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REVIEW

A biogeographical perspective on the variation in mouse lemur density throughout Madagascar

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ABSTRACT

1. Madagascar is home to the smallest primates in the world, the mouse lemurs (*Microcebus* species). Twenty-four species of mouse lemur are currently recognised and are found in variable ecosystems, from dry forests and spiny deserts to humid forests. Due to their widespread distribution and the large number of sympatric species, mouse lemurs can be used as a model to understand the linkages among species richness, population density, and habitat. As all lemurs are threatened by habitat loss and fragmentation, this information can also be used to inform conservation management.

2. We hypothesise that on an island-wide scale, we will find higher population densities in western dry forests than in eastern humid forests because the western dry forests exhibit lower species richness, more sympatric habitat use, and lower resource stability than the eastern humid forests.

3. We conducted a literature review of population density estimates of known mouse lemur species, and used those data to conduct a meta-analysis and estimate overall average population density by geographic region.

4. Our findings suggest that mouse lemur species living in western dry forest generally exhibit higher densities than those in eastern humid forests. This may be partly explained by higher habitat fragmentation in western dry forests, where species co-occur, but is likely to be a function of the magnitude and variability in seasonally available resources in each forest type. Higher seasonality results in less constant food availability and lower levels of environmental predictability, fostering species capable of coping with environmental change and maintaining high densities throughout periods of resource paucity.

5. Our study highlights the importance of conducting *Microcebus* population density research that adheres to standardised methodological approaches. We point to the need for population density estimates for several species for which data are lacking. Such knowledge is important to assess the conservation status of these species, but also to enhance our ability to identify the macro-biogeographical and local ecological drivers of interspecific and intraspecific variability in population density.

INTRODUCTION

A fundamental component of ecology is understanding the spatial variation in community structure and density of animal populations (Andrewartha & Birch 1954). Spatial patterns of animal density are often influenced by a number of abiotic and biotic mechanisms; variation in climate and the connection between habitat type and resource availability are largely responsible for the variation in species distributions (Caughley 1977). However, biotic drivers such as interspecific and intraspecific competition also interact with abiotic factors to influence species distributions and diversity (Lehman et al. 2006, Brown & Yoder 2015, Herrera 2016). Understanding the relative influences of each often requires a substantial amount of information, but is essential to elucidate the driving factors of population dynamics and extinction risk in species of conservation concern (Johnson 1998, Davidson et al. 2009, Steffens & Lehman 2016).

On the island of Madagascar, a number of hypotheses have been asserted to explain the spatial variation in lemur species richness and population density. The differences and separation between eastern humid forests and western dry forests are often cited as leading factors driving these patterns (Humbert 1955, Cornet 1974, Du Puy & Moat 1996, Ganzhorn et al. 2006, Lehman & Fleagle 2006, Yoder & Heckman 2006, Muldoon & Goodman 2015). For arboreal lemur species, the central plateau of Madagascar represents a large barrier of unsuitable habitat, inhibiting dispersal and promoting speciation (Ganzhorn et al. 2006). Historical analyses of the biogeography of lemur species on Madagascar find higher levels of species richness in the eastern humid forests, where lemurs typically have larger geographic ranges than their western congeners (Ganzhorn et al. 2006, Lehman et al. 2016). However, the ecological drivers of the densities of those populations have been relatively unstudied (Ganzhorn et al. 2006, exception: Schäffler & Kappeler 2014). It has been suggested that lemur density is higher in the western dry forests than in the eastern humid forests (Ganzhorn et al. 1999), but little empirical evidence exists to justify this claim and few mechanisms have been established to explain it. The possible relationship between population density and species richness is often overlooked, but may provide some evidence for the large-scale biogeographic patterns observed in Madagascar's primate communities.

Muldoon and Goodman (2015) demonstrate that lemur diversity is an effective indicator of total non-primate mammal community diversity. Given that researchers are often limited to surveying a single forest or particular taxa (e.g. lemurs) due to financial and time constraints, it would have a number of implications for the conservation of a broad range of taxa if lemur population density was to act as a predictor of the population density of other taxa, allowing the selection of priority conservation areas and enabling more efficient assessments of regional biodiversity (Muldoon & Goodman 2015). Therefore, an understanding of the regional variation in lemur population density provides a foundation for future research and for understanding the biogeographic patterns of Madagascar as a whole. Population density and species richness are structured through community-level processes (e.g. food webs, niche divergence, and competition), which are multi-linked and complex (Lawton 1990). In general, community structure is thought to be directionally influenced from regional to local scales, suggesting that variation in population density and species richness is largely explained by and best understood via extrinsic biogeographical patterns, rather than by local processes (Cornell & Lawton 1992, Muldoon & Goodman 2015).

Average population density in the species present at the regional scale is influenced by many factors. In the simplest demographic terms, the basic biological requirements of a species must be met for a population to occupy an area. How readily the resources necessary to meet those requirements are available limits how many individuals of a species may exist in an area. The distribution of these resources, their interactions with abiotic factors, and interspecific and intraspecific competition often limit their availability across the landscape, increasing or decreasing population density along with it (Reed & Bidner 2004). Muldoon and Goodman (2015) found that Madagascar's mammalian community is primarily structured by major habitat type, designated by the amount of rainfall and vegetation structure. Habitat type coincides with the primary east–west humid–dry forest divide that is used to explain differences in lemur species richness (Ganzhorn et al. 2006, Yoder & Heckman 2006). In addition, anthropogenic change in landscape composition heavily influences the amount and distribution of available habitat (Harper et al. 2007). This is especially true in Madagascar, which retains only 10–60% of its original, pre-human forest cover (Lehman & Fleagle 2006, McConnell & Kull 2014). Understanding the patterns in population density and distribution throughout the remaining habitat may help focus conservation initiatives towards priority areas and elucidate the processes of speciation by which so many endemic species came to exist in Madagascar (Kamilar & Beaudrot 2013, Kamilar & Tecot 2016, Rakotoniaina et al. 2016).

