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**The convergent evolution of mammalian reliance on a
'keystone vegetation structure' in Madagascar and Australia**

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The convergent evolution of mammalian reliance on a 'keystone vegetation structure' in Madagascar and Australia

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ABSTRACT

Tree hollow inhabitance is a trait that has evolved multiple times over the course of mammalian evolution, but the selective pressures for this trait are not well-understood, especially in the tropics. In Australia, there are 35 species of tree hollow-inhabiting marsupials (75% of the continent's arboreal marsupials). The adaptive radiation of Australian tree hollow inhabiting mammals is hypothesized to have been driven by thermoregulatory demands and constrained by tree hollow abundance and body size. Because Australia exhibits disparate temperature extremes and the highest tree hollow abundance globally, the continent can support a high diversity of tree hollow inhabiting species. However, tree hollow inhabitance has not been investigated similarly in the tropics, and there is a paucity of data on tree hollow abundance in low-latitude forests. My investigation of tree hollow inhabitance in Madagascar identified 36 species of tree hollow-inhabiting lemurs, comparable to the mammalian tree hollow inhabitant species richness of Australia. I hypothesized that tree hollow inhabitance within Madagascar was driven by thermoregulatory demands and constrained by tree

hollow abundance and body size. I tested this hypothesis by comparing the selective pressures and constraints acting on lemuriform tree hollow inhabitants, lemuriform non-tree hollow inhabitants, and tree hollow inhabitant marsupials in Australia.

Because data on tree hollow abundance are lacking in Madagascar, I used a proxy for tree hollow abundance: mean yearly rainfall, which positively correlates with global tree hollow abundance. Within Madagascar, tree hollow inhabitant sites did not differ in thermoregulatory demands or tree hollow abundance, but non-tree hollow inhabiting lemuriformes were significantly larger than tree hollow inhabiting lemuriformes.

Furthermore, tree hollow inhabitant sites in Madagascar had significantly higher rainfall levels (suggesting high tree hollow abundance) than Australian tree hollow inhabitant sites, but Australian tree hollow inhabitant sites had significantly higher temperature variability (suggesting higher thermoregulatory demands) than tree hollow inhabitant sites in Madagascar. Therefore, the species richness of mammalian tree hollow inhabitants in both regions may be due to different selective pressures.

Because nearly 80% of tree hollow inhabiting lemuriformes are critically endangered, endangered, or vulnerable, understanding the selective pressures and constraints for inhabitation of this keystone vegetation structure is critical to conserving tree hollow inhabitant species threatened with extinction.

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INTRODUCTION

Mammals on every forested continent rely on tree hollows as ‘keystone vegetation structures’ (Tews et al. 2004; Remm & Lohmus 2011). These microhabitats can serve multiple functions for the animals that use them, including thermoregulation (Webb & Shine 1997), predation avoidance (Nilsson 1984), hydration (Sharma et al. 2016), and infant parking (Kappeler 1998). In addition, tree hollows can be evolutionarily preferable to nests due to reduced energy expenditure on sleep site construction (Gibbons & Lindenmayer 2002). However, negative consequences to tree hollow inhabitation exist as well, including increased risk of parasitism (Hokan et al. 2018) and vulnerability to anthropogenic environmental disturbance as compared to alternative sleep sites (Remm & Lohmus 2011). Because the formation of tree hollows suitable for vertebrate occupancy can take more than a century (Gibbons & Lindenmayer 2002), and because tree hollows are most common in unmanaged old growth forests (Remm & Lohmus 2011), many tree hollow inhabitants are now vulnerable to extinction (Ranius et al. 2009).

Tree hollow abundance varies based on climate, disturbance, and the characteristics of individual trees (i.e., age, diameter, health, and species; Gibbons & Lindenmayer 2002; Remm & Lohmus 2011). Gibbons and Lindenmayer (2002) identified three steps in the tree hollow formation process. First, the tree must experience physiological stress or injury, usually through heavy winds or faunal excavation that exposes the core material: heartwood (Baumgartner 1939). Second, the exposed heartwood must decay to form a tree hollow (Carey & Sanderson 1981), a process hypothesized to be expedited by rainfall (Remm & Lohmus 2011). Third, the tree must

be able to persist with the decay, which normally requires larger girth (Gibbons & Lindenmayer 2002). Tree age, diameter, and likelihood of tree hollow formation are positively correlated (Lindenmayer et al. 2017), partially due to the higher propensity of older trees to shed large branches (Jacobs 1955). The thinning of bark and sapwood, which buffers the vulnerable heartwood from wounding, and the slowed growth rate of older trees (Florence 1996), limits heartwood repair and contributes further to tree hollow formation (Jacobs 1955). However, the strongest global predictor of tree hollow abundance is rainfall because moisture allows for faster tree hollow development through the process of fungal heartwood decay (Remm & Lohmus 2011).

Tree hollow inhabitation has evolved convergently and repeatedly over the course of mammalian evolution, yet the selective pressures implicating this global phenomenon are not yet understood. One hypothesis for the evolution of mammalian tree hollow inhabitation posits that the density of tree hollow inhabitants increases in ecoregions with higher thermoregulatory demands due to the buffering qualities of tree hollows (Gibbons & Lindenmayer, 2002). This hypothesis is supported by a number of studies across continents and taxonomic groups that find substantial temperature insulation in tree hollows (e.g., Cawthen et al. 2009; Isaac et al. 2008; Maziarz 2017; Sedgeley 2001). For instance, tree hollows in red mallee (*Eucalyptus oleosa*) on average, buffer temperatures 2.5-4.0°C below ambient temperature during the daytime and 2.0-3.2°C above ambient temperatures at night (O'Connell & Keppel 2016). The thermoregulatory hypothesis is further supported by the behavior of tree hollow inhabitants, for example, the common brushtail possum (*Trichosurus vulpecula*) selectively inhabits tree hollows that buffer from extreme temperatures (Isaac et al.

2008), and the mountain brushtail possum (*T. cunninghami*) is an obligate tree hollow inhabitant in temperate climates (Lindenmayer et al. 1996) but does not inhabit tree hollows in warmer regions (Gibbons & Lindenmayer 2002). Tropical and sub-tropical regions (e.g., Papua New Guinea) are hypothesized to support fewer tree hollow inhabiting species than more temperate regions (e.g., Australia) due to increased thermoregulatory demands in environments with greater temperature variability (Gibbons & Lindenmayer 2002).

