





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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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 km² versus 9,250 and 50,700 km², respectively. Morphometric analyses distinguished unambiguously between sympatric species and detected more subtle but significant differences among sister lineages. Tail length and body size

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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 with 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 fragmentation.

KEYWORDS

conservation, cryptic species, evolution, habitat use, phenotype, sympatry

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 & Salmons, 2018; 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 2020 IUCN assessment, ten species are listed as Endangered, four species are Critically Endangered, while seven are Vulnerable, one is Data Deficient and only two species are categorized as of Least Concern (<https://www.iucnredlist.org>).

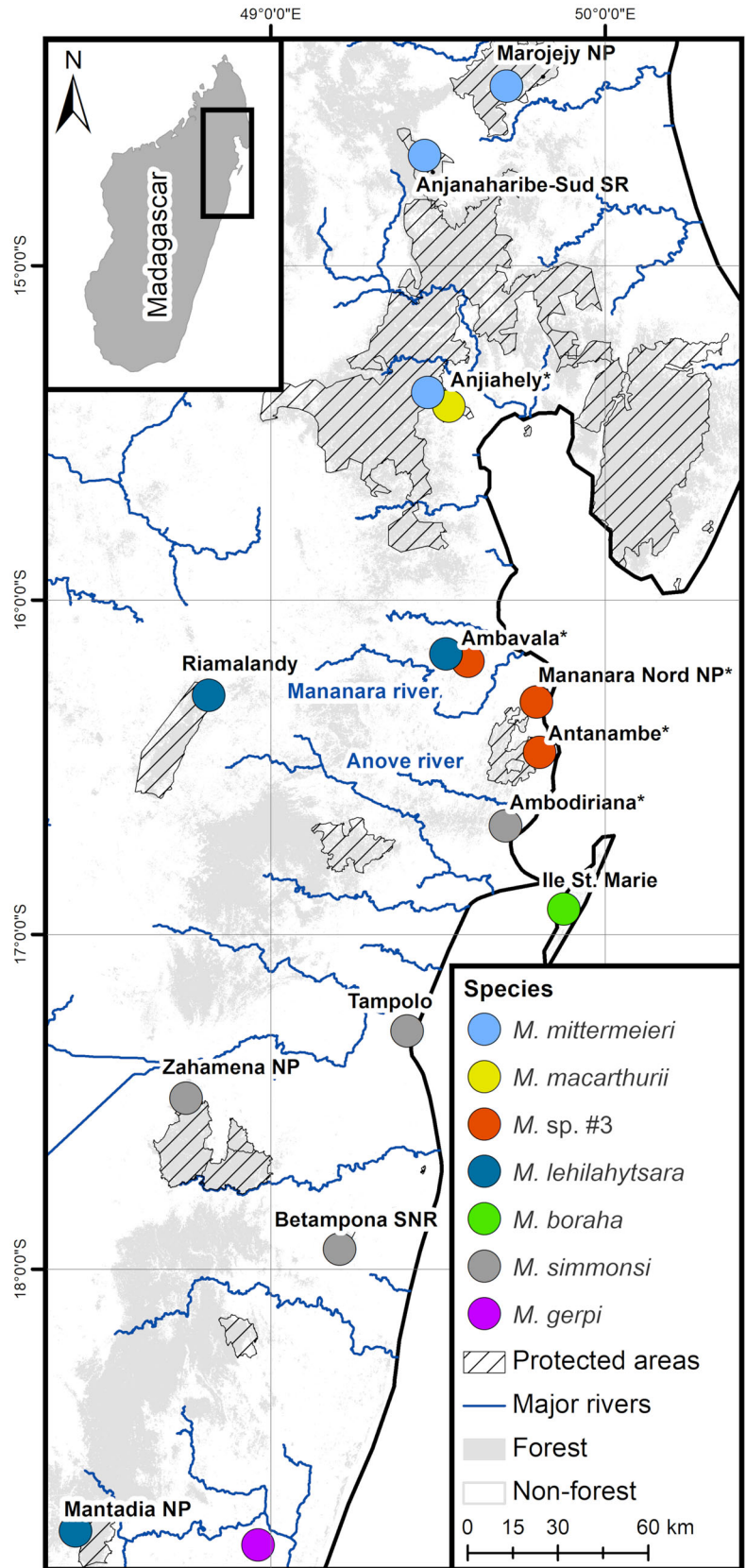
Integrating ecological and distributional data with molecular analyses in mouse lemurs is often difficult, largely because of their cryptic morphology and life history and lack of detailed metadata (Zimmermann & Radespiel, 2014). Analyses of mitochondrial DNA datasets have identified divergent lineages despite similar phenotypes and roughly similar ecological niches, and have led to the description of 12 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 11 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, 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. simmonsii* (Louis et al., 2006) are known to occur. Radespiel et al. (2008) surveyed the forests of the Makira region (Anjahely, 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. simmonsii* (Zahamena NP, Betampona SNR, Tampolo; Louis et al., 2006) and the sympatric species pair *M. macarthurii* and *M. mittermeieri* at Anjahely (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 Anjahely by genomic data in a companion study (Poelstra et al., 2020). Based on a comprehensive data set 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 supported four different lineages: *M. sp. #3*, *M. macarthurii*, *M. lehilahytsara/M. mittermeieri*, and *M. simmonsii*. 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