Of the 108 lemur species inhabiting Madagascar, the most ubiquitous and adaptable are the mouse lemurs (*Microcebus* species). Mouse lemurs are small, arboreal, omnivorous primates that occupy diverse biotic communities in the ecoregions of the island (Kappeler & Rasoloarison 2003). They are nocturnal, seasonally breeding, solitary foragers that are long-lived for their body mass (30–100 g). As recently as 1993, they were thought to comprise only two species (*Microcebus murinus* and *Microcebus rufus*) split between the western and eastern forests of Madagascar (Yoder & Heckman 2006), respectively. Recent phylogenetic studies have redefined a number of populations as distinct species, increasing the number of extant mouse lemur species to 24 (Yoder et al. 2000, 2016, Olivieri et al. 2007, Radespiel et al. 2008, 2011, Rasoloarison et al. 2013, Zimmermann & Radespiel 2014, Hotaling et al. 2016). Many of these species are sympatric, their cryptic nature making field identification difficult, and their overlapping geographic ranges and niches giving rise to unique strategies of habitat partitioning (Fig. 1; Schäffler et al. 2015, Steffens & Lehman 2016). Mouse lemurs are even found in areas heavily affected by human activity, including secondary forests, agricultural lands, and highly disturbed forest edges (Lehman et al. 2006, Radespiel et al. 2006, Herrera et al. 2011). Furthermore, mouse lemurs have not only been found exhibiting high densities in these degraded habitats (Schäffler et al. 2015) but also crowding into favourable habitat patches used by sympatric species when they have no other choice (Steffens & Lehman 2016). Given their flexibility in adapting to heterogeneous environments and conditions, we expect that the higher levels of habitat fragmentation and human activity in the western dry forests (Harper et al. 2007) could lead to higher densities of mouse lemurs there than in the eastern humid forests.

We aim to characterise mouse lemur population density by broad biogeographic region (forest type), thus evaluating whether observed site-level density scales up to climatic region and whether population density corresponds to fundamental patterns of community structuring, similar to species richness (Muldoon & Goodman 2015); the available information relating to fine-scale variation in mouse lemur density is summarised by Steffens and Lehman (2016). We hypothesise that because the western dry forests exhibit lower species richness, more sympatric habitat use, and lower resource stability than eastern humid forests, there will be higher population densities of mouse lemur species in the western dry forests than in the eastern humid forests (Table 1). However, we expect local perturbations to cause variation in mouse lemur densities in both western dry forests and eastern humid forests, such that some sites will be surveyed in the western dry forest at a time when they are in fact lower in mouse lemur population density than sites in the eastern humid forest. In spite of this, we predict that the average population density of mouse lemur species in the western dry forest will be greater than the average population density of mouse lemur species in the eastern humid forest. Therefore, unless mean regional differences are large or within-region variation is small, we expect some similarity in estimated regional average population density.

METHODS

Literature review

We sought to describe the breadth of published research focused on the population density of *Microcebus* species. To do so, we conducted two searches in the ISI Web of Science database, using the following keywords: (1) '*Microcebus*' or 'mouse lemur' and 'abundance' or 'density'; (2) '*Microcebus*' or 'mouse lemur' and 'population'. The searches were conducted on 10 December 2016 and 5 January 2017. Many of the studies identified did not pertain to mouse lemur population density estimates and were removed. Studies in which original research was used to estimate *Microcebus* density or abundance in a specific area are catalogued in Table 2. This literature search missed a large amount of original research, especially field surveys, on *Microcebus* populations published in *Lemur News*, the newsletter of the Madagascar Section of the International Union for Conservation of Nature's Species Survival Commission (IUCN/SSC) Primate Specialist Group. We therefore checked all volumes of *Lemur News* for reports of mouse lemur abundance or density, and included these values in Table 2.

We excluded studies in which population indices, such as encounter rates (e.g. observed species encounters per km of transect), were estimated rather than density. In addition, we noted whether density was estimated by using a modelling or design framework to account for the proportion of the population that was undetected in the survey area. Robust estimation of abundance or density of wild animal populations almost always requires the consideration that individuals within a sampling area will go undetected (Nichols 1992, Anderson 2001). Commonly in wildlife studies, estimation is done using capture–recapture or distance sampling (Malone et al. 2013, Schäffler & Kappeler 2014; see Appendix S1).

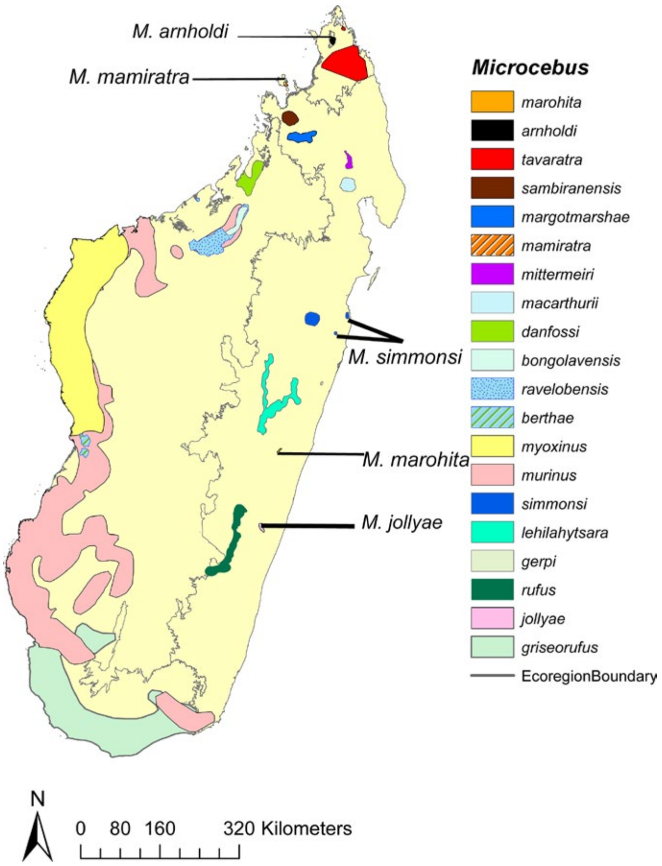

Fig. 1. Geographical ranges in Madagascar, as given by the IUCN, for the *Microcebus* species. Excludes *M. boraha, M. ganzhorni, M. manitatra,* and *M. tanosi*.