An alternative hypothesis for the evolution of mammalian tree hollow inhabitation posits that tree hollow inhabitation is constrained by tree hollow abundance (Gibbons & Lindenmayer 2002). In sites where tree hollow abundance has declined, tree hollow inhabitant species have experienced population reductions (Newton 1994; Marsden & Pilgrim 2002; Gibbons & Lindenmayer 2002; Aitken & Martin 2008; Manning et al. 2013). Thus, ecoregions with lower tree hollow abundance are expected to have lower tree hollow inhabitant species richness (Saunders et al. 1982; Gibbons & Lindenmayer 2002). For instance, avian tree hollow inhabitation is hypothesized to be constrained by tree hollow abundance because there are fewer tree hollow nesting bird species in regions with lower tree hollow densities (e.g., Europe, North America; Saunders et al., 1982). The hypothesis is further supported by the late Miocene expansion of eucalypt forests in Australia (White 1990), which have the highest tree hollow abundance globally (Remm & Lohmus 2011). The domination of this forest type likely allowed the adaptive radiation of Australian tree hollow inhabiting vertebrates (Archer et al. 1991; Gibbons & Lindenmayer 2002). Over 300 species of Australian vertebrates inhabit tree hollows, including 75% of arboreal marsupials, (Smith &

Lindenmayer 1988) indicating that tree hollow abundance is positively correlated with tree hollow inhabitant species richness (Gibbons & Lindenmayer 2002).

Mammalian tree hollow inhabitation may also be constrained by morphology. While tree hollows offer a variety of fitness advantages to invertebrates (e.g., Khazan et al., 2015) and vertebrates (amphibians: e.g., Vences et al. 2019; bats: e.g., Lopez-Baucells 2017; birds: e.g., Nilsson 1984; reptiles: e.g., Lehtinen et al. 2003; and many non-volant mammalian clades: e.g., Svensson et al. 2018), tree hollows are only accessible as keystone resources for small-bodied species. Animals tend to occupy tree hollows with entrance sizes proportional to their body size to reduce predation and competition (Beyer & Goldingay 2006). While no minimum entrance width can be applied across all tree hollow inhabitant clades, a width of 2 cm is hypothesized to be the lower limit for birds and arboreal mammals (Whitford 2002). In contrast, the largest tree hollows have entrance widths up to 75 cm, but tree hollows of this size are rare (Carritt 1999). In a typical study of vertebrate tree hollow inhabitants, tree hollows with entrance widths greater than 10 cm are considered large (e.g., Whitford 2002). In Australia, tree hollow inhabiting mammals range in body size from 0.01 kg (honey possum: *Tarsipes rostratus*) to 3.50 kg (short-eared possum: *T. caninus*) (Gibbons & Lindenmayer 2002). Thus, body size likely acts as an evolutionary constraint of tree hollow inhabitation.

All primate clades except Cattaehini contain species that sleep in tree hollows, but tree hollow inhabitation is most common among strepsirrhines, especially lemuriformes (Kappeler 1998). The common ancestor to all lemuriformes was probably small-bodied, nocturnal, and different from the ancestral loriform (Svensson et al., 2018), in that the ancestral lemuriform likely inhabited tree hollows (Kappeler 1998,

2000). Therefore, as the adaptive radiation of primates occurred in Madagascar, tree hollows were occupied by many new species of small bodied lemurs (Kappeler 1998). No comprehensive list of tree hollow inhabiting lemuriformes exists, despite research on lemuriform tree hollow inhabitation in Madagascar. For instance, the physical characteristics of occupied tree hollows, including height, entrance size, volume, and depth, have been investigated for multiple lemuriformes (e.g., Lutermann et al. 2010; Rasoloharijaona et al. 2008; Rakotomalala et al. 2017; Romanello, in prep.), in addition to research on tree hollow-prone tree species within Madagascar (Salmona et al. 2015; Rakotomalala et al. 2017). Nevertheless, a paucity of information concerning tree hollow abundance across Madagascar exists, and filling this data gap will broaden the contemporary understanding of tree hollow abundance, and therefore, lemuriform evolution.

Australian marsupials are an ideal candidate for a comparative study of tree hollow inhabitation with lemuriformes. While globally, Madagascar and Australia have the most phylogenetically distinct vertebrate assemblages (Bannar-Martin 2015; Holt et al. 2013). The primates of Madagascar and the arboreal marsupials of Australia have substantial niche convergence (Smith & Ganzhorn 1996). For instance, woolly lemurs (e.g., *Avahi laniger*; Goodman & Benstead 2005), and Australian possums (e.g., *T. Vulpecula*; Nowak 2005) are specialized arboreal folivores, and aye-ayes (*Daubentonia madagascariensis*) and the Australian marsupials *Dactylopsila* spp. are both extractive foragers (Ganzhorn et al. 2014), with both pairs occupying the same dietary niche axis (Ganzhorn et al. 2014; Goodman & Benstead 2005; Nowak 2005). The niche overlap between Australian and Malagasy mammals can be explained by environmental comparability because both landmasses contain similarly structured evergreen

rainforest and dry deciduous forest (Bannar-Martin 2015). Furthermore, the biogeographic and evolutionary history of the Australian continent mirrors Madagascar more closely than any primate occupied landmass (Bannar-Martin 2015).

The aim of the study was to test four overarching hypotheses for the convergent evolution of mammalian tree hollow inhabitation in Madagascar and Australia. First, I tested the hypothesis that lemuriform tree hollow inhabitation is driven by thermoregulatory demands. I predicted: temperature range is greater in lemuriform tree hollow inhabitant sites than lemuriform non-tree hollow inhabitant sites. Second, I tested the hypothesis that tree hollow abundance and body size act as evolutionary constraints to lemuriform tree hollow inhabitation. I predicted: tree hollow abundance is higher in lemuriform tree hollow inhabitant sites than lemuriform non-tree hollow inhabitant sites, and lemuriform tree hollow inhabitants have a lower mean body mass than lemuriform non-tree hollow inhabitants. Third, I tested the hypothesis that mammalian tree hollow inhabitation is driven by similar thermoregulatory demands in Madagascar and Australia. I predicted: temperature range is comparable across tree hollow inhabitant sites in Madagascar and Australia. Fourth, I tested the hypothesis that tree hollow abundance and body size act as evolutionary constraints to mammalian tree hollow inhabitation in Madagascar and Australia. I predicted: tree hollow abundance is comparable between tree hollow inhabitant sites in Madagascar and Australia, and tree hollow inhabitants in Madagascar and Australia have a comparable mean body mass.