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



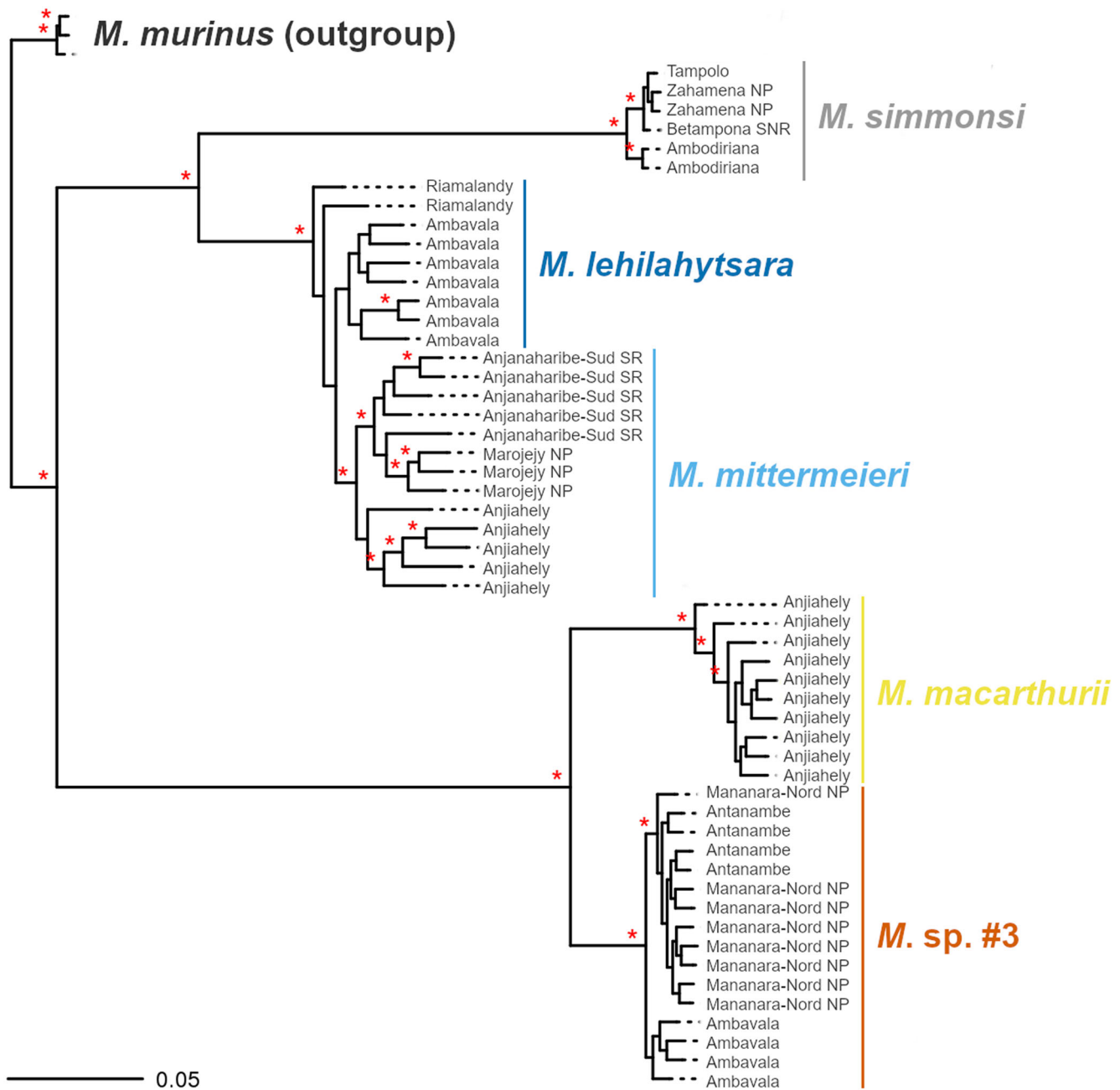


FIGURE 2 Maximum likelihood tree illustrating the phylogenetic relationships between *Microcebus* spp. in northeastern Madagascar as inferred by RAxML (based on nuclear sequence data). Sampling locations are indicated at the tips of the branches. Illustration adapted from Poelstra et al. (2020). NP,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

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 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 (a) providing morphological, ecological and distributional data for the *M. sp. #3* lineage in comparison to all other species from the same region and (b) by formally describing this new species.

2 | METHODS

2.1 | Study region

Northeastern Madagascar is characterized by a humid climate with abundant precipitation ($2,086 \pm SD$ 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 nongovernmental 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., Martin, 1972; Olivieri et al., 2007).

2.2 | *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 Anjahely (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 (Miller et al., 2018; Radespiel et al., 2008; 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 hr 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 (EOO) 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 Nonhuman Primates of the American Society of Primatologists (2001). This study was conducted with permission from institutional and governmental agencies that regulate animal research in Madagascar, Germany, France, Portugal, and the United States.

2.3 | 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, hindfoot 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: (a) adult in contrast to (b) 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

