First density estimates of the Endangered Claire's mouse lemur *Microcebus mamiratra* and recommendations for its conservation

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Abstract Mouse lemurs *Microcebus* spp. are small, nocturnal primates endemic to Madagascar. The genus is extraordinarily diverse, with 25 extant species, several of which have been described recently. The Endangered Claire's mouse lemur *Microcebus mamiratra* was first described in 2006, but, similarly to other newly described mouse lemurs, remains understudied, and estimates of its population size are unavailable, hampering effective conservation management. We conducted line transect distance sampling surveys of *M. mamiratra* across several habitat types in and around Lokobe National Park on the island of Nosy Be in northwestern Madagascar. Using a systematic random design we surveyed 15 transects over a 6-week period in 2023, recording 92 detections from a total survey effort of 46.5 km. We estimate the density of *M. mamiratra* on Nosy Be to be 125.1 individuals/km^2, which extrapolates to an estimate of c. 4,700 individuals across the forested areas of its range on the island. Our results indicate that Nosy Be harbours moderately high densities of *M. mamiratra*, with the highest encounter rates in the unprotected secondary and degraded forests around Lokobe National Park. Our population estimate will inform future conservation status assessments and conservation planning for this range-restricted species and provide a baseline for monitoring population changes over time. We present recommendations for the conservation of *M. mamiratra* and highlight the potential for lemur watching, sustained by the strong tourism industry on Nosy Be, to help protect lemur habitat and generate economic opportunities for local communities.

Fintina Ny tsitsidy *Microcebus* spp. dia biby kely, ary primata mandeha amin'ny alina izay tsy hita maso raha tsy ao Madagasikara. Ity karazana ity dia miavaka ary mbola misy 25 karazana izay miaina ankehitriny, ny ankamaroan'ireo dia vao nofaritana tato anatin'ny taona vitsivitsy izay. Ity tsitsidy izay atahorana ho lany tamingana ity, izay mitondra ny anarana hoe *Microcebus mamiratra* eo amin'ny sehatry ny fikarohana (na fantatra ihany koa hoe Valovi) dia nofaritana voalohany tamin'ny taona 2006, saingy toy ny tsisidy hafa vao nofaritana, dia mbola tsy voadinika tsara izy io ary koa mbola tsy misy ny tombatombana raha ny hamaroan'ny mponina no lazaina, izany dia lasa sakana eo amin'ny fitantanana mahomby amin'ny fiarovana. Ho famahana izany dia, nanao santionana fanadihadiana 'transect line-distance' amin'ny *M. mamiratra* teo anivon'ny karazana toeram-ponenana maromaro, tao amin'ny valanjavaboary Lokobe sy ny manodidina azy ao amin'ny nosy antsoina hoe Nosy Be, izay any amin'ny faritra avaratr'andrefan'i Madagasikara izahay. Izany dia nampiasaina endri-drafitra kisendrasendra, nanaramaso transekta 15 izahay, izay nandritra ny 6-herinandro tamin'ny taona 2023, tamin'ny fitambaran'ny fanadihadiana 46,5 km natao dia 92 no hita avy amin'izany. Tombanana ho 125,1 isam-batana/km^2 ny hakitroky *M. mamiratra* ao Nosy Be, izay nahazahoana antontan'isa 4.700 eo ny tombantomban'ny hakitroka manerana ny faritra misy azy ao amin'ny alafady ao amin'io nosy io. Ny vokatra azonay dia manondro fa i Nosy Be dia manana salan'isa ambony raha ny habetsaky ny *M. mamiratra* no jerena, ary ihany koa manana ny taha ambony indrindra eo amin'ny fahitana io biby io any ivelan'ny ala-fady, na ivelan'ny faritra arovana Lokobe. Ny fanombatombanana ny isan'ny mponina ananana dia hampahafantatra tsaratsara kokoa ny sata mamehy ny fandalinanana ny fiarovana izay mbola ho avy, sy ny drafitra ho fikajiana an'io karazam-biby voaaro io, ary koa manome tombatombana amin'ny fanaraha-maso ny fiovan'ny mponina rehefa mandeha ny fotoana. Izahay dia manolotra tolokevitra ho amin'ny fiarovana an'i *M. mamiratra* ary koa manasongadina ny mety hisian'ny fijerena maso ny gidro (varika), izay tohanan'ny lafiny ara-pizahantany matanjaka ao Nosy Be, mba hanampy ny fiarovana ny toeram-ponenan'ny varika ary koa mba hiteraka tombontsoa ara-toekarena ho an'ny vondron'olona ifotony.

Keywords Claire's mouse lemur, density estimate, distance sampling, lemur conservation, line transect survey, Lokobe National Park, Madagascar, *Microcebus mamiratra*

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Received 30 November 2023. Revision requested 24 January 2024. Accepted 17 April 2024.

Introduction

Molecular genetic and morphological techniques have revealed the extraordinary species diversity of the endemic mouse lemurs of Madagascar (Cheirogaleidae: *Microcebus*; Louis et al., 2008; Groves, 2016; Schüßler et al., 2020). The genus was long considered to comprise just two species, one from the dry forests of the west and south and one from the rainforests of the east (Groves, 2005), but today 25 species are recognized. One consequence of these taxonomic revisions is that the geographical distributions and conservation status of new species, and those from which they are distinguished, must be reassessed (Louis et al., 2006; Rasoloarison et al., 2013), as splitting species often results in proportionately more threatened species with reduced ranges (Agapow et al., 2004). Several newly described mouse lemur species, however, have not been surveyed and population data are incomplete or absent (Setash et al., 2017; Hending, 2021). Population estimates are needed to support IUCN Red List assessments, to allow conservation managers to identify, prioritize and monitor vulnerable species and populations, and to help evaluate conservation programmes (Plumptre & Cox, 2006; Kühl et al., 2008; Rylands et al., 2008, 2020).

Claire's mouse lemur *Microcebus mamiratra* was first described in 2006 (Andriantompohavana et al., 2006) and has been the subject of limited field research (Hasiniaina et al., 2018; Webber et al., 2020; Tinsman et al., 2022). Its geographical range is confined to the humid primary and secondary forests of the Lokobe National Park region on the island of Nosy Be in north-west Madagascar, as well as some small, isolated humid forest fragments on the Malagasy mainland near Manehoka and Ambakirano, east of Nosy Be (Olivieri et al., 2007; Sgarlata et al., 2019; Blanco et al., 2020). Threatened mainly by habitat loss and degradation, it is categorized as Endangered on the IUCN Red List (Blanco et al., 2020). Lemurs have been extirpated from small islands elsewhere in Madagascar, and the population of *M. mamiratra* on Nosy Be is at risk (Goodman, 1993; Hyde Roberts & Daly, 2014). No systematic surveys have been carried out anywhere across its restricted and severely fragmented range, and there are no population size or density estimates (Blanco et al., 2020). Although encounter rates have been reported for *M. mamiratra* (Tinsman et al., 2022), these provide only a relative abundance index and could be affected by differences in detection probability, such as those between observers or environmental variables (Anderson, 2001; Buckland et al., 2008; Campbell et al., 2016).