METHODS

I used Gibbons & Lindenmayer's (2002) dataset on Australian tree hollow inhabitants and compiled data on lemuriform tree hollow inhabitation from published literature and correspondence with researchers (Appendix). I operationally defined a tree hollow inhabitant as any animal that has been documented at least once using tree hollows as regular sleeping, roosting, or nesting sites. Following the International Union for the Conservation of Nature Species Survival Commission (IUCN/SSC) taxonomy, 15 genera and 35 species of Australian tree hollow inhabitant marsupials are represented, as well as all species of lemuriformes, including six genera and 36 species of tree hollow inhabitant lemuriformes. Due to the paucity of data concerning tree hollow abundance across Madagascar, I used mean yearly rainfall, a variable shown to be significantly correlated with tree hollow abundance globally, as a proxy for tree hollow abundance (Remm & Lohmus 2011). Because higher rainfall levels provide more moisture in the environment, heartwood is able to decay more efficiently, thereby forming more tree hollows, justifying the proxy (Remm & Lohmus 2011).

To define tree hollow inhabitant and non-tree hollow inhabitant sites, I visually estimated the approximate latitudinal and longitudinal center of all lemuriform and tree hollow inhabiting Australian marsupial geographic distributions using IUCN/SSC species distribution maps (Figure 1). I then obtained climate data from the nearest weather station. If distributions were non-continuous and separated by more than 200km, I used multiple weather stations to calculate the average across sites. In addition, I obtained morphological data on all lemuriform and Australian marsupial tree hollow inhabitants from the literature.

I addressed the first hypothesis that lemuriform tree hollow inhabitation is driven by thermoregulatory demands using logistic regression to test whether lemuriform tree hollow inhabitation is predicted by mean daily temperature, minimum temperature on record, maximum temperature on record, mean temperature during the hottest month, or mean temperature during the coldest month. I also compared lemuriform tree hollow inhabitant and non-tree hollow inhabitant sites using Welch two sample t-tests for temperature range, and average mean, minimum, and maximum daily temperatures. For the second hypothesis that lemuriform tree hollow inhabitation is constrained by tree hollow abundance and body size, I compared lemuriform tree hollow inhabitant and non-tree hollow inhabitant sites using Welch two sample t-tests for average mean yearly rainfall, average mean rainfall during the driest month, and average mean rainfall during the wettest month. I then compared tree hollow inhabiting lemuriformes to non-tree hollow inhabiting lemuriformes using Welch two sample t-tests for body mass. I addressed the third hypothesis that mammalian tree hollow inhabitation is driven by similar thermoregulatory demands in Madagascar and Australia by comparing lemuriform and Australian marsupial tree hollow inhabitant sites using Welch two sample t-tests for the following variables: temperature range, and average mean, minimum, and maximum daily temperatures. I addressed the fourth hypothesis that tree hollow abundance and body size act as evolutionary constraints to mammalian tree hollow inhabitation in Madagascar and Australia by comparing tree hollow inhabitant sites in Madagascar and Australia using Welch two sample t-tests for average mean yearly rainfall, average mean rainfall during the driest month, and average mean rainfall during the wettest month. I then compared tree hollow inhabitants in Madagascar and Australia using Welch two sample t-tests for body mass.

I log transformed data to comply with the Welch two sample t-test assumption of normality. I conducted all analyses in R version 1.1.456. Means are presented with standard error.

RESULTS

Average daily temperature across all lemuriform tree hollow inhabitant and non-tree hollow inhabitant sites differed by less than 1.0°C. Mean temperature range ($t = 1.41$, $df = 68.81$, $p = 0.163$), as well as average mean ($t = 0.56$, $df = 67.78$, $p = 0.578$; Figure 2), minimum ($t = -0.35$, $df = 68.96$, $p = 0.728$), and maximum temperatures ($t = 1.18$, $df = 62.48$, $p = 0.245$), did not differ between lemuriform tree hollow inhabitant and non-tree hollow inhabitant sites. No model for predicting lemuriform tree hollow inhabitation was significant.

Mean yearly rainfall across all lemuriform sites was 1428.7 ± 69.2 mm. Average mean yearly rainfall did not differ between lemuriform tree hollow inhabitant (1349.4 ± 89.79 mm) and non-tree hollow inhabitant (1510.2 ± 105.3 mm) sites ($t = -0.30$, $df = 54.34$, $p = 0.765$; Figure 3). In addition, mean rainfall range ($t = -0.18$, $df = 67.85$, $p = 0.854$), as well as average rainfall levels during the driest and wettest months of the year, did not differ between lemuriform tree hollow inhabitant and non-tree hollow inhabitant sites ($t = -1.78$, $df = 63.52$, $p = 0.079$; $t = -0.59$, $df = 68.41$, $p = 0.555$).

The average body mass of tree hollow inhabiting lemuriformes (0.54 ± 0.07 kg) was lower than the average body mass of non-tree hollow inhabitant lemuriformes (2.38 ± 0.30 kg; $t = -5.86$, $df = 37.73$, $p < 0.001$; Figure 4). The average body mass of tree hollow inhabiting lemuriformes ranged from 0.03 kg (Madame Berthe's mouse lemur: *Microcebus berthae*) to 1.85 kg (Wright's sportive lemur: *Lepilemur wrightae*), whereas the average body mass of non-tree hollow inhabiting lemuriformes ranged from 0.03 kg (Sambirano mouse lemur: *M. sambiranensis*) to 7.75 kg (Indri: *Indri indri*).

Average mean daily temperature differed between tree hollow inhabitant Australian marsupial sites ($18.71 \pm 0.72^\circ\text{C}$; Figure 5) and tree hollow inhabitant lemuriform sites ($23.61 \pm 0.53^\circ\text{C}$; $t = 5.57$, $df = 56.81$, $p < 0.001$). Minimum temperature was higher in tree hollow inhabitant lemuriform sites ($14.08 \pm 0.61^\circ\text{C}$) than in tree hollow inhabitant Australian marsupial sites ($7.46 \pm 0.86^\circ\text{C}$; $t = 6.33$, $df = 60.98$, $p < 0.001$; Figure 6), but maximum temperature did not differ across sites ($t = 1.86$, $df = 69.00$, $p = 0.067$). Mean temperature range differed between Malagasy and Australian tree hollow inhabitant sites ($t = -6.24$, $df = 65.01$, $p < 0.001$).