Table 1. Relative metrics of factors influencing mouse lemur (*Microcebus* species) population density in Madagascar by ecoregion. Arrows indicate the effect of each characteristic within that region relative to the other region

Characteristic	Western Dry Forests	Eastern Humid Forests
Species richness[1–4]	↓	↑
Seasonality[1,5,6,7]	↑	↓
Number of sympatric species[8,9]	↑	↓
Geographic distribution of lemur species[1,2]	↓	↑
Mouse lemurs use torpor or hibernation[10–14]	↑	↓
Net influence on population density	↑	↓

[1] Ganzhorn et al. (2006), [2] Lehman et al. (2016), [3] Yoder et al. (2000), [4] Muldoon and Goodman (2015), [5] Blanco et al. (2015), [6] Dausmann (2014), [7] Vuarin et al. (2013), [8] Zimmerman et al. (1998), [9] Schmid and Kappeler (1994), [10] Atsalis (1999), [11] Karanewsky (2013), [12] Canale et al. (2012), [13] Karanewsky et al. (2015), [14] Nowack and Dausmann (2015).

For studies conducted prior to recent species designations, we updated the species in the study to reflect the most recent taxonomy if possible. For example, populations of what were previously thought to be *Microcebus murinus* in southeast Madagascar were designated *Microcebus ganzhorni*, *Microcebus tanosi, Microcebus griseorufus*, or *Microcebus manitatra* based on the location of the study, or were analysed as part of a conglomerate group of these species if their species designation could not be identified with relative certainty. We then classified each estimate of density by region, assigning them to either eastern humid forest or western dry forest to allow the estimation of regional density differences.

Species and regional density estimates

We fit a hierarchical Bayesian regression model using the population density estimates from the literature, where mouse lemur density, y_{isr}, indicates the density value i for species s, which belongs to region r (western dry forest or eastern humid forest; Fig. 2). There are 24 currently recognised mouse lemur species; we categorised eight of those species as western dry forest inhabitants and 16 as eastern humid forest species, based on the geographical ranges currently provided by the IUCN (Anonymous 2016). For studies that provided only a range of density estimates, we used the midpoint of that range as the density estimate

Table 2. Published estimates of mouse lemur population density by species and location from the literature search

Species	Location	Region of Madagascar	Dry Forest or Humid Forest	Individuals per ha	Reference	Sampling Method	Detection Accounted For?	Season of Field Work	Wet/Dry Season	Day or Night
Microcebus berthae	Ambadira – dry season	Central west	Dry Forest	0.95	Schäffler and Kappeler (2014)	Transect methods	Y (Program Distance)	June–September	Dry	Night
M. berthae	Ambadira – rainy season	Central west	Dry Forest	1.8	Schäffler and Kappeler (2014)	Transect methods	Y (Program Distance)	June–September	Wet	Night
M. berthae	Ambadira corridor – dry season	Central west	Dry Forest	0.69	Schäffler and Kappeler (2014)	Transect methods	Y (Program Distance)	June–September	Dry	Night
M. berthae	Ambadira corridor – rainy season	Central west	Dry Forest	0.34	Schäffler and Kappeler (2014)	Transect methods	Y (Program Distance)	June–September	Wet	Night
M. berthae	Kirindy – dry season	Central west	Dry Forest	0.55	Schäffler and Kappeler (2014)	Transect methods	Y (Program Distance)	June–September	Dry	Night
M. berthae	Kirindy – rainy season	Central west	Dry Forest	0.57	Schäffler and Kappeler (2014)	Transect methods	Y (Program Distance)	June–September	Wet	Night
M. berthae	Menabe	Southwest	Dry Forest	1 (1.19–0.80)	Schwab and Ganzhorn (2004)	Mark–Recapture (Sherman trap grid)	N	All (once a month for 13 months)	Both	Night
Microcebus griseorufus	Tongaenoro	Southwest	Dry Forest	10	Ralison (2006a)	Transect methods	N	February–April	Wet	Both
M. griseorufus	Tsimanampetsotsa	Southwest	Dry Forest	11.8	Bohr et al. (2011)	Mark–Recapture (Sherman trap grid)	N	April and July	Both	Night
M. griseorufus	Tsimanampetsotsa	Southwest	Dry Forest	4	Bohr et al. (2011)	Mark–Recapture (Sherman trap grid)	N	April and July	Both	Night
Microcebus murinus and *M. griseorufus*	Antabore	Southwest	Dry Forest	3	Ralison (2006a)	Transect methods	N	Feb–April	Wet	Both
M. murinus and *M. griseorufus*	Fiherenana-Manombo Complex	Southwest	Dry Forest	10.78	Gardner et al. (2009)	Transect methods	N	June–September	Dry	Both
M. murinus and *M. griseorufus*	Fiherenana-Manombo Complex	Southwest	Dry Forest	5.46	Gardner et al. (2009)	Transect methods	N	June–September	Dry	Both
M. murinus and *M. griseorufus*	Vombositse	Southwest	Dry Forest	2.73	Ralison (2006a)	Transect methods	N	February–April	Wet	Both