Distance sampling is a powerful method for estimating absolute population density (number of individuals per unit area) and population size (density multiplied by area). It comprises a set of standardized survey techniques, principally line transects and point transects, in which observers record distances to detected objects whilst traversing lines or standing at points that are placed randomly within a survey area (Buckland et al., 1993, 2001, 2004). The detected objects are usually animals of the target species but might be animal cues (e.g. calls) or signs (e.g. nests). Intuitively, we expect that objects become more difficult to detect with increasing distance from the line or point and that some objects might be missed. A key strength of distance sampling is that it accounts for imperfect detection: the distribution of observed distances is used to model a detection function that describes the probability that an object is detected as a function of distance from the line or point, thereby allowing estimation of the proportion of objects missed during the surveys (Buckland et al., 1993, 2001, 2004). This can be particularly advantageous for animals that are otherwise difficult to detect, such as small-bodied and nocturnal mouse lemurs (Meyler et al., 2012; Schäffler & Kappeler, 2014). In primatology, line transects are the most popular form of distance sampling (Plumptre, 2000; Ross & Reeve, 2003; Plumptre et al., 2013). Proper inference in line transect distance sampling relies on the following key assumptions: (1) objects directly on the line are detected with certainty, (2) objects are detected at their initial location, prior to any movement in response to the observer, and (3) distances to detected objects are measured accurately (Buckland et al., 1993, 2001, 2004; Buckland, 2006; Plumptre et al., 2013). A further assumption, relevant for group-living primates, is (4) group sizes (or clusters) are accurately recorded (Buckland et al., 2010). Mouse lemurs are amenable to line transect surveys for several reasons: (1) their tapetum lucidum (reflective eye tissue) and preference for the understorey aid detection on the centreline (Lahann, 2008; Rakotondravony & Radespiel, 2009), (2) they move relatively slowly and often become stationary when observed (Meyler et al., 2012), (3) they are mostly solitary, generally removing the need to estimate cluster size and spread (Buckland et al., 2010; Bessone et al., 2023), and (4) they are generally abundant, so adequate samples sizes can be obtained (Kappeler & Rasoloarison, 2003). Line transect distance sampling also relies on two underlying principles of survey design: (1) randomization (i.e. the lines should be placed randomly, and not subjectively, in the survey area; e.g. systematically spaced parallel lines with a random start point; Marques et al., 2010; Thomas et al., 2010; Hilário et al., 2012), and (2) replication (i.e. an adequate number of lines (at least 10–20) should be placed; Buckland et al., 1993, 2001, 2004; Thomas et al., 2010). In practice, however, surveys are often compromised by time and resource constraints (e.g. rapid assessments), and the key assumptions are routinely violated or cannot be met (Buckland et al., 2010; de Andrade et al., 2019). Recent meta-analyses of published density estimates of mouse lemurs have highlighted that non-standardized designs (e.g. using non-random established trails as transects) and analysis methods (e.g. not accounting for detection probability) are prevalent (Setash et al., 2017; Hending, 2021). Poor survey practices can bias results and inhibit rigorous inference; at worst, they can lead to incorrect conservation status assessments, inappropriate conservation management decisions or the misallocation of limited conservation funds (Elphick, 2008).

Here we provide the first reliable estimates of density and abundance for *M. mamiratra* using line transects, a systematic random survey design and best-practice field protocols. Population estimates will inform future status assessments and conservation actions for this threatened primate. We predict that density estimates for *M. mamiratra* are similar to those reported for other mouse lemur species from the dry and transitional forests of north-west Madagascar, consistent with large-scale regional patterns in mouse lemur densities (Setash et al., 2017). We also predict that encounter rates at Nosy Be are higher in unprotected, anthropogenic habitats than in protected, primary forests, consistent with general patterns in mouse lemur abundance (Hending, 2021).

Study area

Nosy Be is a 321 km² island in the Mozambique channel to the north-west of Madagascar, c. 12 km from the mainland. It is part of the Sambirano Domain, a transitional area between the eastern wet and western dry forests (Sawyer et al., 2015). The climate is tropical with a hot, wet season during October–April and a cooler, dry season during May–September (Cutler, 1965; Andreone et al., 2005). Mean daily temperatures range from 23 °C during July–August to 28 °C during January–February (Birkinshaw, 1995), and mean annual rainfall is 2,250 mm (Andreone et al., 2005). Most of the original forest cover on Nosy Be has been converted to agricultural land, including rice and ylang-ylang crops (Andreone et al., 2005). The 7.4 km² Lokobe National Park protects most of the remaining primary forest, which is classified as low-altitude humid evergreen forest (Hasiniaina et al., 2018). The Park is surrounded by a mosaic of secondary and degraded forest, crop plantations and small villages (Birkinshaw, 1995; Tinsman et al., 2022). Elevation across Nosy Be is 0–430 m, with the primary forests of Lokobe National Park occupying some of the highest slopes (Tinsman et al., 2022). The black lemur *Eulemur macaco* and the Nosy Be or Hawks' sportive lemur *Lepilemur tymerlachsoni* are the only lemurs sympatric with *M. mamiratra* on the island. Nosy Be has been identified as a priority area for lemur conservation (Schwitzer et al., 2013, 2014) and is also one of the most popular tourist destinations in Madagascar (Jędrusik, 2019).

Methods

Survey design and transect placement

We used the *survey design* function in *Distance 7.5 Release 2* (Thomas et al., 2010) to superimpose a grid of points with a random starting position across a map of the extent of occurrence of *M. mamiratra* on Nosy Be, obtained from the most recent IUCN Red List assessment (Blanco et al., 2020). We then used the coordinates of these grid points to place a systematic set of segmented parallel transect lines in and around Lokobe National Park. We placed 16 transects in the survey area (Table 1), but only surveyed 15 of these because of safety concerns at one location (small flooded areas considered unsafe for nocturnal work; T9, Fig. 1). The mean transect length was 815 m (range: 633–1,125 m), which we measured in the field with an open reel tape measure. Some transects were shorter because they crossed impassable terrain such as ravines. Transects covered areas of primary, secondary and degraded forest, and plantations both within and outside the National Park boundaries. We cut the transects in straight lines in a north–south direction, only deviating to avoid dangerous (e.g. boulders) or inaccessible areas (e.g. paddy rice plantations) where necessary. We marked the transects with fluorescent flagging tape so that observers could identify the centreline during surveys. We then waited at least 72 h before surveying, to minimize the effects of disturbance from cutting the transects (Bessone et al., 2023).