TABLE 1 Age classes of *Microcebus* spp. based on their mean body mass in grams (\pm standard deviation)

Species	<i>M. sp. #3</i> (Ambavala–Antanambe)	<i>M. lehilahytsara</i> (Ambavala)	<i>M. lehilahytsara</i> (Mantadia NP)	<i>M. mittermeieri</i> (Anjahely)
Capture time	Aug.–Sept.	Sept.	May–Nov.	Sept.–Dec.
Adults	57.4 \pm 5.6 (N = 18)	43.3 \pm 5.5 (N = 3)	43.8 \pm 4.7 (N = 30)	45.1 \pm 6.2 (N = 22)
Young	45.9 \pm 2.5 (N = 7)	24.4 \pm 5.3 (N = 5)	31.2 \pm 4.0 (N = 12)	21.5 \pm 1.9 (N = 4)

Note: Intraspecific differences between age classes were highly significant in all cases (two-tailed *t* tests: $p < .001$). For *M. macarthurii* and *M. simmonsii* only adult individuals were caught.

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 data set, 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 Anjahely (Radespiel et al., 2008). The morphometric data set 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 anestrus (closed vagina, nonreproductive), pre-estrous (swollen vagina), estrus (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 nonbreeding season, testes increase considerably in size starting about 1–3 months before female estrus (Evasoa et al., 2018). However, testes size was measured slightly differently across our data set (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 interobserver error. It is worth reporting, however, that two researchers contributed data points to more than one species (D. S. and D. W. R.), and that D. S. was trained by D. W. R. Furthermore, there was a strict selection of measurements that fully agreed with collection standards before assembling the data set. Finally, the data set was carefully scanned for outliers and inconsistencies within and across species, and a total of 21 measurements was excluded for this reason before data analyses. Reproductive data can also be found in Table S1.

