarged NA 71-Ju2-2014 AM A7 Ambodrians adult M simmonsi 54 21,0 12,7 35,1 20,7 22,4 6,2 7,4 99,0 22,7 NA 99,0 123,0 enlarged NA 71-Ju2-2014 AM A7 Ambodrians adult M simmonsi 58 22,0 14,4 35,8 20,2 23,4 6,4 10,5 40,8 22,3 NA 87,0 135,0 enlarged NA 71-Ju2-2014 AM A7 Ambodrians adult M simmonsi 50 20,9 12,4 35,8 20,2 23,4 6,4 10,5 40,8 22,3 NA 87,0 135,0 enlarged NA 71-Ju2-2014 AM A7 Ambodrians adult M simmonsi 50 20,9 12,4 35,8 20,2 23,4 6,4 10,5 40,8 22,3 NA 87,0 135,0 enlarged NA 71-Ju2-2014 AM A7 Ambodrians adult M simmonsi 50 20,9 12,4 35,8 20,2 23,4 6,4 10,5 40,8 22,3 NA 87,0 135,0 enlarged NA 71-Ju2-2014 AM A7 Ambodrians adult M simmonsi 50 20,9 12,4 35,8 20,2 23,4 6,4 10,5 40,8 22,3 NA 87,0 135,0 enlarged NA 71-Ju2-2014 AM A7 Ambodrians adult M signos Simmonsi 50 20,9 12,4 35,7 7,7 10,4 41,1 24,0 10,4 103,0 151,0 NA closed 4-Sep-2017 DS 8-Mil-Spat M signos Simmonsi 50 20,9 12,4 35,7 7,7 10,4 41,1 24,0 10,4 103,0 151,0 NA closed 4-Sep-2017 DS 8-Mil-Spat M signos Simmonsi 50 11,6 35,8 20,0 24,9 7,0 10,3 35,3 21,5 8,4 94,0 138,0 enlarged NA 11-Sep-2017 DS 8-Mil-Spat M signos Simmonsi 50 20,0 11,6 35,8 20,0 24,9 7,0 10,3 35,3 21,5 8,4 94,0 138,0 enlarged NA 11-Sep-2017 DS 8-Mil-Spat M signos Simmonsi 50 20,0 24,9 7,0 10,3 35,3 21,5 8,4 94,0 138,0 enlarged NA 11-Sep-2017 DS 8-Mil-Spat M signos Simmonsi 50 20,0 24,9 7,0 10,3 35,3 21,5 8,4 94,0 138,0 enlarged NA 11-Sep-2017 DS 8-Mil-Spat M signos Simmonsi 50 20,0 24,9 27,0 11,4 24,9 36,3 21,5 22,7 7,7 10,1 35,1 35,1 22,7 7,7 10,1 35,1 22,7 7,7 | A3                   | Ambodiriana   |          | F<br>F |               | 43       | 15,5         | 11,5       | 35,1         | 20,2         | 22,2     | 6,8       | 11,0         | 37,8     | 22,7     | NA       | 80,0     | 130,0          | NA                     | closed   | 21-Jun-2014                | AM         |
| A6 Ambodrians adult M simmonsi 54 21,0 12,7 35,1 20,7 22,4 6,2 7,4 39,0 22,7 NA 93,0 123,0 enlarged NA 17-Jul-2014 AM A8 Ambodrians adult M simmonsi 58 22,0 14,4 36,0 20,2 23,7 7,1 10,2 40,1 23,1 NA 95,0 130,0 enlarged NA 17-Jul-2014 AM A8 Ambodrians adult F 93 64 17,0 12,4 39,7 7,2 20,0 25,7 7,5 10,4 41,1 24,0 10,3 16,0 10, | A5                   | Ambodiriana   | adult    | M      | simmonsi      | 43       | 16,7         | 11,5       | 34,6         | 20,1         | 21,9     | 5,7       | 7,3          | 33,2     | 20,6     | NA       | 85,0     | 120,0          | enlarged               | NA       | 2-Jul-2014                 | AM         |