Line transect surveys

Author LDM provided training to all observers on distance sampling theory (e.g. survey design, key assumptions) and field protocols (e.g. equipment use, searching behaviour) at the start of the field season. We conducted nocturnal surveys in the wet season during 17 February–4 April 2023. Beginning at sunset (c. 19.00), teams of 2–3 observers walked a transect in single file at a mean speed of 1–2 km/h, pausing during heavy rainfall. Observers stopped to scan the survey area at regular intervals, concentrating search effort on and near the line. We used headlamps to locate mouse lemurs by reflective eye shine and binoculars to distinguish *M. mamiratra* from other wildlife. Observers would temporarily leave the transect line to confirm the identification of detections as required. For each mouse lemur detected, we recorded cluster size and perpendicular distance from the transect line on a standardized datasheet. We measured perpendicular distances with a laser rangefinder and paced distances < 4 m (the minimum range of the rangefinder). We recorded detections of each mouse lemur individually (i.e. cluster size of 1), including where we detected mouse lemurs in groups of 2–3 (Buckland et al., 2001, 2010). We recorded only visual detections. We surveyed each transect 2–5 times. We regularly changed team composition to minimize between-team observer variability. We stored field data electronically and verified the data daily. Although *M. mamiratra* is not believed to undergo prolonged periods of torpor (Tinsman et al., 2022), we conducted our surveys outside the dry season, when mouse lemurs typically exhibit this

  doi:10.1017/S0030605324000772

TABLE 1 Summary of transects surveyed, including predominant habitat type, whether the transect was within the boundaries of Lokobe National Park (Nosy Be, north-western Madagascar; Fig. 1), transect length, number of times the transect was surveyed, total survey effort (*L*), total number of *Microcebus mamiratra* detected (*n*) and encounter rate (*n*/*L*).

Transect ID	Predominant habitat type	Within Lokobe National Park boundaries?	Length (m)	Number of times surveyed	*L* (km)	*n*	*n*/*L*
T1	Secondary/degraded forest and plantation	No	961	2	1.92	0	0.00
T2	Secondary/degraded forest and plantation	No	773	5	3.87	26	6.73
T3	Plantation	No	855	3	2.57	3	1.17
T4	Plantation	No	845	2	1.69	0	0.00
T5	Secondary/degraded forest and plantation	No	792	5	3.96	3	0.76
T6	Secondary/degraded forest and plantation	No	805	5	4.03	19	4.72
T7	Secondary/degraded forest and plantation	No	925	4	3.70	17	4.59
T8	Secondary/degraded forest	No	775	4	3.10	0	0.00
T9[1]	Secondary/degraded forest	No	780	NA	NA	NA	NA
T10	Secondary/degraded forest and plantation	No	812	5	4.06	1	0.25
T11	Primary forest, secondary/degraded forest and plantation	No	1,125	4	4.50	7	1.56
T12	Primary forest and secondary/degraded forest	Yes	717	3	2.15	3	1.39
T13	Primary forest	Yes	633	3	1.90	2	1.05
T14	Primary forest	No	684	3	2.05	3	1.46
T15	Primary forest and secondary/degraded forest	No	838	5	4.19	7	1.67
T16	Secondary/degraded forest and plantation	No	713	4	2.85	1	0.35
Total					46.53	92	1.98

[1]Not surveyed after placement because of safety concerns.

behaviour (Dausmann & Warnecke, 2016), hence there should be no torpor-related availability bias (Hending et al., 2023).

Data analysis: distance software

We used the conventional distance sampling engine in *Distance* to estimate *M. mamiratra* density and abundance. We pooled individual surveys and detections for each transect line, and recorded effort as line length multiplied by the number of times the line was surveyed (Buckland et al., 2008). We plotted histograms of the perpendicular distances as part of an exploratory data analysis phase. We then grouped distance data into suitable distance cut points for analysis and right-truncated 10% to remove outliers and facilitate modelling (Buckland et al., 2001; Thomas et al., 2010). We then fitted the following model and adjustment combinations: uniform key function with cosine series expansion, half-normal key function with cosine and Hermite polynomial series expansion, and hazard-rate key function with simple polynomial series expansion. We visually assessed the candidate models and compared them using χ^2 goodness-of-fit tests and the Akaike information criterion (Akaike, 1973).

Analysis of habitat on Nosy Be

The geographical range maps in the IUCN Red Lists are minimum convex polygons of the extent of occurrence of a species and not necessarily its area of occupancy, and as a result could include areas of unsuitable habitat (e.g. non-forest, villages; Schwitzer et al., 2014). We therefore estimated forest cover within the extent of occurrence of *M. mamiratra* on Nosy Be using Global Forest Watch (2023), and we used this forested area as a proxy for suitable mouse lemur habitat in our abundance extrapolation. Forest cover was calculated as the tree cover extent in 2000 ($>$ 30% canopy density; Hansen et al., 2013; see also Estrada et al., 2018; Mekonnen et al., 2020; Markolf et al., 2022) within the range data shapefile obtained from the IUCN Red List (Blanco et al., 2020) plus or minus net tree cover change during 2000–2022 (Potapov et al., 2022).

Results

We recorded 92 *M. mamiratra* detections in a total survey effort of 46.5 km (Table 1). This exceeds the recommended minimum sample size of 60–80 detections (Buckland et al., 2001).

Since 2000, c. 14.5 km^2 (28%) of forest cover has been lost within the range of *M. mamiratra* on Nosy Be. We estimate that 37.3 km^2 of forest cover remains, an area similar to the maximum area of occupancy of the species on the island.

Our distance analyses generated a mean density estimate of 125.1 individuals/km^2 (95% CI 65.3–239.5, coefficient of variation 0.32). The half-normal key function with cosine