Table 2 *(Continued)*

Species	Location	Region of Madagascar	Dry Forest or Humid Forest	Individuals per ha	Reference	Sampling Method	Detection Accounted For?	Season of Field Work	Wet/Dry Season	Day or Night
M. murinus	Bemaraha	Central west	Dry Forest	2.2–2.8	Ausilio and Raveloanrinoro (1998)	Unknown	N	Unknown		Unknown
M. murinus	Anjamena	Northwest	Dry Forest	0.85 ± 0.02	Muller et al. (2000)	Transect methods	N	April–August	Both	Both
M. murinus	Ankarafantsika	Northwest	Dry Forest	0.80–1.20	Radespiel et al. (2001)	Mark–Recapture (Sherman trap grid)	N	August–October	Dry	Night
M. murinus	Ankarafantsika	Northwest	Dry Forest	0–2.23	Rakotondravony and Radespiel (2009)	Transect methods	Y (relative density given effective strip width)	4–5 Weeks during dry season	Dry	Night
M. murinus	Ankarafantsika	Northwest	Dry Forest	0.29–5.28	Rakotondravony and Radespiel (2009)	Transect methods	Y (relative density given effective strip width)	4–5 Weeks during dry season	Dry	Night
M. murinus	Ankarafantsika	Northwest	Dry Forest	0.86–4.76	Rakotondravony and Radespiel (2009)	Transect methods	Y (relative density given effective strip width)	4–5 Weeks during dry season	Dry	Night
M. murinus	Ankarafantsika	Northwest	Dry Forest	1.67	Radespiel (2000)	Mark–Recapture (Sherman trap grid)	N	August–October	Dry	Night
M. murinus	Morondava	Central west	Dry Forest	3.43	Fleagle et al. (1999)					
M. murinus	Ankarafantsika	Northwest	Dry Forest	1.05 ± 0.83	Steffens and Lehman (2016)	Transect Methods	N	June–November	Dry	Night
M. murinus and *M. myoxinus*	Andranomanitsy Forest	Northwest	Dry Forest	6.67	Ralison (2007)	Transect methods	N	October	Dry	Both
M. murinus and *M. myoxinus*	Anjamena	Northwest	Dry Forest	0.85 ± 0.02	Muller et al. (2000)	Transect methods	N	April–August	Both	Both
Microcebus danfossi	Between Sofia River and Maevarano River	Northwest	Dry Forest	2.2–5.0	Randrianambinina et al. (2010)	Transect methods	N	May–December	Both	Night

Table 2 *(Continued)*

Species	Location	Region of Madagascar	Dry Forest or Humid Forest	Individuals per ha	Reference	Sampling Method	Detection Accounted For?	Season of Field Work	Wet/Dry Season	Day or Night
Microcebus ravelobensis	Ankarafantsika	Northwest	Dry Forest	0.94 ± 0.77	Steffens and Lehman (2016)	Transect Methods	N	June–November	Dry	Night
M. ravelobensis	Ankarafantsika	Northwest	Dry Forest	7.3–10.5	Weidt et al. (2004)	Mark–Recapture (Sherman trap grid)	Y (MNA and Jolly-Seber for open populations)	May–October	Dry	Night
M. ravelobensis	Ankarafantsika	Northwest	Dry Forest	0.37–9.38	Rakotondravony and Radespiel (2009)	Transect methods	Y (relative density given effective strip width)	4–5 Weeks during dry season	Dry	Night
M. ravelobensis	Ankarafantsika	Northwest	Dry Forest	0–4.41	Rakotondravony and Radespiel (2009)	Transect methods	Y (relative density given effective strip width)	4–5 Weeks during dry season	Dry	Night
M. ravelobensis	Ankarafantsika	Northwest	Dry Forest	0–2.44	Rakotondravony and Radespiel (2009)	Transect methods	Y (relative density given effective strip width)	4–5 Weeks during dry season	Dry	Night
Microcebus tavaratra	Ankarana	Northwest	Humid Forest	0.67–2.20	Hawkins et al. (1990)	Transect methods	N	October–November	Wet	Both
M. tavaratra	Bekaraoka	Northwest	Humid Forest	0.82 ± 0.1	Meyler et al. (2012)	Transect methods	N	July–August	Dry	Night
M. tavaratra	Solaniampilana	Northwest	Humid Forest	1.79 ± 0.27	Meyler et al. (2012)	Transect methods	N	July–August	Dry	Night
M. ganzhorni or *M. manitatra*	Petriky	Southeast	Humid Forest	6.53	Malone et al. (2013)*	Transect methods	Y (Program Distance)	April–July	Both	Night
M. ganzhorni or *M. manitatra*	Petriky	Southeast	Humid Forest	4.75	Malone et al. (2013)*	Transect methods	Y (Program Distance)	April–July	Both	Night
M. ganzhorni	Mandena	Southeast	Humid Forest	6.8	Norscia unpublished data; see Norscia et al. (2006)*					
M. ganzhorni or *M. tanosi*	Ste Luce	Southeast	Humid Forest	3	Donati (2002), Norscia et al. (2006)*	Transect methods	N	December	Wet	Both

Table 2 *(Continued)*

Species	Location	Region of Madagascar	Dry Forest or Humid Forest	Individuals per ha	Reference	Sampling Method	Detection Accounted For?	Season of Field Work	Wet/Dry Season	Day or Night
M. ganzhorni, M. tanosi, or *M. griseorufus*	Anka	Southeast	Humid Forest	3.16	Norscia et al. (2006)*	Transect methods	N	January	Wet	Both
M. ganzhorni, M. tanosi, or *M. griseorufus*	Mahavelo	Southeast	Humid Forest	2.21	Ralison (2006a)*	Transect methods	N	February–April	Wet	Both
M. ganzhorni, M. tanosi, or *M. griseorufus*	Vohondava	Southeast	Humid Forest	10.46–10.77	Ralison (2006a)*	Transect methods	N	February–April	Wet	Both
M. ganzhorni, M. tanosi, or *M. griseorufus*	Andohahela	Southeast	Humid Forest	1.41	Rasoarimanana (2005), Feistner and Schmid (1999)*	Transect methods	N	October–December	Wet	Both
M. ganzhorni, M. tanosi, or *M. griseorufus*	Andrendahy	Southeast	Humid Forest	5.69	Ralison (2006a)*	Transect methods	N	February–April	Wet	Both
M. griseorufus	Berenty	Southeast	Humid Forest	2.2–4.3	Génin (2008)	Mark–Recapture (Sherman trap grid)	N	All	Both	Night
Microcebus rufus	Andringitra	Southeast	Humid Forest	0.73–3.97	Sterling and Ramaroson (1996)	Transect methods	N	September–October	Dry	Both
M. rufus	Beakora Forest	Southeast	Humid Forest	0.06	Rabeson et al. (2006)	Transect methods	N	January–February	Wet	Both
M. rufus	Ranomafana	Southeast	Humid Forest	0.23 ± 0.04	Wright et al. (2012)	Transect methods	Unknown	2004–2009	Unknown	Unknown
M. rufus	Ranomafana	Southeast	Humid Forest	0.164	Herrera et al. (2011)	Transect methods	N	June–July	Dry	Both
M. rufus	Ranomafana	Southeast	Humid Forest	0.43	Zohdy et al. unpublished data; see Appendix S1)	Spatial Capture–Recapture	Y	October–November	Dry	Night