2.4 | Statistical analyses of morphometrics

We performed a principal component analysis (PCA) and linear discriminant analysis (LDA) as well as analysis of variance (ANOVA) with Tukey post hoc tests for pairwise 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 data set. 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. simmonsii*. We further only used a subset of 11 *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

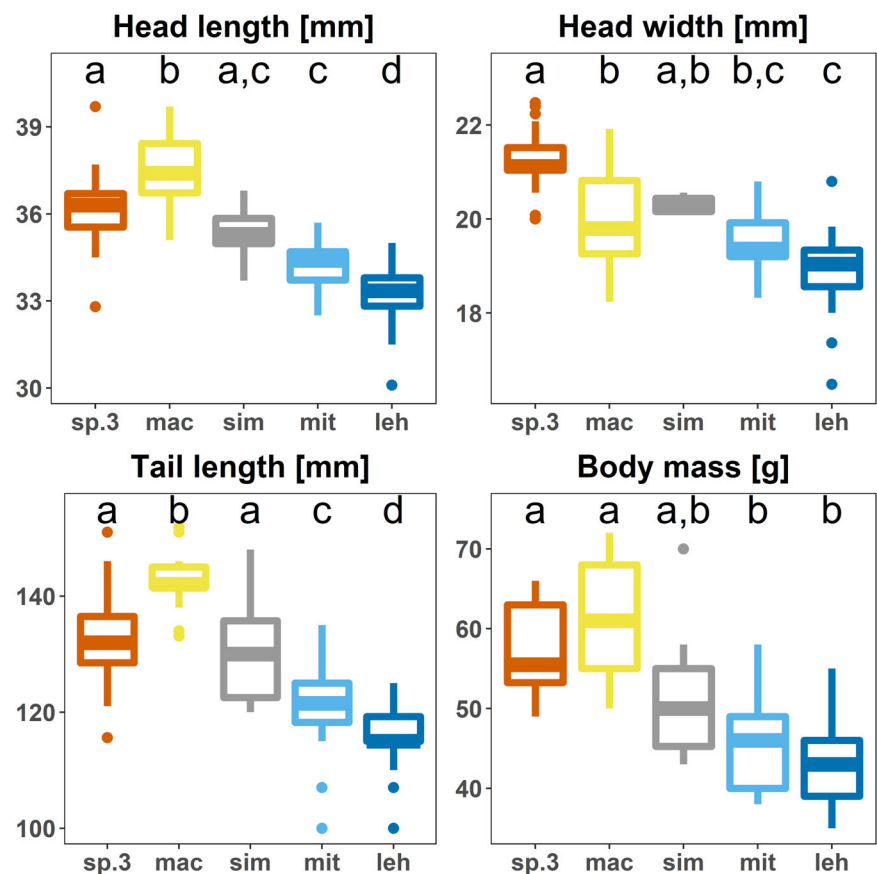
3.1 | Distribution of *Microcebus* spp. in northeastern Madagascar

First, we confirmed the presence of mouse lemurs at four locations previously not surveyed in our study region (Figures 1 and 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. macarthurii*/*M. mittermeieri* in Anjahely 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. simmonsii*. 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. simmonsii*, were found in lowland as well as montane rainforests (Table 2). The estimated EOO is much smaller for the two lowland species (*M. macarthurii* [560 km²] and *M. sp. #3* [1,500 km²]) compared with *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.

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

Taxon	Locations	Altitude	EOO	References
<i>M. mittermeieri</i>	Marojejy NP, Anjanaharibe-Sud SR, Anjiahely	350–1,056	9,250	Louis et al. (2006); Radespiel et al. (2008); Weisrock et al. (2010); this study
<i>M. macarthurii</i>	Anjiahely	350–400	560	Radespiel et al. (2008); this study
<i>M. lehilahytsara</i>	Ambavala, Riamalandy, Mantadia NP, Ambohitantely, Ankafobe, Tsinjoarivo	233–1,552	50,700	Kappeler et al. (2005); Weisrock et al. (2010); Yoder et al. (2016); this study
<i>M. sp. #3</i>	Ambavala, Mananara-Nord NP, Antanambe	42–356	1,500	This study
<i>M. simmonsii</i>	Ambodiriana, Tampolo, Zahamena NP, Betampona SNR	19–956	13,250	Louis et al. (2006); this study

Note: Combined EOO for *M. lehilahytsara* and *M. mittermeieri* is estimated with 66,800 km². Coordinates of the locations are given in Table S2.