| AB Ambodrians adult F sp 3 64 17,0 124, 93,7 20,0 26,7 7,5 10,4 41,1 24,0 10,4 103,0 151,0 enlarged NA closed 4-Sep-2017 DS B-MM-B34 Ambavalls adult M sp 3 66 17,6 13,7 37,7 20,0 26,7 7,5 10,4 41,1 24,0 10,6 95,6 130,0 enlarged NA 6-Sep-2017 DS B-MM-B34 Ambavalls adult M sp 3 63 18,0 11,8 36,8 20,0 24,9 7,0 10,3 93,3 21,5 8,4 94,0 133,0 enlarged NA 1-Sep-2017 DS B-MM-B34 Ambavalls adult M sp 3 63 18,0 11,8 36,8 20,0 24,9 7,0 10,3 93,3 21,5 8,4 94,0 133,0 enlarged NA 1-Sep-2017 DS B-MM-B34 Ambavalls adult M sp 3 63 11,5 35,8 21,3 23,7 7,6 9,0 37,4 20,8 9,9 9,2 6 135,0 enlarged NA 1-Sep-2017 DS B-M-B-C1 Ambavalls adult M sp 3 62 15,3 11,5 35,8 21,3 23,7 7,6 9,0 37,4 20,8 9,9 9,2 6 135,0 enlarged NA 1-Sep-2017 DS A-MM-A12 Antinambe adult M sp 3 50 18,7 13,5 35,9 21,6 23,2 7,0 11,4 38,4 22,9 11,6 95,9 128,0 enlarged NA 1-Sep-2017 DS A-MM-A24 Antinambe adult M sp 3 54 18,0 11,5 35,8 21,3 22,7 7,6 11,4 38,4 22,9 10,4 94,0 137,0 enlarged NA 1-Sep-2017 DS A-MM-A34 Antinambe adult M sp 3 53 17,6 12,1 32,8 21,3 22,7 7,6 11,4 38,4 22,9 10,4 94,0 137,0 enlarged NA 1-Sep-2017 DS A-MM-A34 Antinambe adult M sp 3 53 17,6 12,1 32,8 21,3 22,7 7,0 11,4 38,4 22,9 10,4 94,0 137,0 enlarged NA 1-Sep-2017 DS A-MM-A34 Antinambe adult M sp 3 53 17,6 12,1 32,8 21,3 22,7 7,0 11,4 38,4 22,9 10,4 94,0 137,0 enlarged NA 1-Sep-2017 DS A-MM-A34 Antinambe adult M sp 3 53 17,6 12,1 32,8 21,3 22,7 7,7 8,1 11,0 44,0 23,0 8,7 100,1 133,0 enlarged NA 1-Sep-2017 DS A-MM-A34 Antinambe adult M sp 3 53 18,5 12,1 32,8 21,3 22,7 7,7 8,1 11,0 44,0 23,0 8,7 100,1 133,0 enlarged NA 1-Sep-2017 DS A-MM-A34 Antinambe adult M sp 3 53 18,5 12,1 32,8 21,3 22,7 7,7 8,1 11,0 44,0 23,0 8,7 100,1 133,0 enlarged NA 1-Sep-2017 DS A-MM-A34 Antinambe adult M sp 3 53 18,5 12,1 32,8 21,3 22,4 8,1 9,1 10,1 40,1 22,6 10,9 82,8 14,6 14,7 44,6 14,7 44,7 44,7 44,7 44,7 44,7 44,7 44,7  |                      |               |          |        |               |          |              |            |              |              |          |           |              |          |          |          |          |                | enlarged               |          |                            |            |
| B-MM-B34 Ambavalla adult M sp3 66 17,6 13,7 37,7 23,0 26,0 8,2 10,0 41,7 24,5 10,6 9,5 8 130,0 enlarged NA 6-Sep-2017 DS B-MM-B34 Ambavalla adult M sp3 63 18,0 11,8 36,8 20,0 24,9 7,0 10,3 39,3 21,5 8,4 94,0 138,0 enlarged NA 13-Sep-2017 DS B-MM-B34 Ambavalla adult F sp3 64 18,0 12,5 98,3 11,5 35,8 21,3 22,7 7,6 9,0 37,4 20,8 9,9 9,2 6 135,0 enlarged NA 13-Sep-2017 DS A-MM-A12 Anthanambe adult F sp3 64 18,0 12,5 98,3 21,1 22,8 8,2 10,6 39,2 23,0 8,9 96,3 132,0 NA closed NA 13-Sep-2017 DS A-MM-A14 Anthanambe adult M sp3 50 18,7 13,5 35,7 21,4 24,9 7,3 10,1 38,1 22,5 11,6 95,9 128,0 enlarged NA 13-Aug-2017 DS A-MM-A14 Anthanambe adult M sp3 51,7 13,5 35,7 21,4 24,9 7,3 10,1 38,1 22,5 11,6 95,9 128,0 enlarged NA 13-Aug-2017 DS A-MM-A13 Anthanambe adult M sp3 53 17,6 12,1 32,8 21,3 22,7 7,0 11,4 