Table 2 *(Continued)*

Species	Location	Region of Madagascar	Dry Forest or Humid Forest	Individuals per ha	Reference	Sampling Method	Detection Accounted For?	Season of Field Work	Wet/Dry Season	Day or Night
M. rufus	Ranomafana	Southeast	Humid Forest	0.65	Zohdy et al. unpublished data; see Appendix S1)	Spatial Capture–Recapture	Y	October–November	Dry	Night
M. rufus	Ranomafana	Southeast	Humid Forest	1.1	Reed (1999)					
M. rufus	Vohibola III	Southeast	Humid Forest	0.24 ± 0.06	Lehman et al. (2006)	Transect methods	N	June–October and May–November	Both	Both
M. rufus	Vohibola III	Southeast	Humid Forest	0.12 ± 0.08	Lehman et al. (2006)	Transect methods	N	June–October and May–November	Both	Both
M. rufus	Vohibola III	Southeast	Humid Forest	0.48 ± 0.09	Lehman et al. (2006)	Transect methods	N	June–October and May–November	Both	Both
Microcebus mittermeiri	Marojejy	Northeast	Humid Forest	0.07–0.24	Sterling and McFadden (2000)*	Transect methods	N	October–November	Dry	Both
M. simmonsi	Réserve Spéciale de Marotandrano	Northeast	Humid Forest	3.75	Ralison (2006b)*	Transect methods	N	November	Dry	Both
Microcebus spp.	Makira Forest Block	Northeast	Humid Forest	0–1.23	Rasolofoson et al. (2007)	Transect methods	N	Unknown	Unknown	Both
Microcebus spp. and *Allocebus* spp.	Makira-Masoala	Northeast	Humid Forest	0.391	Murphy et al. (2016)	Transect methods	Y (Program Distance)	All	Both	Both
Microcebus spp.	Iketra	Northeast	Humid Forest	0.39 ± 0.09	Sterling and Rakotoarison (1998)*	Transect methods	N	January–February	Wet	Both

*Studies in which species' names were changed to reflect current taxonomy. MNA = minimum number alive.

$$\begin{array}{ll}
\text{Data process:} & \log(y_{\mathrm{isr}}) \sim \mathrm{Normal}(\mu_{\mathrm{isr}}, \sigma) \\
\text{Species-level process:} & \mu_{\mathrm{isr}} = \alpha_{\mathrm{sr}} + w_i' \beta_1 \\
\text{Region-level process:} & \alpha_{\mathrm{sr}} \sim \begin{cases} \mathrm{Normal}(\mu_{\mathrm{Dry}}, \tau_{\mathrm{Dry}}), & \text{when } r = 1, \text{ Dry Forest} \\ \mathrm{Normal}(\mu_{\mathrm{Humid}}, \tau_{\mathrm{Humid}}), & \text{when } r = 2, \text{ Humid Forest} \end{cases} \\
\text{Priors:} & \sigma \sim \mathrm{Uniform}(0, 10),\ \tau_{.} \sim \mathrm{Uniform}(0,10),\ \mu_{.} \sim \mathrm{Normal}(0, 100)
\end{array}$$

Fig. 2. A hierarchical Bayesian model to estimate biogeographic-regional population density in *Microcebus* species.

(i) for that species (s). Our model is multi-level to allow simultaneous inference of mean-level species densities (μ) and regional densities (α), which properly accounts for species-level variation. We also include a covariate to evaluate the effect of sampling method (w), which indicates whether the density was estimated while accounting for imperfect detection of individuals. Regardless of species, we expect higher densities when accounting for individuals that went undetected in the sample or when accounting for the area surveyed (e.g. using distance sampling methods); this hypothesis would be supported if β_1 was found to be greater than zero (Fig. 2). Due to sample size constraints, we could not evaluate regional differences in density in different seasons. Because we are ignoring seasonal variation, we expect to find more similarity in regional density estimates, but we still expect differences to exist due to major climatic differences and levels of habitat heterogeneity between the regions.

Bayesian modelling provides a coherent way to model positive support data, such as animal densities, using the log transformation (Stow et al. 2006). The model was fit in the R programming language using the R package 'rjags', which interfaces with the program JAGS (Plummer 2013). Parameters were estimated using Markov chain Monte Carlo methods, simulating samples from the full conditional distributions. We initialised five independent chains with random starting values; each chain was run for 20000 iterations. We assessed convergence visually by examining trace plots and using the Gelman-Rubin statistic (Gelman & Rubin 1992); values below 1.1 indicate parameter convergence. We summarised posterior distributions using the posterior mode (i.e. the most probable value) as our measure of central tendency, and calculated 95% highest posterior density intervals (HPDI) as measures of variation. To evaluate the hypothesis that mouse lemur density is, on average, higher in the western dry forest than in the eastern humid forest, we compared the regional posterior probability distributions; specifically, we calculated P(Dry Forest > Humid Forest) as $\frac{\sum((\mu_{Dry}-\mu_{\mathrm{Humid}})>0)}{20000}$. If regional distributions were exactly the same, the value would be 0.5; higher values would indicate support for the hypothesis, and a value of 1 would indicate that the two distributions do not overlap at all and are therefore completely different.