FIGURE 3 Selected morphometric measurements of *Microcebus* spp. in northeastern Madagascar. Comparison based on one-way ANOVA ($p < .001$ for all parameters) and grouping (letters above values) according to Tukey post hoc tests. Plots for all parameters in Figure S1. ANOVA, analysis of variance; leh, *M. lehilahytsara* (at Mantadia NP); mac, *M. macarthurii* (at Anjiahely); mit, *M. mittermeieri* (at Anjiahely); sim, *M. simmonsii* (at Ambodiriana); sp.3, *M. sp. #3* (at Ambavala and Antanambe)

3.2 | Morphometric distinction between lineages

All morphometric parameters differed significantly among lineages (ANOVA; $p < .001$; 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, hindfoot, and third toe length (Figure 3 and Figure S1; Table 3). *M. simmonsii* 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 with conspecifics from Mantadia NP or *M. mittermeieri* from Anjiahely (i.e., body length, tail length; Table 3).

TABLE 3 Morphometric measurements of *Microcebus* spp. in northeastern Madagascar (mean \pm standard deviation)

Variables (in mm)	<i>M. sp. #3</i> (N = 18, at Ambavala, Mananara-Nord NP and Antanambe, this study)	<i>M. macarthurii</i> (N = 14, at Anjahely, this study and Radespiel et al., 2008)	<i>M. simmonsii</i> (N = 8, at Ambodiriana, this study)	<i>M. mittermeieri</i> (N = 22, at Anjahely, Radespiel et al., 2008)	<i>M. lehilahytsara</i> (N = 29, at Mantadia NP, Randrianambinina, 2001)	<i>M. lehilahytsara</i> (N = 3, at Ambavala, this study)
Ear length	17.2 \pm 0.8 a	18.0 \pm 0.8 a,c	19.5 \pm 2.7 b,c	18.3 \pm 1.4 a,c	20.0 \pm 1.1 b	17.9 \pm 0.2
Ear width*	12.7 \pm 1.0 a	10.6 \pm 1.3 b	12.6 \pm 0.9 a	12.1 \pm 0.8 a	12.3 \pm 0.9 a	11.8 \pm 1.1
Head length	36.2 \pm 1.4 a	37.5 \pm 1.3 b	35.3 \pm 0.9 a,c	34.3 \pm 0.8 c	33.2 \pm 1.0 d	35.2 \pm 1.3
Head width	21.5 \pm 0.9 a	20.0 \pm 1.5 b	20.4 \pm 0.2 a,c	19.3 \pm 0.7 b,c	18.6 \pm 1.0 c	20.0 \pm 1.2
Snout length	10.7 \pm 1.2 a	9.6 \pm 1.4 a	10.0 \pm 1.8 a	7.8 \pm 0.9 b	4.9 \pm 0.6 c	9.6 \pm 0.7
Interorbital dist.*	24.7 \pm 1.1 a	23.6 \pm 1.5 a,b	22.6 \pm 0.7 b	20.6 \pm 1.1 c	20.1 \pm 0.6 c	21.6 \pm 2.0
Intraorbital dist.*	7.7 \pm 0.5 a	7.1 \pm 0.6 a,b	6.5 \pm 0.6 b	6.6 \pm 0.7 b	5.8 \pm 0.5 c	7.1 \pm 0.6
Lower leg length*	39.9 \pm 1.9 a	39.9 \pm 1.3 a	38.7 \pm 3.0 a	35.4 \pm 1.5 b	35.7 \pm 1.3 b	37.5 \pm 0.9
Hindfoot length*	22.7 \pm 1.1 a	23.3 \pm 1.5 a	23.4 \pm 2.7 a	20.2 \pm 1.3 b	20.3 \pm 1.0 b	20.7 \pm 0.5
Third toe length*	9.8 \pm 1.2 a	9.5 \pm 0.9 a	NA \pm NANA	7.9 \pm 0.5 b	7.1 \pm 0.6 c	8.0 \pm 0.2
Tail length	132.7 \pm 9.0 a	142.6 \pm 5.5 b	130.6 \pm 9.6 a	121.5 \pm 8.3 c	115.2 \pm 5.1 d	108.7 \pm 19.7
Body length*	93.3 \pm 6.3 a	89.9 \pm 7.0 b	89.2 \pm 6.1 a,c	70.9 \pm 4.5 c	71.3 \pm 4.5 d	80.6 \pm 6.4
Body mass (g)	57.4 \pm 5.6 a	61.1 \pm 7.8 a	51.8 \pm 9.1 a,b	45.1 \pm 6.2 b	43.8 \pm 4.7 b	43.3 \pm 5.5