38,4 22,9 10,4 94,0 137,0 enlarged NA 13-Aug-2017 DS A-MM-A13 Anthanambe adult M sp3 53 17,6 12,1 32,8 21,3 22,4 8,1 9,1 40,1 22,6 10,9 82,8 146,0 enlarged NA 17-Aug-2017 DS A-MM-A13 Anthanambe adult M sp3 53 17,6 12,1 32,8 21,3 22,4 8,1 9,1 40,1 22,6 10,9 82,8 146,0 enlarged NA 17-Aug-2017 DS A-MM-A13 Anthanambe adult M sp3 53 16,5 12,1 37,4 20,7 24,0 8,1 9,9 39,8 23,0 7,9 83,3 146,0 enlarged NA 24-Aug-2017 DS MBB 019 Manamara Nord adult M sp3 55 17,4 NA 35,7 21,6 NA NA 13,8 NA   | A8                   | Ambodiriana   |          | M      | simmonsi      |          | 20,9         | 12,4       | 35,8         | 20,2         | 23,4     | 6,4       | 10,5         | 40,8     | 22,3     | NA       | 87,0     | 135,0          | enlarged               | NA       | 17-Jul-2014                | AM         |
| B-MM-B24 Ambavalla adult M sp3 62 15.3 11.5 58,8 21.3 22.7 7,6 9.0 37,4 20.8 9,9 9.26 135,0 enlarged NA 15-Sep-2017 DS A-MM-A12 Anthanambe adult F sp3 64 18.0 12.5 98,3 23,1 22.8 8,2 10.6 39,2 23.0 8,9 99.5 138,0 enlarged NA 15-Aug-2017 DS A-MM-A14 Anthanambe adult M sp3 54 18.0 13.5 35,9 21.6 23.2 7,0 11.4 38,4 22.9 10.6 95,9 128.0 enlarged NA 15-Aug-2017 DS A-MM-A14 Anthanambe adult M sp3 54 18.0 13.5 35,9 21.6 23.2 7,0 11.4 38,4 22.9 10.4 99,0 137.0 enlarged NA 17-Aug-2017 DS A-MM-A13 Anthanambe adult M sp3 53 17,6 14,7 34.5 22.0 24.7 8,1 11.0 44.0 23.0 8,7 10.1 133.0 enlarged NA 17-Aug-2017 DS A-MM-A13 Anthanambe adult M sp3 55 17.0 12.1 32.8 2.1 3 25.4 8,1 9,1 40,1 22.6 10.9 82.8 146.0 enlarged NA 17-Aug-2017 DS A-MM-A13 Anthanambe adult M sp3 55 17.0 12.1 32.8 21.3 25.4 8,1 9,1 40,1 22.6 10.9 82.8 146.0 enlarged NA 22-Aug-2017 DS A-MM-A13 Anthanambe adult M sp3 55 17.0 12.1 32.8 21.3 22.7 5, 9,1 39,4 21.5 10.4 88,7 135.0 enlarged NA 22-Aug-2017 DS A-MM-B10 20 Manamara North adult M sp3 55 17.4 NA 35.7 21.6 NA NA 13.8 NA  | B-MM-B34             | Ambavala      | adult    | M      | sp3           | 66       | 17,6         | 13,7       | 37,7         | 23,0         | 26,0     | 8,2       | 10,0         | 41,7     | 24,5     | 10,6     | 95,6     | 130,0          | enlarged               | NA       | 6-Sep-2017                 | DS         |
| A-MM-A-12 Antanambe adult M sp3 50 18,7 13,5 86,7 21,4 24,9 7,3 10,1 38,1 22,5 11,6 95,9 128,0 enlarged NA 13-Aug-2017 DS A-MM-A-34 Antanambe adult M sp3 54 18,0 13,5 35,9 21,6 23,2 7,0 11,4 38,4 22,9 10,4 94,0 137,0 enlarged NA 17-Aug-2017 DS A-MM-A-34 Antanambe adult M sp3 63 17,6 14,7 34,5 22,0 24,7 8,1 11,0 44,0 23,0 8,7 100,1 133,0 enlarged NA 17-Aug-2017 DS A-MM-A-13 Antanambe adult M sp3 53 17,6 12,1 32,8 21,3 25,4 8,1 9,1 40,1 22,6 10,9 82,8 146,0 enlarged NA 27-Aug-2017 DS A-MM-A-13 Antanambe adult M sp3 55 17,0 12,1 32,8 21,3 25,4 8,1 9,1 40,1 