Rainfall patterns differed between Madagascar and Australia. Mean yearly rainfall was lower in tree hollow inhabitant sites in Australia (1037.6 ± 96.8 mm) than in Madagascar ($t = 2.68$, $df = 64.93$, $p = 0.009$; Figure 7). Lemuriform tree hollow inhabitant sites had higher rainfall variability than Australian marsupial tree hollow inhabitant sites ($t = 5.13$, $df = 65.945$, $p < 0.001$): in Madagascar, average rainfall was lower in the driest month than it was in Australia ($t = -2.43$, $df = 63.83$, $p = 0.018$; Figure 8) and rainfall was higher in the wettest month in Madagascar compared to Australia ($t = 4.79$, $df = 65.83$, $p < 0.001$; Figure 9).

The average body mass of tree hollow inhabiting Australian marsupials ranged from the honey possum (0.01 kg), which was less than half as heavy as the smallest tree hollow inhabiting lemur, to the short-eared possum (3.50 kg), which was nearly twice as heavy as the largest tree hollow inhabiting lemur. Nevertheless, the average body mass of tree hollow inhabiting Australian marsupials (0.64 ± 0.16 kg) did not differ from the

average body mass of tree hollow inhabitant lemuriformes (0.54 ± 0.07 kg; $t = -0.53$, $df = 46.90$, $p = 0.60$; Figure 10).

DISCUSSION

Despite tree hollows being a global 'keystone vegetation structure' (Tews et al. 2004; Remm & Lohmus 2011), little is known about the selective pressures and constraints acting on tree hollow inhabitant species. By comparatively investigating tree hollow inhabitation in Madagascar and Australia, I tested existing hypotheses to explain the widespread convergent evolution of mammalian tree hollow inhabitation. Contrary to the hypothesis that tree hollow inhabitant sites have greater thermoregulatory demands and a higher abundance of tree hollows, I found no difference in ecology between tree hollow inhabitant and non-tree hollow inhabitant sites within Madagascar. By contrast, tree hollow inhabitant sites in Australia and Madagascar differed in their ecology, suggesting tree hollow inhabitation likely convergently evolved in both regions due to different selective pressures and constraints. My findings also suggest that the ability of Australian marsupials and lemuriformes to inhabit tree hollows is constrained by their morphology. Substantial variation in the selective pressures and constraints acting on mammalian tree hollow inhabitation, combined with the long-term development of tree hollows, demonstrates the potential complexity of mammalian tree hollow inhabitant conservation initiatives, and highlights the need for further research on mammalian tree hollow inhabitant ecology.

Thermoregulatory demands were comparable between tree hollow inhabitant and non-tree hollow inhabitant sites within Madagascar, and Australian tree hollow inhabitant sites had substantially lower minimum temperatures and greater temperature variability than tree hollow inhabitant sites in Madagascar. Thus, while lemuriformes presumably benefit from the temperature buffering qualities of tree

hollows (Blanco & Rahalinarivo 2010; Lutermann et al. 2010), selective pressure for structural thermoregulatory assistance is substantially reduced within Madagascar relative to Australia. Madagascar's tropical temperature regime allows the average lemuriform tree hollow inhabitant to experience approximately half the temperature variation experienced by Australian marsupial tree hollow inhabitants. Because Madagascar has higher tree hollow inhabitant species richness and is approximately 13 times smaller than Australia, my results challenge the hypothesis that increased thermoregulatory demands drive high tree hollow inhabitant species richness. Further research on the drivers of mammalian tree hollow inhabitation in the tropics is necessary to develop an accurate understanding of the global convergent evolution of tree hollow inhabitation.

While evidence exists to support the hypothesis that tree hollow inhabitation is constrained by tree hollow abundance in Australia (Gibbons & Lindenmayer 2002), my results indicate that lemuriform tree hollow inhabitation is not constrained by tree hollow abundance because tree hollow abundance, as assessed by rainfall, did not differ between lemuriform tree hollow inhabitant and non-tree hollow inhabitant sites. Tree hollow abundance was substantially higher in tree hollow inhabitant sites in Madagascar than Australia, but because lemuriform tree hollow inhabitant sites varied so greatly in tree hollow abundance, alternative constraints likely influence lemuriform tree hollow inhabitation. Factors such as competition, environmental exposure, and parasite avoidance vary based on rainfall and can effectively reduce tree hollow abundance thereby constraining tree hollow inhabitation. Therefore, investigating tree hollow availability, or the number of habitable tree hollows, may be a more useful

metric than either tree hollow abundance or the total number of tree hollows because environmental variables, such as rainfall, effectively alter tree hollow abundance.

Competition for access to tree hollows can potentially explain why tree hollow abundance is unrelated to mammalian tree hollow inhabitation in Madagascar. Lemuriform species richness is higher in humid and sub-humid forests than in succulent woodland, spiny thicket, and dry deciduous forest (Muldoon & Goodman 2015). Therefore, interspecific competition for tree hollow access likely increases in regions with higher rainfall, and thus higher tree hollow abundance. Because interspecific competition between sympatric primate species often leads to sleep site niche partitioning (e.g., Justa et al. 2019), regions of Madagascar with higher tree hollow abundance may have reduced tree hollow inhabitant species richness. However, bats (Lopez-Baucells 2017), frogs (Vences et al. 2019), lizards (Lehtinen et al. 2003), and other tree hollow inhabitants in Madagascar may also outcompete primates for access to these sleep sites in regions with higher rainfall, and therefore, higher levels of biodiversity. The European honeybee, for instance, competitively excludes birds and mammals from suitable tree hollow sleep sites (Mawson & Long 1994; Oldroyd et al. 1994). Because increased tree hollow abundance may correlate with increased tree hollow competition, tree hollow abundance is effectively reduced, thereby further constraining tree hollow inhabitation. While tree hollow inhabitant populations have been hypothesized to be limited by the abundance of suitable tree hollows (Gibbons & Lindenmayer 2002), my results suggest interspecific competitive exclusion may play a role in tree hollow inhabitant population dynamics, and therefore tree hollow inhabitant species richness.