Note: Comparisons are based on one-way analysis of variance (ANOVA; $p < .001$ 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, and N = 6 at Antanambe.

*N = 11 for *M. sp. #3*.

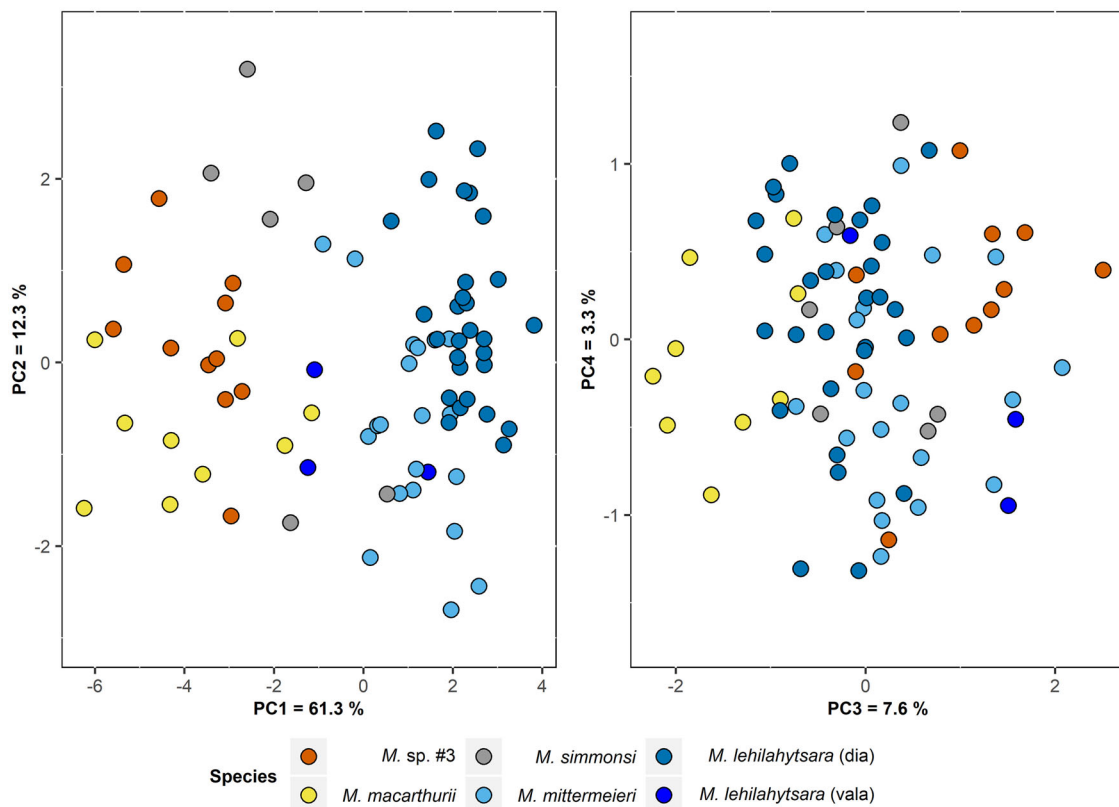


FIGURE 4 Principal component analysis including all morphometric parameters (except third toe length) showing PC1/PC2 (left) and PC3/PC4 (right). Small (*M. mittermeieri* and *M. lehilahytsara*) and large (*M. sp. #3* and *M. macarthurii*) lineages differ along PC1, with some differentiation of *M. mittermeieri* 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: $F = 36.88$; $df = 77$; $p < .001$). dia, Mantadia NP; PERMANOVA, permutational multivariate analysis of variances; vala, Ambavala