22,6 10,9 82,8 146,0 enlarged NA 27-Aug-2017 DS A-MM-A-13 Antanambe adult M sp3 55 17,0 12,1 32,8 21,3 25,4 8,1 9,1 40,1 22,6 10,9 83,3 146,0 enlarged NA 27-Aug-2017 DS A-MM-A-13 Antanambe adult M sp3 55 17,4 NA 35,7 21,6 NA NA 133,8 NA NA NA NA NA NA 131,9 enlarged NA 13-Aug-2015 MBB MBB 020 Maranama_Norm adult M sp3 54 16,5 NA 35,4 21,4 NA NA 11,1 NA NA NA NA 131,9 enlarged NA 13-Aug-2015 MBB MBB 021 Maranama_Norm adult M sp3 54 16,5 NA 35,4 21,4 NA NA 11,1 NA NA NA NA 131,0 enlarged NA 13-Aug-2015 MBB MBB 022 Maranama_Norm adult M sp3 46 17,5 NA 35,5 22,1 NA NA 11,1 NA NA NA NA NA NA NA 131,0 enlarged NA 15-Aug-2015 MBB MBB 023 Maranama_Norm adult M sp3 46 17,5 NA 35,5 22,1 NA NA 11,7 NA NA NA NA NA 131,0 enlarged NA 15-Aug-2015 MBB MBB 025 Maranama_Norm adult M sp3 46 17,5 NA 35,5 22,1 NA NA 11,7 NA NA NA NA NA 13,0 enlarged NA 15-Aug-2015 MBB MBB 025 Maranama_Norm adult M sp3 46 17,0 NA 35,5 22,1 NA NA 11,7 NA NA NA NA NA 11,0 enlarged NA 15-Aug-2015 MBB MBB 026 Maranama_Norm adult M sp3 46 17,0 NA 35,5 22,8 NA NA NA 11,7 NA NA NA NA NA 11,0 enlarged NA 15-Aug-2015 MBB MBB 026 Maranama_Norm adult M sp3 57 17,0 NA 35,5 22,8 NA NA NA 11,7 NA NA NA NA NA NA NA 11,0 enlarged NA 25-Aug-2015 MBB MBB 026 Maranama_Norm adult M sp3 57 17,0 NA 35,5 22,8 NA  | B-MM-B24             | Ambavala      | adult    | M      | sp3           | 62       | 15,3         | 11,5       | 35,8         | 21,3         | 23,7     | 7,6       | 9,0          | 37,4     | 20,8     | 9,9      | 92,6     | 135,0          | enlarged               | NA       | 13-Sep-2017                | DS         |
| A-MM-A-34 Antanambe adult M sp3 63 17,6 14,7 9.4,5 22,0 24,7 8.1 11.0 44,0 23,0 8,7 100,1 133,0 enlarged NA 17-Aug-2017 DS A-MM-A13 Antanambe adult M sp3 53 17,6 12,1 32,8 21,3 25,4 8.1 9,1 40,1 22,6 10,9 82,8 146,0 enlarged NA 22-Aug-2017 DS A-MM-A13 Antanambe adult M sp3 52 18,5 12,1 37,4 20,7 24,0 8,1 9,9 98,8 23,0 7,9 83,3 146,0 enlarged NA 22-Aug-2017 DS A-MM-A13 Antanambe adult F sp3 56 17,0 12,4 36,3 20,1 24,2 7,5 9,1 39,4 21,5 10,4 88,7 135,0 NA closed 24-Aug-2017 DS MBB 019 Mananama, Nord adult M sp3 55 17,4 NA 36,7 21,6 NA NA 133,8 NA NA NA NA NA 131,9 enlarged NA 15-Aug-2015 MBB MBB 020 Mananama, Nord adult M sp3 54 16,5 NA 35,4 21,4 NA NA 11,1 NA NA NA NA NA 131,0 enlarged NA 15-Aug-2015 MBB MBB 021 Mananama, Nord adult M sp3 54 16,5 NA 35,4 21,4 NA NA 11,1 NA   | A-MM-A12             | Antanambe     | adult    | M      | sp3           | 50       | 18,7         | 13,5       | 36,7         | 21,4         | 24,9     | 7,3       | 10,1         | 38,1     | 22,5     | 11,6     | 95,9     | 128,0          | enlarged               | NA       | 13-Aug-2017                | DS         |