RESULTS

Literature review

Our search resulted in 33 studies that addressed some aspect of the population density of mouse lemurs. These studies provided 59 estimates of density, of which 29 were in western dry forests, 24 in eastern humid forests, and six in spiny forest. Estimates of population density from the spiny forest region in the south-eastern corner of Madagascar were excluded from the analysis due to sample size constraints and a lack of research coverage within this area. Current estimates of mouse lemur density are the result of multiple different sampling methodologies and taxonomies, spanning a range of several decades. Density estimates remain unavailable for 11 of the 24 mouse lemur species (*Microcebus bongolavensis, Microcebus jollyae, Microcebus lehilahytsara, Microcebus mamiratra, Microcebus sambiranensis, Microcebus marohita, Microcebus tanosi, Microcebus gerpi, Microcebus manitatra, Microcebus boraha,* and *Microcebus ganzhorni*), and interpretation is made difficult by the fact that more than 20 species were recognised since the year 2000. Nine of the density estimates from the south-eastern corner of Madagascar could not be identified to the species level based on updated taxonomy, requiring that we analyse them together (see Fig. 3, Table 3). One or more density estimates exist for nine species of mouse lemur, regardless of taxonomy used. Sampling methodology, whether or not density estimates accounted for probability of detection, season of sampling, and time of day that sampling occurred are reported for comparison (Table 2). In the majority of the population density estimates (46 estimates of the resulting 59), transects were used to estimate mouse lemur density as opposed to mark–recapture techniques, and for only 16 of the 59 estimates, the probability of detection was accounted for when calculating density. In three studies, individuals were identified to genus only, and so they were excluded from the Bayesian regression analysis.

Spatial variation in mouse lemur density

Our findings reveal that population density in *Microcebus* species varies from 0.06 individuals of *Microcebus rufus*

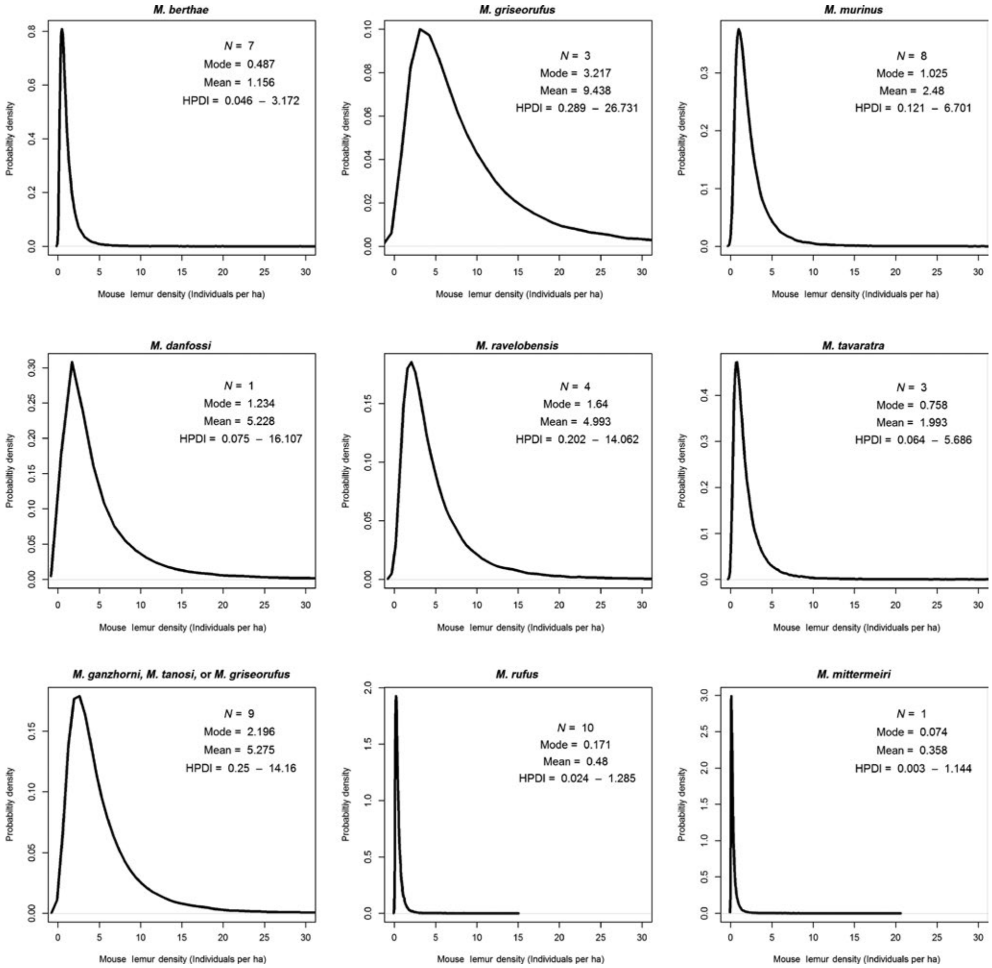

Fig. 3. Posterior distributions of population density estimates by species of *Microcebus* lemur in Madagascar.

Table 3. Posterior modes and lower and upper 95% highest posterior density intervals (HPDI) of the average population density of mouse lemurs (*Microcebus* species) from published results

Species	Most probable average population density	Lower 95% HPDI	Upper 95% HPDI
M. berthae	0.476	0.047	3.244
M. griseorufus	3.006	0.227	26.431
M. murinus	0.973	0.092	6.357
M. danfossi	1.308	0.090	16.029
M. ravelobensis	1.433	0.186	10.784
M. tavaratra	0.744	0.060	5.829
M. ganzhorni, M. tanosi, or M. griseorufus	2.187	0.209	14.455
M. rufus	0.225	0.018	1.316
M. mittermeiri	0.074	0.003	1.203

per hectare in the eastern humid forest of Beakora to 11.8 individuals of *Microcebus griseorufus* per hectare in the western dry forests of Tsimanampetsotsa National Park. The mode of the regional density distribution for western dry forests resulting from the Bayesian regression was 2.00 (HPDI = 3.01e-03 – 6.87) individuals per hectare, whereas the mode of the density distribution for eastern humid forests was 0.446 (HPDI = 1.32e-06 – 6.16) individuals per hectare. This results in a 0.808 probability that western dry forest regional estimates are greater than eastern humid forest regional estimates, indicating support for our hypothesis. The species-level density estimates resulting from the Bayesian regression ranged from 0.07 (*Microcebus mittermeiri*) to 3.21 (*Microcebus griseorufus*) individuals per hectare (Table 3, Fig. 3). When including a covariate for sampling method (w), the regression coefficient (β_1) was 0.237 (HPDI = −0.4284 to 0.7806), indicating no evidence that the type of sampling methodology affected a study's density estimate.