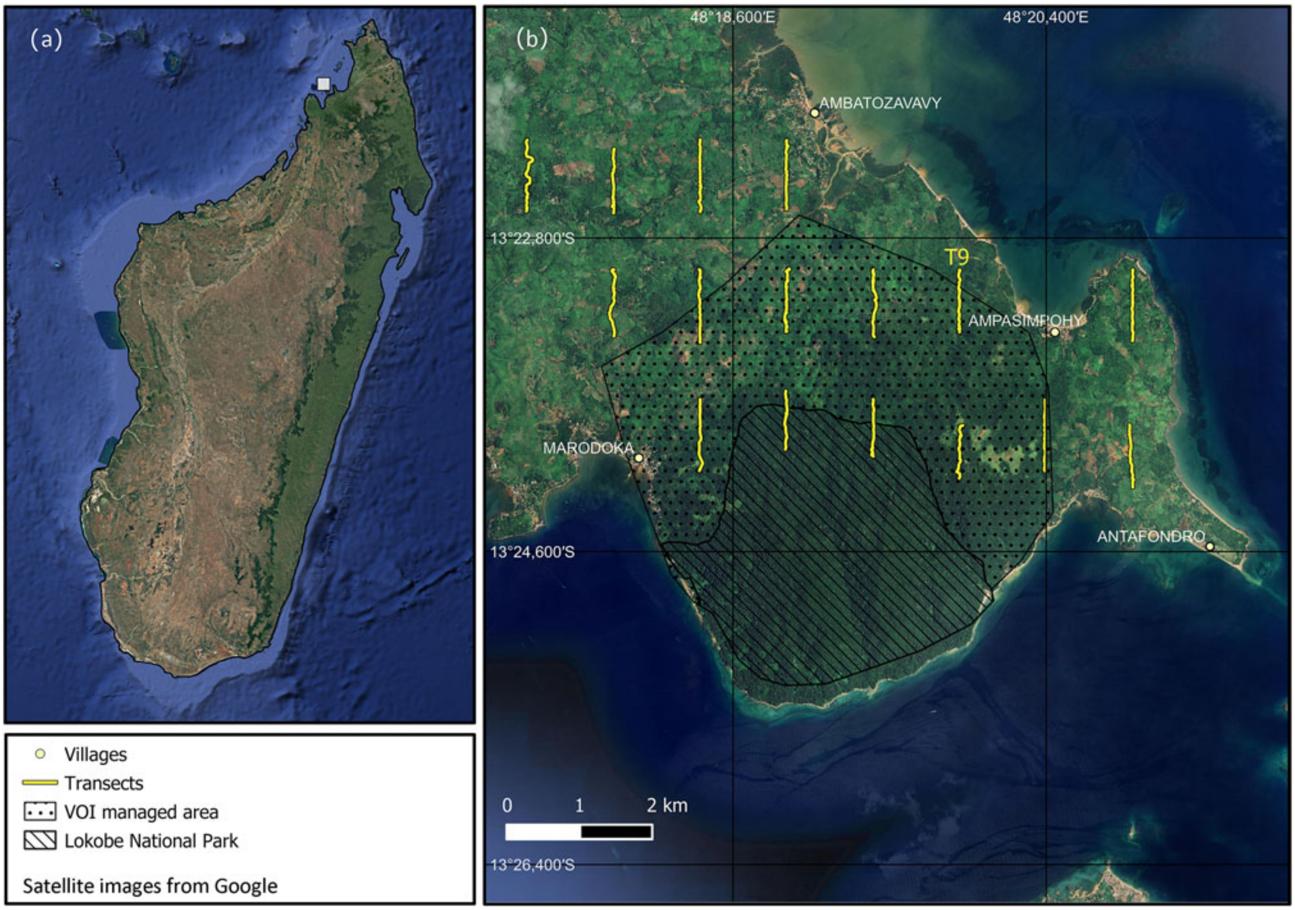

FIG. 1 (a) Madagascar, showing the location of Nosy Be, and (b) the survey area and line transects (Table 1). Transect IDs: top row T1–T4, middle row T5–T10, bottom row T11–T16. VOI, Vondron'Olona Ifotony.

adjustment provided the best fit to the data ($\chi^2 = 2.06$, df = 3, P = 0.56; detection probability = 0.23; effective strip width = 7.05; Fig. 2). Extrapolating this density estimate across the forested area within the extent of occurrence of *M. mamiratra* on Nosy Be yields a population of c. 4,700 individuals.

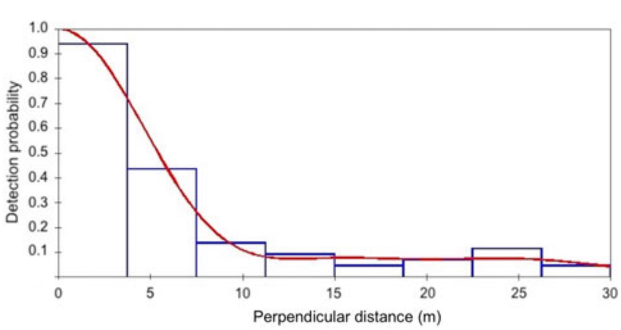

FIG. 2 Histogram showing the detection probability of *Microcebus mamiratra* as a function of perpendicular distance from the transect line on Nosy Be, north-west Madagascar (Fig. 1). The columns represent grouped detections of *M. mamiratra* and the curve represents the detection function. Data were right-truncated by 10%.

Discussion

We report the first population estimates for *M. mamiratra*, an Endangered and little-known mouse lemur of north-west Madagascar. We applied randomization and replication in our survey design and employed survey protocols that ensured we met the key assumptions of distance sampling, allowing valid inference and extrapolation from our results. Our population data will inform future conservation status assessments and management decisions and provide a starting point for monitoring local population changes over time. More broadly, our study also helps to address the need for baseline population data for newly described mouse lemurs, and our use of standardized survey methods facilitates meaningful inter-site and interspecific comparisons (Setash et al., 2017; Hending, 2021).

Our density estimates for *M. mamiratra* (125.1 individuals/km^2) are intermediate compared to those of other mouse lemurs (see Setash et al., 2017, Hending, 2021 and Hending et al., 2022b for summaries of published *Microcebus* spp. population densities). Mouse lemur densities are generally higher for western dry forest species and lower for eastern humid forest species, probably driven by

  doi:10.1017/S0030605324000772

regional differences in habitat (e.g. increased fragmentation and seasonality in western dry forests), species richness and mouse lemur physiology, amongst other factors (Setash et al., 2017). Consistent with these large-scale regional patterns, and as predicted, *M. mamiratra* densities were broadly similar to those reported for other species from the dry and transitional forests of north-west Madagascar. For example, densities of 30 individuals/km² have been reported for what is probably the Sambirano mouse lemur *Microcebus* cf. *sambiranensis* at Sahamalaza-Iles Radama National Park (Hending et al., 2022b), 378 individuals/km² for Danfoss' mouse lemur *Microcebus danfossi* in the Sofia region (Randrianambinina et al., 2010; Hending et al., 2022b) and 80 and 265 individuals/km² for the northern rufous mouse lemur *Microcebus tavaratra* at various sites in the Daraina region (Meyler et al., 2012). Although *M. mamiratra* has been described, at least anecdotally, as rare within its range (Mittermeier et al., 2010; Blanco et al., 2020; see also McKelvey et al., 2008), our results indicate this is not the case, at least for the Nosy Be population, insofar as rarity relates to low abundance (Drever et al., 2012). The misconception that *M. mamiratra* is rare could relate to its low detectability; mouse lemurs are small, mostly solitary, inconspicuous and can be difficult to detect at distance, particularly in dense forest and wet weather (Fig. 2; Schäffler & Kappeler, 2014; Deppe, 2020). This serves to highlight the value of distance sampling methods that model and incorporate detectability and only require perfect detection on the transect centre line or point.