Tree hollow abundance and lemuriform tree hollow inhabitation may also be unrelated due to environmental exposure. Tree hollow inhabitation is hypothesized to be more common in species living in open environments (Alerstam & Hogstedt 1981; Strahan 1983; Gibbons & Lindenmayer 2002). For example, tree hollow-nesting bird species are significantly more likely to live in open environments than non-tree-hollow-nesting bird species (Alerstam & Hogstedt 1981). Furthermore, the spotted cuscus (*Phalanger maculates*) and the green ringtail possum (*Pseudocheirus archeri*) occur in dense tropical rainforests of New Guinea and do not occupy tree hollows, while their closest living relatives occupying Australian eucalyptoid forests with high exposure, nearly all inhabit tree hollows (Strahan, 1983). Despite higher tree hollow abundance in environments with high rainfall levels (Remm & Lohmus 2011), tree hollow inhabiting lemuriform species richness may be high in lower rainfall regions due to increased environmental exposure and therefore more intense selective pressure for predation avoidance through tree hollow inhabitation.

Additionally, mammalian parasite avoidance may reduce selective pressure for tree hollow inhabitation in regions with higher rainfall levels, and therefore, higher tree hollow abundance. Tree hollows containing water can harbor parasites (Gibbons & Lindenmayer 2002), and many mammals actively avoid parasites that are damaging to their health (e.g., Hausfater & Meade 1982). Milne Edwards' sportive lemur (*L. edwardsi*) has a higher prevalence and diversity of endoparasitic helminths than the sympatric western woolly lemur (*A. occidentalis*) because the sportive lemur sleeps in tree hollows and has high sleep site fidelity (Hokan et al. 2018). Additionally, the grey mouse lemur (*M. murinus*) abandons tree hollow sleep sites at the onset of regular heavy rainfall (Lutermann et al. 2010). While the grey mouse lemur shows preference for tree hollows

over alternative sleep sites for thermoregulatory purposes, at the onset of heavy rainfall the species inhabits nests or open sites likely as tactic of water, and thus parasite avoidance (Lutermann et al. 2010). Therefore, environmental factors such as high rainfall levels may reduce selective pressure for tree hollow inhabitation in regions with greater tree hollow abundance. Because tree hollow abundance is not a reliable indicator of tree hollow inhabitation within Madagascar, evidence to support the hypothesis that tree hollow abundance constrains tree hollow inhabitation within Madagascar is lacking. In fact, my results indicate rainfall is a potentially substantial constraint on lemuriform tree hollow inhabitation in sites with high tree hollow abundances. Therefore, because there is no evidence to support the hypothesis that tree hollow abundance is the primary evolutionary constraint for lemuriform tree hollow inhabitation, alternative considerations should be investigated. For example, the species richness of tree hollow inhabitant lemuriformes could be explained by phylogenetic niche conservatism (Kappeler 1998) rather than thermoregulation or tree hollow abundance.

Contrary to Remm & Lohmus (2011), my results may also suggest that mean yearly rainfall is not a good proxy for tree hollow abundance within Madagascar. Their global analysis indicated that mean yearly rainfall was the best global predictor of tree hollow abundance, but tropical sites were excluded from the analysis due to data deficiencies. Thus, further research on tree hollow abundance across the tropics is needed to address the accuracy of global predictors of tree hollow abundance. Within Madagascar, rainfall may fail to predict tree hollow abundance due to variation in stochastic disturbances like cyclones. Tree hollow formation is induced by physiological stress or injury (Baumgartner 1939), and heavy winds during cyclones can cause

substantial trunk and limb breakage (Gibbons & Lindenmayer 2002). Thus, in regions that experience more frequent or intense cyclones, i.e. the tropics, tree hollow abundance may be greater than in regions with fewer or less intense disturbances. Remm & Lohmus (2011) did not include cyclone impacts in their modelling, other than the effect of cyclones on mean yearly rainfall levels, but noted the potential of such disturbances to strongly influence tree hollow abundance. Between 1980 and 2007, an average of 12.5 cyclones formed yearly in the southwest Indian Ocean, and 48 cyclones made landfall in Madagascar (Mavume et al. 2010). The effects of stochastic disturbance on tree hollow abundance are undocumented in Madagascar; however, frequent disturbance likely plays a significant role in the abundance of tree hollows, and the survival of tree hollow inhabitants. Because Madagascar's dry forests were affected by nearly half of all cyclones from 1961 to 2000 (Waeber et al. 2015), sites with lower mean yearly rainfall may have comparable or higher tree hollow abundance than sites with higher mean yearly rainfall, thereby contradicting the rainfall proxy rather than the hypothesis that tree hollow abundance constrains tree hollow inhabitation.

Another way in which the rainfall proxy could be a poor predictor of global tree hollow abundance is variation in anthropogenic disturbance. Remm & Lohmus (2011) found that anthropogenic disturbances also alter tree hollow abundance: tree hollow abundance increases with forest "naturalness" (Remm & Lohmus 2011). Managed forests, i.e. those which have experienced cutting, have significantly lower tree hollow abundance than natural forests, i.e. those which have not experienced cutting (Remm & Lohmus 2011). However, as stated previously, Remm & Lohmus (2011) did not include tropical sites in their analysis, thus disturbance could play a different role in tree hollow abundance within tropical sites. The extent of forest cover prior to human arrival on

Madagascar is difficult to estimate, however, from 1953 to 2000 the island's forest cover was reduced from 27% to 17%, a loss of 61,000 km² (Lowry et al. 1997; Harper et al. 2007; Moat & Smith 2007). Thus, natural forest is highly limited in Madagascar and understanding the distribution of natural versus managed forests may provide a more reliable predictor of tree hollow abundance than mean yearly rainfall. If rainfall is indeed a poor proxy, the possibility remains that tree hollow abundance is a constraint for lemuriform tree hollow inhabitation.