| A-MM-A13 Arlanambe adult M sp3 52 18,5 12,1 37,4 20,7 24,0 8,1 9,9 38,8 23,0 7,9 83,3 146,0 enlarged NA 24-Aug-2017 DS AMB 019 Mananama, Nord adult M sp3 55 17,4 NA 35,7 21,4 NA NA 131,8 NA NA NA NA NA 131,9 enlarged NA 15-Aug-2015 MBB MBB 020 Mananama, Nord adult M sp3 55 17,4 NA 35,7 21,4 NA NA 11,1 NA NA NA NA NA 131,0 enlarged NA 15-Aug-2015 MBB MBB 021 Mananama, Nord adult M sp3 54 16,5 NA 35,4 21,4 NA NA 11,1 NA NA NA NA NA 131,0 enlarged NA 15-Aug-2015 MBB MBB 021 Mananama, Nord adult M sp3 54 16,5 NA 35,4 21,4 NA NA 10,0 NA  | A-MM-A34             | Antanambe     | adult    | M      | sp3           | 63       | 17,6         | 14,7       | 34,5         | 22,0         | 24,7     | 8,1       | 11,0         | 44,0     | 23,0     | 8,7      | 100,1    | 133,0          | enlarged               | NA       | 17-Aug-2017                | DS         |
| A-MB-681 Artinamene adult F sp3 56 17,0 12.4 88,3 20,1 24.2 7,5 9,1 39,4 21,5 10,4 88,7 135,0 NA closed 25-Aug-2017 DS MBB MBB 020 Mananara Nord adult M sp3 55 17,4 NA 35,7 21,6 NA NA 13.8 NA NA NA NA 131,0 enlarged NA 15-Aug-2015 MBB MBB 020 Mananara Nord adult M sp3 54 16,4 NA 35,7 21,4 NA NA NA 11,1 NA NA NA NA 131,0 enlarged NA 15-Aug-2015 MBB MBB 022 Mananara Nord young F sp3 46 16,3 NA 35,4 21,4 NA NA 10,0 NA NA NA NA 131,0 enlarged NA 15-Aug-2015 MBB MBB 022 Mananara Nord young F sp3 46 16,3 NA 35,5 21,1 NA NA 11,7 NA NA NA NA 12,0 NA closed 16-Aug-2015 MBB MBB 022 Mananara Nord young M sp3 54 16,4 NA 35,5 21,4 NA NA NA 11,7 NA NA NA NA 12,0 enlarged NA 15-Aug-2015 MBB MBB 024 Mananara Nord young F sp3 46 17,6 NA 35,2 21,6 NA NA 11,6 NA NA 11,6 NA NA NA 134,0 enlarged NA closed 16-Aug-2015 MBB MBB 024 Mananara Nord young F sp3 46 15,3 NA 35,4 21,8 NA NA 11,6 NA NA NA NA NA NA 134,0 NA closed 18-Aug-2015 MBB MBB 026 Mananara Nord young F sp3 46 15,4 NA 35,6 22,8 NA NA 11,7 NA NA NA NA NA 12,0 enlarged NA 22-Aug-2015 MBB MBB 026 Mananara Nord young F sp3 46 15,4 NA 35,6 22,8 NA NA 11,7 NA NA NA NA NA 11,0 enlarged NA 22-Aug-2015 MBB MBB 026 Mananara Nord young F sp3 46 15,4 NA 35,6 22,8 NA NA 11,7 NA NA NA NA NA NA 11,0 enlarged NA 22-Aug-2015 MBB MBB 028 Mananara Nord young F sp3 46 15,4 NA 35,6 22,8 NA   | A-MM-A13             | Antanambe     | adult    | M      | sp3           | 52       | 18,5         | 12,1       | 37,4         | 20,7         | 24,0     | 8,1       | 9,9          | 39,8     | 23,0     | 7,9      | 83,3     | 146,0          | enlarged               | NA       | 24-Aug-2017                | DS         |