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 Anjahely. Again, *M. simmonsii* 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 data set. These five clusters corresponding to the five lineages were significantly different from each other as indicated by the PERMANOVA ($F = 36.88$; $df = 77$; $p < .001$).

The LDA model (a priori assignment of species) could also statistically distinguish between the five lineages (Wilk's lambda = 0.005; $F = 10.338$; $p < .001$). Four distinct clusters that included *M. lehilahytsara*, *M. macarthurii*, *M. mittermeieri*, and *M. sp. #3* are illustrated in Figure 5. *M. simmonsii* 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. simmonsii* (Table S4). The first two discriminant functions explained together 86.9% of the variation between the groups.

3.3 | Reproductive status

At Anjahely, 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 3 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 two out of three females were in estrus. Juveniles weighing 20–24 g were captured in the population in mid-December (Figure 6).

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 toward deepening our understanding of mouse lemur diversity in this understudied hotspot of microendemism.

4.1 | Distribution of *Microcebus* spp. in northeastern Madagascar

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 Anjahely (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 EOO, 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. simmonsii 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 (Figures 1 and 2) which expands its EOO by almost fivefold. The northern range limit for *M. simmonsii* 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 responsible for this pattern: (a) competitive exclusion at the geographic limits of the respective species ranges (Beaudrot et al., 2013; Hardin, 1960) or (b) an altitudinal range limit of both species below 640–700 m a.s.l. corresponding to the source region of the Anove River (DS, unpublished 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, unpublished data). Moreover, *M. simmonsii* 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. simmonsii* 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. simmonsii* (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.). Before 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. simmonsii* (Louis et al., 2006), *M. gerpi* (Radespiel et al., 2012), and *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 Anjahely)) requires further investigation concerning the relative importance of competitive exclusion, different habitat preferences, or distributional barriers, all of which have remained unexplored so far.

4.2 | 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 and

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; Moloro 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 and 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 Anjahely, 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 Anjahely 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 vs. lowland rainforest) or a morphological gradient across its entire range. These hypotheses, however, will require further testing.

M. simmonsii 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. simmonsii* 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 data set to the holotype specimen for *M. simmonsii* (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. simmonsii* 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. simmonsii* 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.

4.3 | 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 anestrus 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 7 weeks of age (Radespiel, Zimmermann & Wittkowski, unpublished data). Adding these 7 weeks (49 days) to about 57 days of gestation (for *M. lehilahytsara*, Wrogemann & Zimmermann, 2001; for *M. rufus*, Blanco, 2008), this could point toward 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 M. B. B. (unpublished 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, that is, 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 with 23°C), lower minimum temperature (9°C compared with 15°C) and a higher annual temperature range (19°C compared with 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 with 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 (Anjahely: 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 Anjahely. Reproductive observations of two *M. mittermeieri* females from another low elevation forest (Marojejy NP east site, ~200 m a.s.l.; M. B. B., unpublished 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 three 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.; M. B. B., unpublished 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 with 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. mamiatra* 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 lineages showed highly similar schedules in both cases.

4.4 | 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 Section 5).