While my results indicate thermoregulatory demands and tree hollow abundance are unrelated to tree hollow inhabitation in Madagascar, I found morphology to be related to tree hollow inhabitation similarly in both Madagascar and Australia. Body size likely acts as a constraint on mammalian tree hollow inhabitation because body mass was significantly lower in tree hollow inhabiting lemuriformes than non-tree hollow inhabiting lemuriformes, and the body mass of lemuriform tree hollow inhabitants and Australian marsupial tree hollow inhabitants was not significantly different. While very large animals, such as the Japanese black bear (*Ursus thibetanus japonicus*; 72 kg), have been documented using tree hollows as sleep / hibernation sites (Itoh et al. 2010), as body mass increases, the abundance of tree hollows suitable for occupancy decreases (Gibbons & Lindenmayer 2002). Large tree hollows are rare, and the low abundance of large tree hollows, exacerbated by the long-term tree hollow formation process (e.g., large tree hollows remain rare in eucalyptus >220 years; Gibbons & Lindenmayer 2002), likely causes reduced selective pressure for tree hollow inhabitation in large bodied species. For example, in the spiny thicket ecoregion of southwestern Madagascar, tree hollows serve as temperature buffers against hot mid-day temperatures for Verreaux's sifaka (*Propithecus verreauxi*; 3 kg), but the species does

not use tree hollows as regular sleep sites and has not been documented using tree hollows in other ecoregions (Chloe Chen-Krauss *pers. comm.*). Therefore, while large bodied animals draw similar benefits from tree hollows, the abundance of large tree hollows likely limits selective pressure for reliance on this sleep site type. However, due to the recent extinction of approximately two-thirds of lemuriform species within the spiny thicket ecoregion of Madagascar (Crowley, 2010), tree hollow inhabitant morphology results may be skewed; however, the large body size of the extinct lemurs make tree hollow occupancy highly unlikely.

Because tree hollows require long-term development (Gibbons & Lindenmayer 2002), they are most abundant in uncut old growth forests, leaving tree hollow inhabiting species especially vulnerable to extinction (Remm & Lohmus 2011). Within the lemuriform clade, 80% of tree hollow inhabitants are critically endangered, endangered, or vulnerable (Romanello *in prep*). While artificial tree hollows have been shown to expand limiting resource availability for tree hollow inhabiting lemuriformes in the short-term (Andrews et al. 1998; Valerie Clark *pers. comm.*), targeted protections for hollow-prone tree species, found to be effective in North America (Engstrom et al. 1996), have yet to be implemented in Madagascar where nearly 50% of forest is estimated to be within 100m from an edge (Vieilledent et al. 2018). Understanding the site-specific drivers of tree hollow inhabitation will allow for the improvement of conservation techniques within Madagascar and across all forested continents.

FIGURES

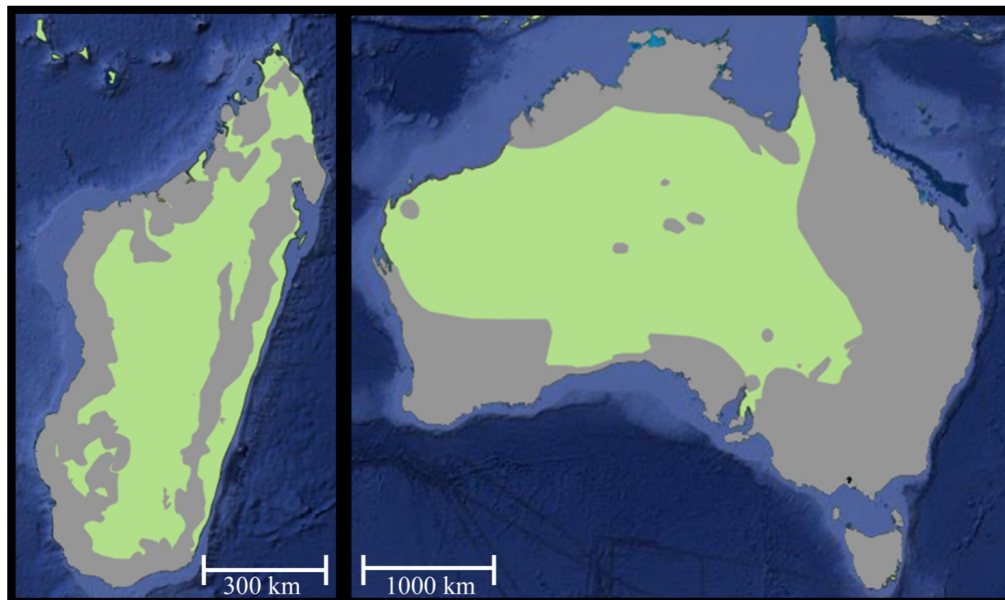


Figure 1: Map of tree hollow inhabitant species distributions for lemuriformes and Australian mammals respectively. Gray regions are inhabited. Spatial data obtained from iucnredlist.org.

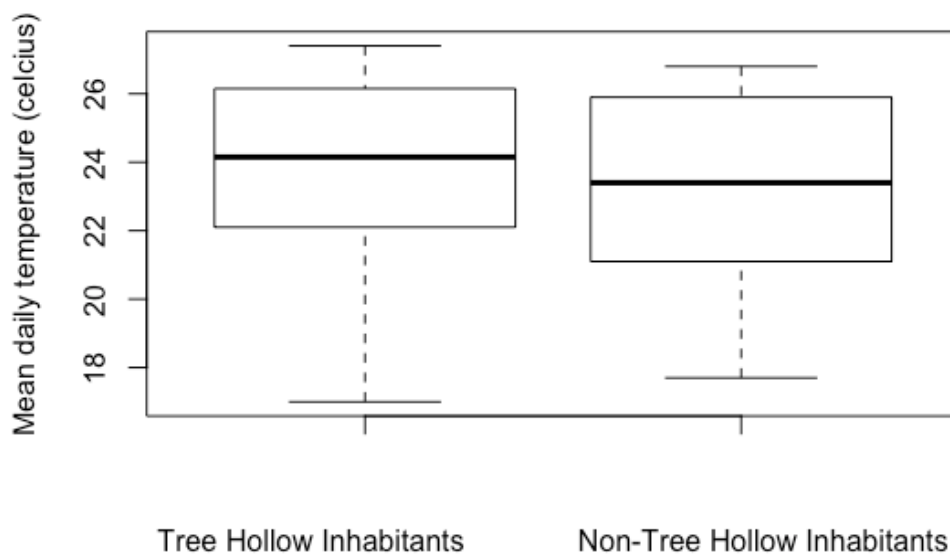


Figure 2: Mean daily temperatures did not significantly differ between tree hollow inhabitant and non-tree hollow inhabitant lemuriform sites (minimum, first quartile, median, third quartile, maximum).



Figure 3: Mean yearly rainfall levels did not significantly differ between tree hollow inhabitant and non-tree hollow inhabitant lemuriform sites (minimum, first quartile, median, third quartile, maximum; dots represent outliers).