Our survey area included protected and unprotected areas and several habitat types, covering much of the extent of occurrence of *M. mamiratra* on Nosy Be. As predicted, the transects with the highest encounter rates were in unprotected secondary and degraded forests in the north-west of our survey area, outside the Lokobe National Park boundaries and proximate to areas of human activity (Table 1; Fig. 1). This suggests that *M. mamiratra*, similarly to other mouse lemurs, may prefer disturbed forests and anthropogenic habitats. Mouse lemurs are generally highly adaptable and can be common in such habitats, including agricultural crops (Hending et al., 2018; Knoop et al., 2018; Andriambeloson et al., 2021). Unlike other cheirogaleids, mouse lemur density generally has a positive relationship with anthropogenic disturbance and a negative relationship with forest cover, and densities are generally higher in unprotected than protected areas (Hending, 2021). Moreover, some mouse lemurs show tolerance to forest edges, a common microhabitat feature of the fragmented secondary and degraded forests in our study site (Lehman et al., 2006; Burke & Lehman, 2015). We also observed that the transects with high encounter rates were adjacent to transects where *M. mamiratra* was never or seldom observed (Table 1; Fig. 1). It has also been found that encounter rates of *M. mamiratra* are highly variable (Tinsman et al., 2022). This uneven spatial distribution may be explained by variation in forest microhabitat structures that are important to mouse lemur survival (Rendigs et al., 2003; Fredsted et al., 2004).

Conservation recommendations and future directions

Nosy Be is a priority area for lemur conservation, and our results indicate that its population of *M. mamiratra* comprises c. 4,700 individuals at a moderately high density. Importantly, the highest encounter rates occurred in the unprotected secondary and degraded forests surrounding Lokobe National Park, some of which are managed by Vondron'Olona Ifotony (Fig. 1), a village-based association for forest management. We encourage conservation managers to continue to work with local communities and private landowners to preserve all remaining forest habitats. Several landowners and village presidents we spoke with during informal discussions expressed an interest in lemur conservation; for example, some landowners maintained small forested areas on their plantations having observed lemurs using them. Direct payments to households could help incentivize forest management and ensure local people are adequately compensated for the high opportunity costs borne through conservation restrictions (Milne & Niesten, 2009; Wendland et al., 2010; Gross-Camp et al., 2012; Schwitzer et al., 2013; Poudyal et al., 2018; Estrada et al., 2022). However, this would require significant, long-term investment, typically from international donors, and such schemes have so far achieved only limited success in Madagascar (Sommerville et al., 2010; Rasolofoson et al., 2015). Because Nosy Be is a popular tourist destination, there is also potential for nocturnal lemur watching ecotourism to help protect lemur habitat, generate income for local communities and foster residents' appreciation of lemurs (Ormsby & Mannle, 2006; Schwitzer et al., 2014; Wright et al., 2014; Waters et al., 2023). Madagascar National Parks has recently commenced nocturnal tours at Lokobe National Park (G. Bakarizafy, pers. comm., 2023), and with the support of local stakeholders this could be extended to community-led initiatives outside the Park (Razanatsoa et al., 2021). The conservation success stories of community-run organizations elsewhere in Madagascar (e.g. Association Mitsinjo in Andasibe and Anja Reserve in the south-central highlands) could be emulated in Nosy Be by integrating ecotourism with other initiatives, including forest restoration, scientific training and capacity building, and environmental education (Schwitzer et al., 2013; Dolch et al., 2015; Gould & Andrianomena, 2015).

Currently, Lokobe National Park is the only protected area in which *M. mamiratra* occurs (Blanco et al., 2020). Although the Park has good infrastructure and is well resourced, it is small, and it is doubtful whether it alone can ensure the long-term viability of the species (Olivieri et al.,

  doi:10.1017/S0030605324000772

2007). Future surveys of the isolated mainland populations and their habitats, which are currently under no formal protection, could identify suitable locations for establishing additional protected areas (Olivieri et al., 2007) and restoring forest connectivity to maximize the capacity of the species to respond to future climate change (Hannah et al., 2008; Hending et al., 2022a). *Microcebus mamiratra* is also reported to occupy mangrove habitats (Gardner, 2016), and although our surveys did not incorporate this habitat type, future research could elucidate the relative importance of mangroves to this species.

Lokobe National Park itself is difficult to survey. The terrain is steep, and slippery underfoot in the wet season, with several ravines and large boulders complicating access and transect placement. Although we were able to place transects in the northern parts of the Park, we abandoned attempts to do so in the south as it was too difficult to cut straight transects and potentially unsafe for nocturnal work. Future surveys in Lokobe National Park could consider point transect surveys, which would allow observers to use safe and accessible routes when navigating between points (Axel & Maurer, 2011).

In conclusion, Nosy Be harbours significant numbers of Claire's mouse lemur, an Endangered primate with a restricted and severely fragmented geographical range. To safeguard its long-term survival, we recommend: (1) a focus of conservation efforts in Nosy Be on the unprotected secondary and degraded forests, with consideration given to direct household payments for conservation and to ecotourism initiatives, and (2) future surveys of the mainland populations and their habitats, with a view to establishing additional protected areas and forest connectivity.

Author contributions Study design: all authors; fieldwork: LDM, HR, ESN; data analysis: LDM; writing: LDM, AMB.

Acknowledgements This research project was funded by Re:wild's Lemur Conservation Action Fund and the Australian National University's Primate Conservation Travel Grant, for which we are grateful. We thank the Ministère de l'Environnement et du Dèveloppement Durable for research permission and Dr Jean Freddy Ranaivoarisoa and the Mention Anthropobiologie et Développement Durable at the University of Antananarivo for their assistance obtaining the permit; the directors of Lokobe National Park, Gérard Bakarizafy and Landisoa Randimbison; the staff of Madagascar National Parks, Franck Tanasi Tombomanana, Omar Mohamad Assany, Said Mohamad Assany and Joël Tianjara; our guides from the Comités Locaux du Parc at Nosy Be, Udo-Heiss Jaozafy, Tavandra Mohibo Mamoudou, Avilaza, Kadra Odile, Alphonsine Tina and Mohammad; the landowners and village presidents of Marodoka, Antafondro, Ampasipohy and Ambatozavavy for permission to access and conduct our research on their lands; and two anonymous reviewers for their constructive comments.

Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards, was approved by the Australian National University's Animal Experimentation Ethics Committee (protocol #A2022/30) and was carried out in accordance with applicable national laws of Madagascar and Australia. Research permission was obtained from the Ministère de l'Environnement et du Développement Durable (#346/22/MEDD/SG/DGGE/DAPRNE/SCBE.Re).

Data availability The data that support the results of this study are available from the corresponding author upon reasonable request.

References

Agapow, P.-M., Bininda-Emonds, O.R.P., Crandall, K.A., Gittleman, J.L., Mace, G.M., Marshall, J.C. et al. (2004) The impact of species concept on biodiversity studies. *The Quarterly Review of Biology*, 79, 161–179.

Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. In *Second International Symposium on Information Theory* (eds B.N. Petrov & F. Csaki), pp. 267–281. Akadémiai Kiadó, Budapest, Hungary.

Anderson, D.R. (2001) The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin*, 29, 1294–1297.