The studied taxa were found in a variety of habitat types, ranging from nearly undisturbed to selectively logged forest, from shrubby secondary regrowth 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 EOO. *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, that is, *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 EOO. 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

5.1 | Systematics

Order: Primates (Linnaeus 1758)

Suborder: Strepshirini (É. Geoffroy 1812)

Family: Cheirogaleidae (Gray 1873)

Genus: *Microcebus* (É. Geoffroy 1828)

Species: *Microcebus jonahi* species nova

5.2 | Holotype

B34, adult male, captured on September 06, 2017 by D. S. Tissue samples, hair samples, as well as e-voucher photos of the animal are stored at the Institute of Zoology, University of Veterinary Medicine Hanover, Germany. The animal itself was released after field handling, sampling, and photographing, since its taxonomic distinctiveness was not recognized at the time of capture. Field measurements (all lengths measured in mm): ear length: 17.6, ear width: 13.7, head length: 37.7, head width: 23.0, snout length: 10.0, intraorbital distance: 8.2, interorbital distance: 26.0, lower leg length: 41.7, hindfoot length: 24.5, third toe length: 10.6, body length: 95.6, tail length: 130.0, body mass: 66 g. The population around Ambavala is designated as the source population for physical specimens in support of the holotype.

5.3 | Type locality

Forest near the rural village of Ambavala (S 16° 12.307', E 49° 35.371'), in a community protected forest at about 342 m a.s.l. approx. 20 km west of Mananara Avaratra (Mananara-Nord), Province of Analanjirifo, Madagascar.

5.4 | Paratypes

(a) BD1, adult female, captured in the community protected forest of Antsiradrano (near Ambavala) on September 04, 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 September 11, 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.

5.5 | Description

Microcebus jonahi is a large-bodied, reddish-brown, and small-eared mouse lemur (Figure 7). This species has short and dense fur.

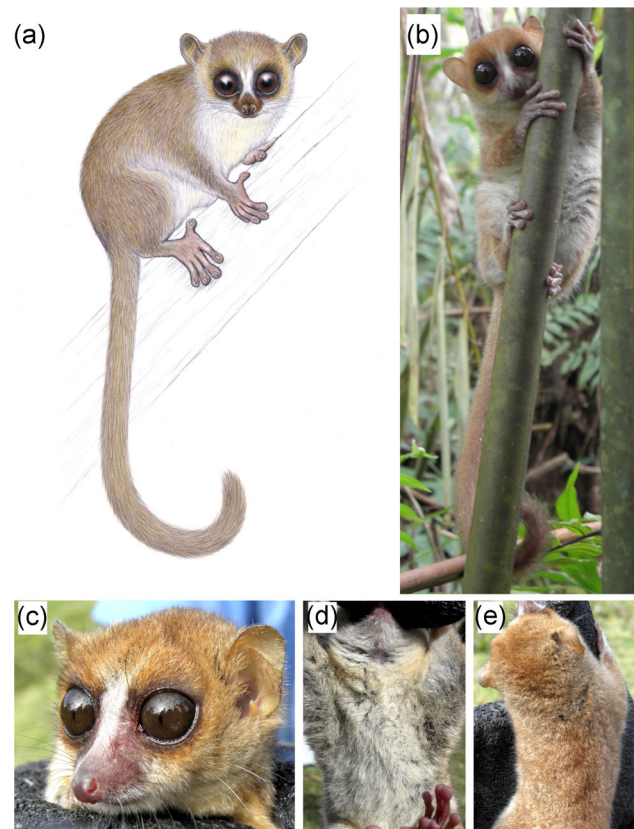


FIGURE 7 Outer morphology of *Microcebus jonahi*. (a) Drawing of an adult individual; (b) Habitus of adult female (paratype individual BD1); (c–e) Close-ups of adult male (holotype B34). Illustration copyright by Stephen D. Nash/IUCN SSC Primate Specialist Group; used with permission. Photos by D. Schüßler

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 toward 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 whitish-gray 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.

5.6 | 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 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).

5.7 | Diagnosis

M. jonahi can be distinguished from other taxa in northeastern Madagascar by morphometric features and genomic distinctiveness. Compared with 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, unpublished 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. simmonsii*, by its shorter ear length and its larger inter- and intraorbital 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 (Poelstra et al., 2020).

5.8 | Etymology

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.

5.9 | Vernacular name

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

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY

The raw data that support the findings of this study are contained in the supplementary material.

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SUPPORTING INFORMATION

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