| MBB 020 Mananara Nord adult MB 93         54         16.4         NA         35,7         21,4         NA         NA         11.1         NA         NA         NA         NA         13.10         enlarged engle NA         15.4ug-2015         MBB MB 02M Mananara Nord young Fall Nord Nord NA         NA         13.10         enlarged engle NA         15.4ug-2015         MBB MB 02M MB NA   |                      |               |          |        | sp3<br>sp3    |          |              | 12,4<br>NA |              |              |          | 7,5<br>NA |              |          |          |          |          |                |                        |          | 26-Aug-2017<br>13-Aug-2015 |            |
| MBB 022         Mananara Nord young         F         sp3         46         16.3         NA         35.5         22.1         NA         NA         11.7         NA         NA         NA         12.0         NA         closed         16.4ug-2015         MBB           MBB 024         Mananara Nord young         F         sp3         46         17.6         NA         35.2         21.6         NA         NA         11.6         NA         NA         NA         NA         14.0g-2015         MBB           MBB 025         Mananara Nord young         F         sp3         47         15.4         NA         36,4         21,8         NA         NA         11.6         NA         NA         NA         NA         NA         NA         14.0g-2015         MBB         MBB 027         Mananara Nord young         NA         15.4         NA         36,4         21,8         NA         NA         11.6         NA  | MBB 020              | Mananara_Nore | d adult  | M      | sp3           | 54       | 16,4         | NA         | 35,7         | 21,4         | NA       | NA        | 11,1         | NA       | NA       | NA       | NA       | 131,0          | enlarged               | NA       | 15-Aug-2015                | MBB        |
| MBB 024 Mananara Norl young F sp3 47 15.4 NA 58.4 21.8 NA NA 11.6 NA NA NA NA NA 134,0 NA closed 15-Aug-2015 MBB MBB 026 Mananara Norl adult M sp3 53 16.9 NA 55.5 22.6 NA NA 11.7 NA NA NA NA NA 11.7 NA NA NA NA NA 11.7 NA   | MBB 022              | Mananara_Nore | d young  | F      | sp3           | 46       | 16,3         | NA         | 36,5         | 22,1         | NA       | NA        | 11,7         | NA       | NA       | NA       | NA       | 122,0          | NA                     | closed   | 16-Aug-2015                | MBB        |
| MBB 026 Mananara Nord adult M sp3 57 17.0 NA 36,7 21,3 NA NA 12.4 NA NA NA NA 115.6 enlarged NA 22,4ug-2015 MBB MBB 028 Mananara Nord adult M sp3 64 17.1 NA 35.6 22.0 NA NA 9.4 NA NA NA NA NA 12.1 enlarged NA 22,4ug-2015 MBB MBB 028 Mananara Nord adult M sp3 64 17.1 NA 35.5 22.8 NA NA 11.2 NA NA NA NA 12.1 enlarged NA 22,4ug-2015 MBB MBB 028 Mananara Nord young M sp3 44 16.3 NA 35.9 20.9 NA NA 11.7 NA NA NA NA 12.1 enlarged NA 22,4ug-2015 MBB MBB 030 Mananara Nord young F