Andreone, F., Guarino, F.M. & Randrianirina, J.E. (2005) Life history traits, age profile, and conservation of the panther chameleon, *Furcifer pardalis* (Cuvier 1829), at Nosy Be, NW Madagascar. *Tropical Zoology*, 18, 209–225.

Andriambeloson, J.B., Blanco, M.B., Andriantsalohimisantatra, A., Rivoharison, T.V., Walker, N., Birkinshaw, C. & Yoder, A.D. (2021) Living in tiny fragments: a glimpse at the ecology of Goodman's mouse lemurs (*Microcebus lehilahytsara*) in the relic forest of Ankafobe, Central Highlands, Madagascar. *Primates*, 62, 887–896.

Andriantompohavana, R., Zaonarivelo, J.R., Engberg, S.E., Randriamampionona, R., McGuire, S.M., Shore, G.D. et al. (2006) Mouse lemurs of northwestern Madagascar with a description of a new species at Lokobe Special Reserve. *Occasional Papers, Museum of Texas Tech University*, 259a, 1–23.

Axel, A.C. & Maurer, B.A. (2011) Lemurs in a complex landscape: mapping species density in subtropical dry forests of southwestern Madagascar using data at multiple levels. *American Journal of Primatology*, 73, 38–52.

Bessone, M., Kühl, H.S., Hohmann, G., Herbinger, I., N'Goran, K.P., Asanzi, P. et al. (2023) Assessing the effects of survey-inherent disturbance on primate detectability: recommendations for line transect distance sampling. *Primates*, 64, 107–121.

Birkinshaw, C.R. (1995) *The importance of the black lemur, Eulemur macaco (Lemuridae, Primates), for seed dispersal in Lokobe Forest, Madagascar*. PhD thesis. University College, London, UK.

Blanco, M., Dolch, R., Ganzhorn, J., Greene, L.K., Le Pors, B., Lewis, R. et al. (2020) *Microcebus mamiratra*. In *The IUCN Red List of Threatened Species* 2020. dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T136206A115581016.en.

Buckland, S.T. (2006) Point-transect surveys for songbirds: robust methodologies. *The Auk*, 123, 345–357.

Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993) *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, London, UK.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2001) *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. (2004) *Advanced Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, Oxford, UK.

Buckland, S.T., Marsden, S.J. & Green, R.E. (2008) Estimating bird abundance: making methods work. *Bird Conservation International*, 18, S91–S108.

Buckland, S.T., Plumptre, A.J., Thomas, L. & Rexstad, E.A. (2010) Design and analysis of line transect surveys for primates. *International Journal of Primatology*, 31, 833–847.

Burke, R.J. & Lehman, S.M. (2015) Edge effects on morphometrics and body mass in two sympatric species of mouse lemurs in Madagascar. *Folia Primatologica*, 85, 277–291.

Campbell, G., Head, J., Junker, J. & Nekaris, K.A.I. (2016) Primate abundance and distribution: background concepts and methods. In *An Introduction to Primate Conservation* (eds S. Wich & A.J. Marshall), pp. 79–110. Oxford University Press, Oxford, UK.

Cutler, E.B. (1965) Sipunculids of Madagascar. *Cahiers ORSTOM Océanographie*, 3, 51–63.

Dausmann, K.H. & Warnecke, L. (2016) Primate torpor expression: ghost of the climatic past. *Physiology*, 31, 398–408.

de Andrade, A.C., Marques, T.A. & Buckland, S.T. (2019) Spider monkeys, the misunderstood assumptions of distance sampling and the pitfalls of poor field design. *Biodiversity and Conservation*, 28, 4119–4121.

Deppe, A.M. (2020) Brown mouse lemurs (*Microcebus rufus*) may lack opportunities to learn about predator calls. *Folia Primatologica*, 91, 452–462.

Dolch, R., Ndriamiary, J., Ratolojanahary, T., Randrianasolo, M. & Ramanantenasoa, I.A. (2015) Improving livelihoods, training para-ecologists, enthralling children: earning trust for effective community-based biodiversity conservation in Andasibe, eastern Madagascar. *Madagascar Conservation & Development*, 10, 21–28.

Drever, C.R., Drever, M.C. & Sleep, D.J.H. (2012) Understanding rarity: a review of recent conceptual advances and implications for conservation of rare species. *The Forestry Chronicle*, 88, 165–175.

Elphick, C.S. (2008) How you count counts: the importance of methods research in applied ecology. *Journal of Applied Ecology*, 45, 1313–1320

Estrada, A., Garber, P.A., Gouveia, S., Fernández-Llamazares, Á, Ascensão, F., Fuentes, A. et al. (2022) Global importance of Indigenous peoples, their lands, and knowledge systems for saving the world's primates from extinction. *Science Advances*, 8, eabn2927.

Estrada, A., Garber, P.A., Mittermeier, R.A., Wich, S., Gouveia, S., Dobrovolski, R. et al. (2018) Primates in peril: the significance of Brazil, Madagascar, Indonesia and the Democratic Republic of the Congo for global primate conservation. *PeerJ*, 6, e4869.

Fredsted, T., Pertoldi, C., Olesen, J.M., Eberle, M. & Kappeler, P.M. (2004) Microgeographic heterogeneity in spatial distribution and mtDNA variability of gray mouse lemurs (*Microcebus murinus*, Primates: Cheirogaleidae). *Behavioral Ecology and Sociobiology*, 56, 393–403.

Gardner, C.J. (2016) Use of mangroves by lemurs. *International Journal of Primatology*, 37, 317–332.

Global Forest Watch (2023) *World Resources Institute*. globalforestwatch.org [accessed 1 September 2023].

Goodman, S.M. (1993) A reconnaissance of Ile Sainte Marie, Madagascar: the status of the forest, avifauna, lemurs and fruit bats. *Biological Conservation*, 65, 205–212.

Gould, L. & Andrianomena, P. (2015) Ring-tailed lemurs (*Lemur catta*), forest fragments, and community-level conservation in south-central Madagascar. *Primate Conservation*, 29, 67–73.

Gross-Camp, N.D., Martin, A., McGuire, S., Kebede, B. & Munyarukaza, J. (2012) Payments for ecosystem services in an African protected area: exploring issues of legitimacy, fairness, equity and effectiveness. *Oryx*, 46, 24–33.

Groves, C.P. (2005) The taxonomy of primates in the laboratory context. In *The Laboratory Primate* (ed. S. Wolfe-Coote), pp. 3–15. Elsevier Academic Press, San Diego, USA.

Groves, C.P. (2016) The taxonomy of Cheirogaleidae: an ever-expanding species list. In *The Dwarf and Mouse Lemurs of Madagascar: Biology, Behavior and Conservation Biogeography of the Cheirogaleidae* (eds S.M. Lehman, U. Radespiel & E. Zimmermann), pp. 21–52. Cambridge University Press, Cambridge, UK.