DISCUSSION

Spatial variation in density

Our findings represent the first empirical evidence of large-scale regional variation in mouse lemur density in Madagascar. While the posterior distributions describing regional population density do overlap, the posterior modes (highest probability values) are quite different and the majority (0.81 probability) of evidence suggests that generally, mouse lemur densities are higher in the western dry forests than in the eastern humid forests (Fig. 4). Appreciable differences in dominant habitat structure and climatic events in eastern humid forests and western dry forests generate very different mammalian community structures, and therefore densities (Ganzhorn et al. 1997, Muldoon & Goodman 2015, Kamilar & Tecot 2016). We expect that for species whose niches and geographic ranges overlap in part or in whole, resources become more limited and each species exists at a lower density than it would alone. However, sympatric species have been shown to coexist by expanding their ranges during the dry season (when resources are limited) to use both degraded and non-degraded habitat (Schäffler et al. 2015). This suggests that species with higher ecological flexibility that are able to exploit a variety of habitats might be capable of existing in higher densities, even when little non-degraded habitat remains.

As habitat becomes more fragmented and fragments decline in size, Island Biogeography Theory states that densities of all species should decline as well (MacArthur & Wilson 1967, Chiarello & de Melo 2001, Steffens & Lehman 2016). However, this may not be the case in a group of species that are known to tolerate edge effects and utilise degraded habitat. Steffens and Lehman (2016) observed a positive relationship between density of the sympatric species *Microcebus murinus* and *Microcebus ravelobensis* in a fragmented landscape, contrasting with the findings of Rakotondravony and Radespiel (2009), who found a negative relationship between the densities of the two species in continuous forest. This suggests that the more fragmented the landscape, the more crowded the fragments become, regardless of what interspecific interactions would have taken place in a more pristine environment. Coincidentally, Harper et al. (2007) showed that a drastic increase in fragmentation occurred throughout the western dry forests primarily from the 1950s to the 1990s, and found that "dry forests were by all measures the most fragmented forest type throughout the study period, and…fragmentation of the humid forest increased only slightly from the 1970s–c. 2000." While all of the studies from which we obtained density estimates took place after 1990, higher rates of fragmentation in the west probably play a role in the higher regional density of mouse lemurs we observed. In addition, the twofold

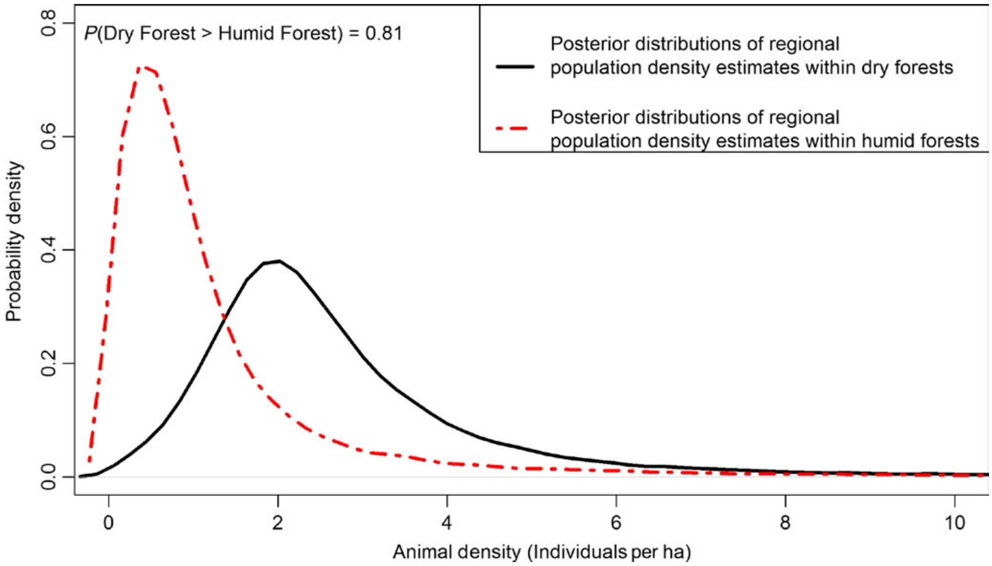

Fig. 4. Posterior distributions of regional population density estimates. [Colour figure can be viewed at wileyonlinelibrary.com]

difference in mouse lemur species richness from the east to the west coincides with our current understanding of species richness–density relationships. At the regional scale, we saw lower population density in areas of higher species richness, potentially caused by niche and geographic range overlap. Although we do not fully understand the extent of mouse lemurs' geographic range overlap, given the recent updates to their taxonomy we expect that habitat partitioning will probably play a larger role in order for species with overlapping niches to coexist as more habitat becomes degraded across Madagascar, and is already likely to be an important driver of population density (Schäffler et al. 2015).