sp3 44 14.2 NA 35,7 20,4 NA NA NA 11.7 NA NA NA NA 13.1,0 NA dosed 24,4ug-2015 MBB MBB 030 Mananara Nord young M sp3 50 17.2 NA 36,4 20,5 NA NA 11.9 NA NA NA NA 13.1,0 NA NA NA 13.1,0 NA NA NA 12.1,0 enlarged NA 22,4ug-2015 MBB NBB 030 Mananara Nord young M sp3 50 17.2 NA 36,4 20,5 NA NA 11.9 NA NA NA NA 12.7 enlarged NA 24,4ug-2015 MBB  | MBB 024              | Mananara_Nore | d young  | F      | sp3           | 47       | 15,4         | NA         | 36,4         | 21,8         | NA       | NA        | 11,6         | NA       | NA       | NA       | NA       | 134,0          | NA                     | closed   | 18-Aug-2015                | MBB        |
| MBB 028 Mananara Nord adult M sp3 64 17,1 NA 36,5 22,8 NA NA 11,2 NA NA NA 121,2 enlarged NA 23-Aug-2015 MBB MBB 029 Mananara Nord young M sp3 44 16,3 NA 55,9 20,9 NA NA 11,7 NA NA NA NA 127,0 enlarged NA 23-Aug-2015 MBB MBB 030 Mananara Nord young F sp3 42 14,2 NA 35,7 20,4 NA NA 10,5 NA NA NA NA 131,0 NA closed 24-Aug-2015 MBB MBB 031 Mananara Nord young M sp3 50 17,2 NA 36,4 20,5 NA NA 11,9 NA NA NA NA 12,7 enlarged NA 24-Aug-2015 MBB  | MBB 026              | Mananara Nore | d adult  | M      | sp3           | 57       | 17,0         | NA         | 36,7         | 21,3         | NA       | NA        | 12,4         | NA       | NA       | NA       | NA       | 115,6          | enlarged               | NA       | 22-Aug-2015                | MBB        |
| MBB 030 Mananana Nord young F sp3 42 14.2 NA 35,7 20,4 NA NA 10,5 NA NA NA 131,0 NA closed 24-Aug-2015 MBB MBB 031 Mananana Nord young M sp3 50 17,2 NA 36,4 20,5 NA NA 11,9 NA NA NA NA 12,7 enlarged NA 24-Aug-2015 MBB  | MBB 028              | Mananara_Nore | d adult  | М      | sp3           | 64       | 17,1         | NA         | 36,5         | 22,8         | NA       | NA        | 11,2         | NA       | NA       | NA       | NA       | 121,2          | enlarged               | NA       | 23-Aug-2015                | MBB        |
|  | MBB 030              | Mananara_Nore | young    | F      | sp3           | 42       | 14,2         | NA         | 35,7         | 20,4         | NA       | NA        | 10,5         | NA       | NA       | NA       | NA       | 131,0          | NA                     | closed   | 24-Aug-2015                | MBB        |
| MBB 032 Mananara_Nord adult M sp3 49 16,4 NA 35,5 21,6 NA NA 11,0 NA NA NA 126,0 enlarged NA 24-Aug-2015 MBB   |                      |               |          | M      | sp3<br>sp3    | 50<br>49 | 17,2<br>16,4 | NA<br>NA   | 36,4<br>35,5 | 20,5<br>21,6 | NA<br>NA | NA<br>NA  | 11,9<br>11,0 | NA<br>NA | NA<br>NA | NA<br>NA | NA<br>NA | 128,7<br>126,0 | enlarged<br>enlarged   | NA<br>NA | 24-Aug-2015<br>24-Aug-2015 | MBB<br>MBB |