Hannah, L., Dave, R., Lowry, P.P., Andelman, S., Andrianarisata, M., Andriamaro, L. et al. (2008) Climate change adaptation for conservation in Madagascar. *Biology Letters*, 4, 590–594.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A. et al. (2013) High-resolution global maps of 21st-century forest cover change. *Science*, 342, 850–853.

Hasiniaina, A.F., Scheumann, M., Rina Evasoa, M., Braud, D., Rasoloharijaona, S., Randrianambinina, B. & Zimmermann, E. (2018) High frequency/ultrasonic communication in a Critically Endangered nocturnal primate, Claire's mouse lemur (*Microcebus mamiratra*). *American Journal of Primatology*, 80, e22866.

Hending, D. (2021) Environmental drivers of Cheirogaleidae population density: remarkable resilience of Madagascar's smallest lemurs to habitat degradation. *Ecology and Evolution*, 11, 5874–5891.

Hending, D., Andrianiaina, A., Rakotomalala, Z. & Cotton, S. (2018) The use of vanilla plantations by lemurs: encouraging findings for both lemur conservation and sustainable agroforestry in the Sava Region, northeast Madagascar. *International Journal of Primatology*, 39, 141–153.

Hending, D., Holderied, M., McCabe, G. & Cotton, S. (2022a) Effects of future climate change on the forests of Madagascar. *Ecosphere*, 13, e4017.

Hending, D., Randrianarison, H., Andriamavosoloarisoa, N.N.M., Ranohatra-Hending, C., McCabe, G., Cotton, S. & Holderied, M. (2022b) A new population of mouse lemurs (*Microcebus* sp.) from north-western Madagascar, with population size and density estimates. *Primate Conservation*, 36, 103–111.

Hending, D., Randrianarison, H., Andriamavosoloarisoa, N.N.M., Ranohatra-Hending, C., Solofondranohatra, J.S., Tongasoa, H.R. et al. (2023) Seasonal differences in the encounter rate of the fat-tailed dwarf lemur (*Cheirogaleus medius*) in the transitional forests of northwest Madagascar: implications for reliable population density assessment. *International Journal of Primatology*, 44, 482–498.

Hilário, R.R., Rodrigues, F.H.G., Chiarello, A.G. & Mourthé, I. (2012) Can roads be used as transects for primate population surveys? *Folia Primatologica*, 83, 47–55.

Hyde Roberts, S. & Daly, C. (2014) A search for the missing sportive lemurs of Nosy Komba, north west Madagascar. *Lemur News*, 18, 13–15.

Jędrusik, M.H. (2019) Nosy Be (Madagascar) and the neighbouring islands versus tourism development. *Miscellanea Geographica*, 23, 23–32.

Kappeler, P.M. & Rasoloarison, R.M. (2003) Microcebus mouse lemurs [Tsidy]. In *The Natural History of Madagascar* (eds S.M. Goodman & J.P. Benstead), pp. 1310–1315. University of Chicago Press, Chicago, USA.

Knoop, S., Chikhi, L. & Salmona, J. (2018) Mouse lemurs' use of degraded habitat: a review of the literature. *Lemur News*, 21, 20–31.

Kühl, H., Maisels, F., Ancrenaz, M. & Williamson, E.A. (2008). *Best Practice Guidelines for Surveys and Monitoring of Great Ape*

Populations. IUCN Species Survival Commission Primate Specialist Group, Gland, Switzerland.

Lahann, P. (2008) Habitat utilization of three sympatric cheirogaleid lemur species in a littoral rain forest of southeastern Madagascar. *International Journal of Primatology*, 29, 117–134.

Lehman, S.M., Rajaonson, A. & Day, S. (2006) Edge effects and their influence on lemur density and distribution in southeast Madagascar. *American Journal of Physical Anthropology*, 129, 232–241.

Louis, E.E., Engberg, S.E., Lei, R., Geng, H., Sommer, J.A., Randriamampionona, R. et al. (2006) Molecular and morphological analyses of the sportive lemurs (family Megaladapidae: genus *Lepilemur*) reveals 11 previously unrecognized species. Museum of Texas Tech University, *Special Publications*, 49, 1–47.

Louis, E.E., Engberg, S.E., McGuire, S.M., McCormick, M.J., Randriamampionona, R., Ranaivoarisoa, J.F. et al. (2008) Revision of the mouse lemurs, *Microcebus* (Primates, Lemuriformes), of northern and northwestern Madagascar with descriptions of two new species at Montagne d'Ambre National Park and Antafondro Classified Forest. *Primate Conservation*, 23, 19–38.

Markolf, M., Schäffler, L. & Kappeler, P. (2022) *Microcebus berthae*. In *The IUCN Red List of Threatened Species* 2022. dx.doi.org/10.2305/IUCN.UK.2022-1.RLTS.T41573A215090010.en.

Marques, T.A., Buckland, S.T., Borchers, D.L., Tosh, D. & McDonald, R.A. (2010) Point transect sampling along linear features. *Biometrics*, 66, 1247–1255.

McKelvey, K.S., Aubry, K.B. & Schwartz, M.K. (2008) Using anecdotal occurrence data for rare or elusive species: the illusion of reality and a call for evidentiary standards. *BioScience*, 58, 549–555.

Mekonnen, A., Fashing, P.J., Bekele, A. & Stenseth, N.C. (2020) Distribution and conservation status of Boutourlini's blue monkey (*Cercopithecus mitis boutourlinii*), a vulnerable subspecies endemic to western Ethiopia. *Primates*, 61, 785–796.

Meyler, S.V., Salmona, J., Ibouroi, M.T., Besolo, A., Rasolondraibe, E., Radespiel, U. et al. (2012) Density estimates of two endangered nocturnal lemur species from northern Madagascar: new results and a comparison of commonly used methods. *American Journal of Primatology*, 74, 414–422.

Milne, S. & Niesten, E. (2009) Direct payments for biodiversity conservation in developing countries: practical insights for design and implementation. *Oryx*, 43, 530–541.

Mittermeier, R.A., Louis Jr, E.E., Richardson, M.J., Schwitzer, C., Langrand, O., Rylands, A.B. et al. (2010) *Lemurs of Madagascar*. Conservation International, Arlington, USA.

Olivieri, G., Zimmermann, E., Randrianambinina, B., Rasoloharijaona, S., Rakotondravony, D., Guschanski, K. & Radespiel, U. (2007) The ever-increasing diversity in mouse lemurs: three new species in north and northwestern Madagascar. *Molecular Phylogenetics and Evolution*, 43, 309–327.

Ormsby, A. & Mannle, K. (2006) Ecotourism benefits and the role of local guides at Masoala National Park. Madagascar. *Journal of Sustainable Tourism*, 14, 271–287.

Plumptre, A.J. (2000) Monitoring mammal populations with line transect techniques in African forests. *Journal of Applied Ecology*, 37, 356–368.

Plumptre, A.J. & Cox, D. (2006) Counting primates for conservation: primate surveys in Uganda. *Primates*, 47, 65–73.