Population densities in mouse lemur species are likely to be driven largely by food availability and climate, but life-history theory may also offer clues as to how many individuals an area can support. The eastern humid forests are characterised by heavier precipitation (1500–6000 mm per year vs. 500–2000 mm per year in the western dry forests; Ganzhorn et al. 2006), by less abrupt habitat zones than exist in the western dry forests (Goodman & Ganzhorn 2003), and by lower seasonality, which results in more constant food availability and higher levels of environmental predictability (Table 1; Blanco et al. 2015). Less predictable habitats characteristic of western dry forests tend to favour species with faster life-history strategies that exhibit high levels of ecological flexibility (Dausmann 2014, Vuarin & Henry 2014). Mouse lemurs that evolved in these unpredictable environments display a fast life-history strategy; they have evolved to coincide their reproduction with pulses in resources, and have the ability to cope with limited resources for extended periods of time (Speakman 2008, Canale et al. 2012). There is evidence that mouse lemurs in the western dry forests hibernate (Schmid & Kappeler 1998) and are therefore more protected from predators and other extrinsic mortality factors than lemurs that do not hibernate (Karanewsky & Wright 2015). While there is also some evidence to support the idea that eastern humid forest mouse lemurs use torpor (Atsalis 1999, Karanewsky 2013, Dausmann 2014, Karanewsky & Wright 2015), there has not yet been conclusive evidence of true hibernation in eastern mouse lemurs. Given this tendency towards torpor and seasonal hibernation, it would appear that mouse lemurs are adapted to a heterogeneous environment (Canale et al. 2012). This energy-conserving adaptation, more evidenced in western mouse lemur species, may also result in higher densities of mouse lemurs being supported (Schmid & Kappeler 1998). Rather than exhibiting a 'boom and bust' pattern of population density characteristic of other fast-lived species (Schmidt & Ostfeld 2003), mouse lemurs may be capable of coping with extreme conditions for extended periods of time and can therefore forego the 'bust', maintaining relatively high densities.

Our estimates of regional mouse lemur density illustrate a large-scale discrepancy that is likely to be driven by differences in habitat, species richness, and physiology between east and west. We were unable to account for seasonality in our analysis, however, which is likely to influence the small-scale density estimates underlying our regional estimates (Lehman 2009). Studies carried out at different times of the year might have resulted in extremely different estimates of mouse lemur density. For example, Schäffler and Kappeler (2014) estimated the density of *Microcebus berthae* in Ambadira to be 0.95 individuals per hectare during the dry season and 1.8 individuals per hectare during the rainy season. Surveys done during the hottest period of the dry season are difficult to compare to those done during the hottest period of the rainy season, given the effects of precipitation on primate density (Pinto et al. 2009). In addition, lemur density is likely to be affected by external factors not within the scope of our analysis, including the density patterns of other primate and non-primate taxa, the ecological history of a site, the human history of a site, and the methodological approach in a given study. The influences we were not able to account for have the potential to confuse large-scale effects of region on density estimates, and warrant further study to ascertain how these factors scale up to affect mouse lemur density at the regional scale. Our results are limited by the fact that they absorb this seasonal variation and we caution that they should be interpreted as such.

Conservation implications

As anthropogenic disturbance continues to alter the habitat structure throughout Madagascar, a deeper understanding of how various levels of disturbance affect mouse lemur density, demography, and behaviour will be imperative. Since the 1950s, the humid and dry forests of Madagascar have lost 43% and 41% of their area, respectively (Harper et al. 2007). These rates of deforestation have increased steadily over time (Harper et al. 2007), and without drastic intervention or targeted restoration efforts, it is likely that extinction rates of many endemic species will also increase. In the eastern humid forests, fragmentation is responsible for an increase in abundance of exotic or invasive species (e.g. *Rattus rattus*; Ramanamanjato & Ganzhorn 2001) and geospatial modelling predicts a large number of lemur range contractions in the coming decades (Brown & Yoder 2015). These range changes may influence the densities of individual species as well as interspecific interactions, resulting in novel population dynamics. Our results suggest that managers should target areas of high species richness (e.g. the eastern humid forest of Madagascar) as potential restoration sites. Given their inclination towards lower mouse lemur density, they are already at higher risk for species extinction, and preserved or restored habitat in these areas has the potential to protect a higher number of species than it does in areas of lower species richness and higher population density (such as the western dry forest of Madagascar).

Methodological impacts and suggestions

A significant result highlighted by this research was the necessity for more rigorous sampling protocols when density estimates are the ultimate goal. We were surprised to find that whether researchers accounted for the undetected proportion of the population when estimating density did not seem to have a general effect on producing higher or lower density estimates. However, we still caution researchers to consider more robust sampling designs and modelling approaches when estimating animal abundance or density. For example, relatively recent advances in modelling methodology of distance sampling data allow for more robust estimates of lemur density given proper sampling protocols, and should be utilised in lieu of convenience or judgment sampling (Buckland et al. 2010, Thomas et al. 2010). Established trails were used as line transects in many of the studies from which density estimates were obtained (e.g. Norscia et al. 2006, Ralison 2006a,b), and very few researchers accounted for detection probability when calculating density (N = 5 studies; Table 2). These non-standard survey designs and analysis methods inhibit rigorous inference, and substantial bias can occur should one fail to meet the assumptions of line transect sampling. Researchers should adhere to formal methods of line transect sampling and basic principles of survey design in future studies of mouse lemur density (Buckland et al. 2001, 2010). Lastly, we also encourage researchers to refrain when possible from estimating population indices (Anderson 2001), which are not generally comparable and thus not of value to meta-analyses.

CONCLUSIONS

This research highlights the spatial variation occurring in mouse lemur density while taking into account current taxonomy, sampling methodology, and regional habitat differences. The species included here are the focus of long-term research efforts; however, many mouse lemur species remain understudied and their conservation statuses remain unknown. This study revealed that population densities of mouse lemurs are higher in the western dry forests than in the eastern humid forests, but further research is warranted to determine causal mechanisms driving this disparity. Lemurs are known to act as indicator species for mammalian communities (Muldoon & Goodman 2015), and a thorough understanding of the drivers of mouse lemur demographics may become an essential conservation tool for a broad range of taxa. Future research efforts should focus on estimating density for more recently designated species of mouse lemur, and on tracking the impacts of anthropogenic disturbance on population densities of mouse lemurs and other species of lemur to determine whether they exhibit similar patterns. In addition, these studies should follow standardised guidelines for sampling design and analysis if strong inferences are to be made. Understanding spatial variation in mouse lemur density gives us a broader perspective on the biogeographic drivers of primate community structure, and on priority areas for further conservation effort in Madagascar's increasingly changing environment.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Ranomafana National Park Mouse Lemur Density Estimate 2007–2010.