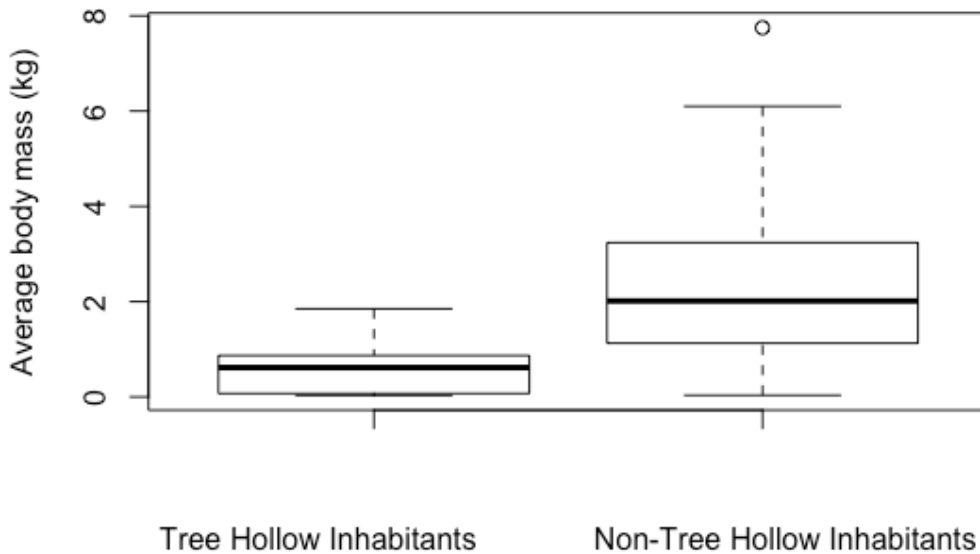


Figure 4: Mean body mass significantly differed between tree hollow inhabitant and non-tree hollow inhabitant lemuriformes (minimum, first quartile, median, third quartile, maximum; dots represent outliers).

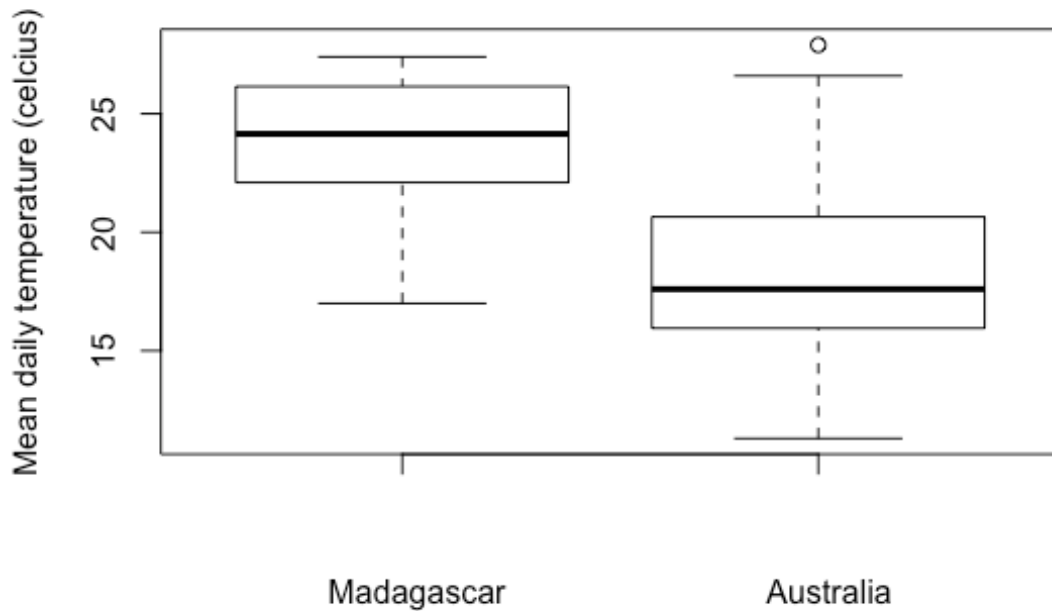


Figure 5: Mean daily temperature significantly differed between tree hollow inhabitant sites in Madagascar and Australia (minimum, first quartile, median, third quartile, maximum; dots represent outliers).

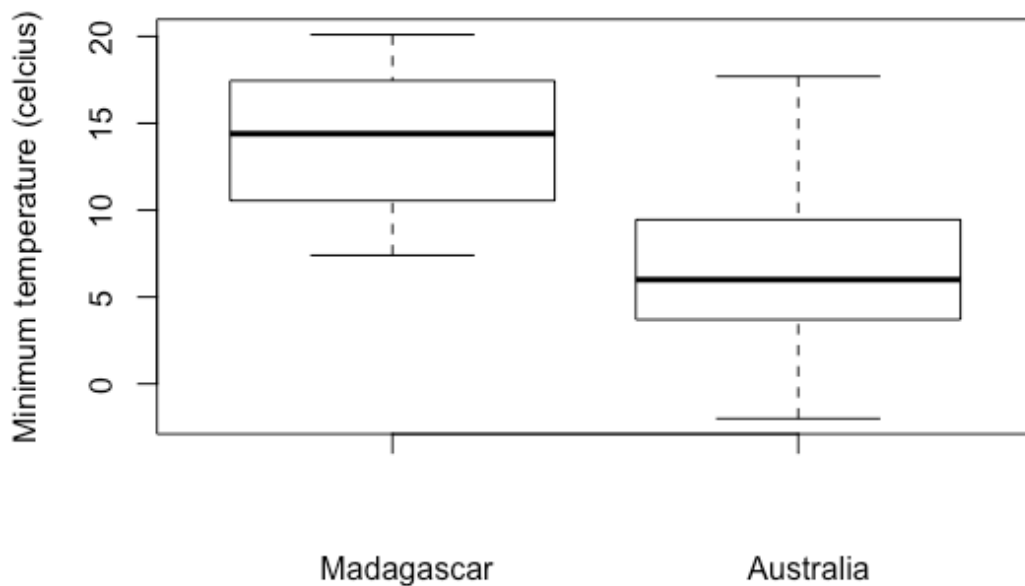


Figure 6: Minimum temperature significantly differed between tree hollow inhabitant sites in Madagascar and Australia (minimum, first quartile, median, third quartile, maximum).