Plumptre, A.J., Sterling, E.J. & Buckland, S.T. (2013) Primate census and survey techniques. In *Primate Ecology and Conservation: A Handbook of Techniques* (eds E.J. Sterling, N. Bynam & M.E. Blair), pp. 10–26. Oxford University Press, Oxford, UK.

Potapov, P., Hansen, M.C., Pickens, A., Hernandez-Serna, A., Tyukavina, A., Turubanova, S. et al. (2022) The global 2000–2020 land cover and land use change dataset derived from the Landsat archive: first results. *Frontiers in Remote Sensing*, 3, 856903.

Poudyal, M., Jones, J.P.G., Rakotonarivo, O.S., Hockley, N., Gibbons, J.M., Mandimbiniaina, R. et al. (2018) Who bears the cost of forest conservation? *PeerJ*, 6, e5106.

Rakotondravony, R. & Radespiel, U. (2009) Varying patterns of coexistence of two mouse lemur species (*Microcebus ravelobensis* and *M. murinus*) in a heterogenous landscape. *American Journal of Primatology*, 71, 928–938.

Randrianambinina, B., Rasoloharijaona, S., Rakotondravony, R., Zimmermann, E. & Radespiel, U. (2010) Abundance and conservation status assessments of two newly described lemur species in northwestern Madagascar (*Microcebus danfossi*, *Lepilemur grewcockorum*). *Madagascar Conservation & Development*, 5, 95–102.

Rasoloarison, R.M., Weisrock, D.W., Yoder, A.D., Rakotondravony, D. & Kappeler, P.M. (2013) Two new species of mouse lemurs (Cheirogaleidae: *Microcebus*) from eastern Madagascar. *International Journal of Primatology*, 34, 455–469.

Rasolofoson, R.A., Ferraro, P.J., Jenkins, C.N. & Jones, J.P.G. (2015) Effectiveness of community forest management at reducing deforestation in Madagascar. *Biological Conservation*, 184, 271–277.

Razanatsoa, E., Andriantsaralaza, S., Holmes, S.M., Rakotonarivo, O.S., Ratsifandrihamanana, A.N., Randriamiharisoa, L. et al. (2021) Fostering local involvement for biodiversity conservation in tropical regions: lessons from Madagascar during the COVID-19 pandemic. *Biotropica*, 53, 994–1003.

Rendigs, A., Radespiel, U., Wrogemann, D. & Zimmermann, E. (2003) Relationship between microhabitat structure and distribution of mouse lemurs (*Microcebus* spp.) in northwestern Madagascar. *International Journal of Primatology*, 24, 47–64.

Ross, C. & Reeve, N. (2003) Survey and census methods: population distribution and density. In *Field and Laboratory Methods in Primatology: A Practical Guide* (eds J.M. Setchell & D.J. Curtis), pp. 91–109. Oxford University Press, Oxford, UK.

Rylands, A.B., Mittermeier, R.A. & Williamson, E.A. (2020) Primate conservation—new reports from the field. *Oryx*, 54, 751–752.

Rylands, A.B., Williamson, E.A., Hoffmann, M. & Mittermeier, R.A. (2008) Primate surveys and conservation assessments. *Oryx*, 42, 313–314.

Sawyer, R.M., Mena, H.E. & Donati, G. (2015) Habitat use, diet and sleeping site selection of *Lepilemur tymerlachsoni* in a disturbed forest of Nosy Be: preliminary observations. *Lemur News*, 19, 25–30.

Schäffler, L. & Kappeler, P.M. (2014) Distribution and abundance of the world's smallest primate, *Microcebus berthae*, in central western Madagascar. *International Journal of Primatology*, 35, 557–572.

Schüßler, D., Blanco, M.B., Salmona, J., Poelstra, J., Andriambeloson, J.B., Miller, A. et al. (2020) Ecology and morphology of mouse lemurs (*Microcebus* spp.) in a hotspot of microendemism in northeastern Madagascar, with the description of a new species. *American Journal of Primatology*, 82, e23180.

Schwitzer, C., Mittermeier, R.A., Davies, N., Johnson, S., Ratsimbazafy, J., Razafindramanana, J. et al. (2013) *Lemurs of Madagascar: A Strategy for Their Conservation 2013–2016*. IUCN Species Survival Commission Primate Specialist Group, Bristol Conservation and Science Foundation, and Conservation International, Bristol, UK.

Schwitzer, C., Mittermeier, R.A., Johnson, S.E., Donati, G., Irwin, M., Peacock, H. et al. (2014) Averting lemur extinctions amid Madagascar's political crisis. *Science*, 343, 842–843.

Setash, C.M., Zohdy, S., Gerber, B.D. & Karanewsky, C.J. (2017) A biogeographical perspective on the variation in mouse lemur density throughout Madagascar. *Mammal Review*, 47, 212–229.

Sgarlata, G.M., Salmona, J., Le Pors, B., Rasolondraibe, E., Jan, F., Ralantoharijaona, T. et al. (2019) Genetic and morphological diversity of mouse lemurs (*Microcebus* spp.) in northern Madagascar: the discovery of a putative new species? *American Journal of Primatology*, 81, e23070.

Sommerville, M., Milner-Gulland, E.J., Rahajaharison, M. & Jones, J.P.G. (2010) Impact of a community-based payment for environmental services intervention on forest use in Menabe, Madagascar. *Conservation Biology*, 24, 1488–1498.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L. et al. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47, 5–14.

Tinsman, J., Volampeno, S., Ganas-Swaray, J., Gann, D., Andrianirina, N., Chamizo, M. et al. (2022) Habitat use by the island lemurs of Nosy Be, Madagascar. *American Journal of Primatology*, 84, e23362.

Waters, S., Hansen, M.F., Setchell, J.M., Cheyne, S., Mittermeier, R.A., Ang, A. et al. (2023) *Responsible Primate Watching for Tourists*. IUCN Species Survival Commission Primate Specialist Group Section on Human–Primate Interactions, Gland, Switzerland.

Webber, A.D., Solofondranohatra, J.S., Razafindramoana, S., Fernández, D., Parker, C.A., Steer, M. et al. (2020) Lemurs in cacao: presence and abundance within the shade plantations of northern Madagascar. *Folia Primatologica*, 91, 96–107.

Wendland, K.J., Honzák, M., Portela, R., Vitale, B., Rubinoff, S. & Randrianarisoa, J. (2010) Targeting and implementing payments for ecosystem services: opportunities for bundling biodiversity conservation with carbon and water services in Madagascar. *Ecological Economics*, 69, 2093–2107.

Wright, P.C., Andriamihaja, B., King, S.J., Guerriero, J. & Hubbard, J. (2014) Lemurs and tourism in Ranomafana National Park, Madagascar: economic boom and other consequences. In *Primate Tourism: A Tool for Conservation?* (eds A. Russon & J. Wallis), pp. 123–146. Cambridge University Press, Cambridge, UK.