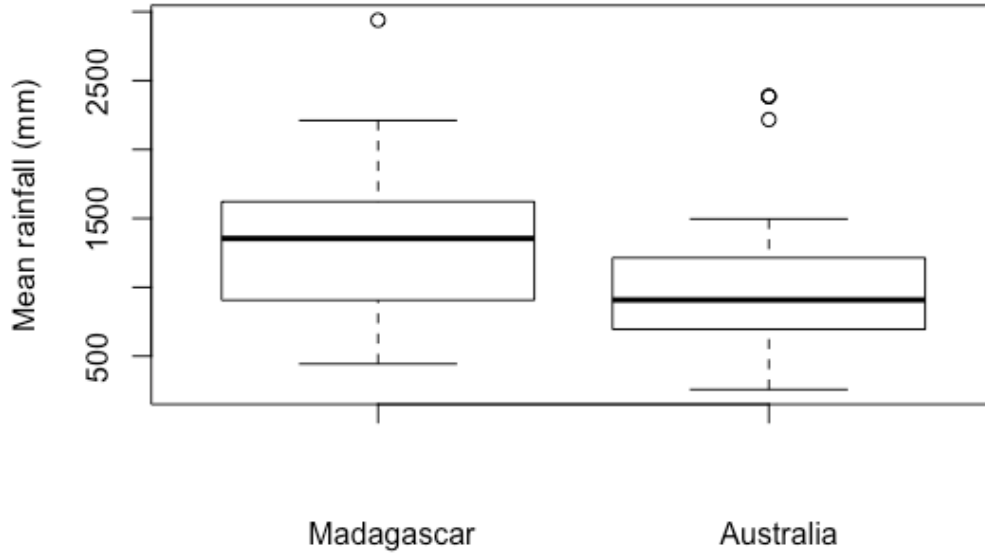


Figure 7: Mean yearly rainfall levels significantly differed between tree hollow inhabitant sites in Madagascar and Australia (minimum, first quartile, median, third quartile, maximum; dots represent outliers).

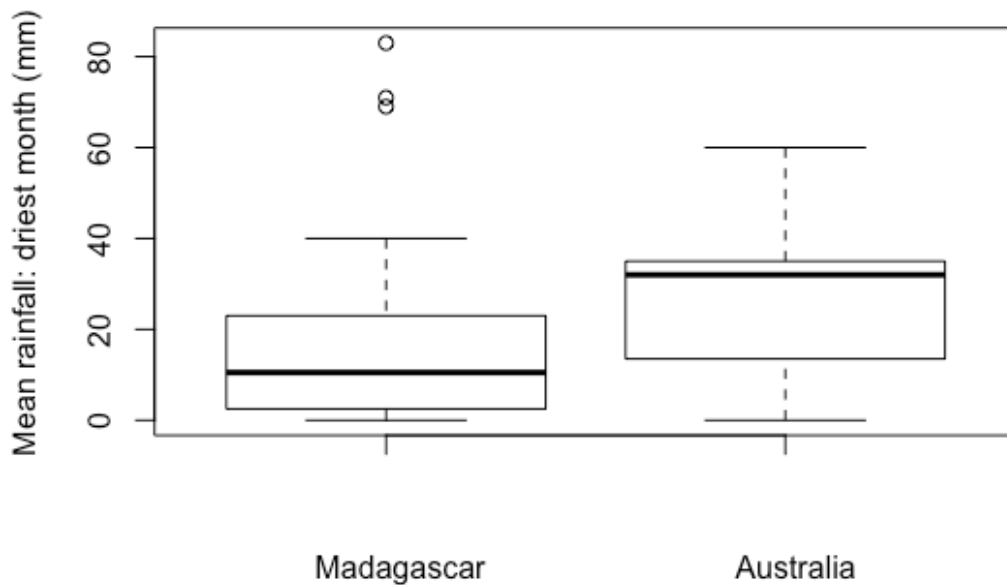


Figure 8: Mean rainfall during the driest month significantly differed between tree hollow inhabitant sites in Madagascar and Australia (minimum, first quartile, median, third quartile, maximum; dots represent outliers).

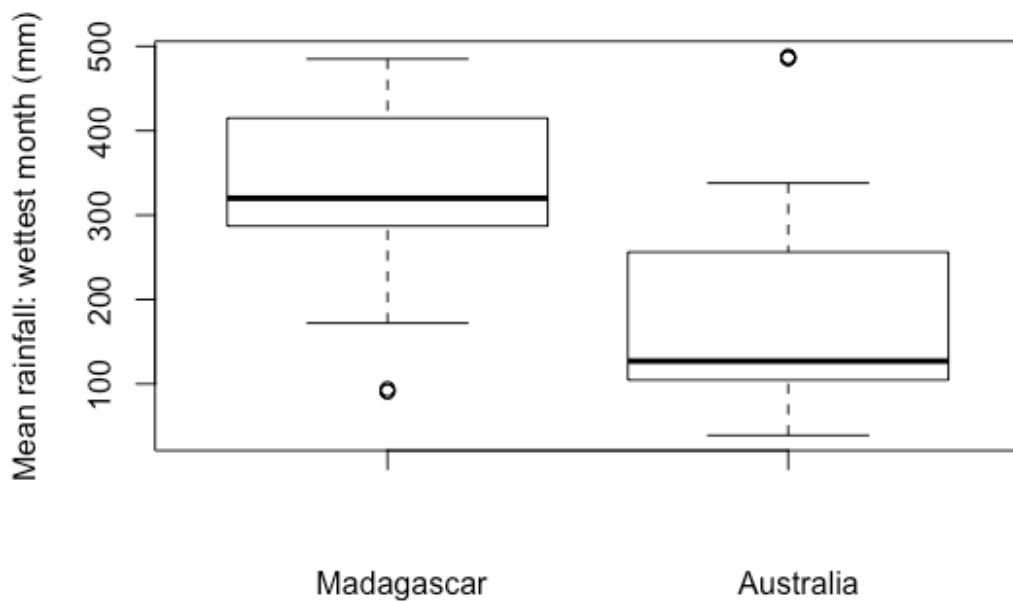


Figure 9: Mean rainfall during the wettest month significantly differed between tree hollow inhabitant sites in Madagascar and Australia (minimum, first quartile, median, third quartile, maximum; dots represent outliers).

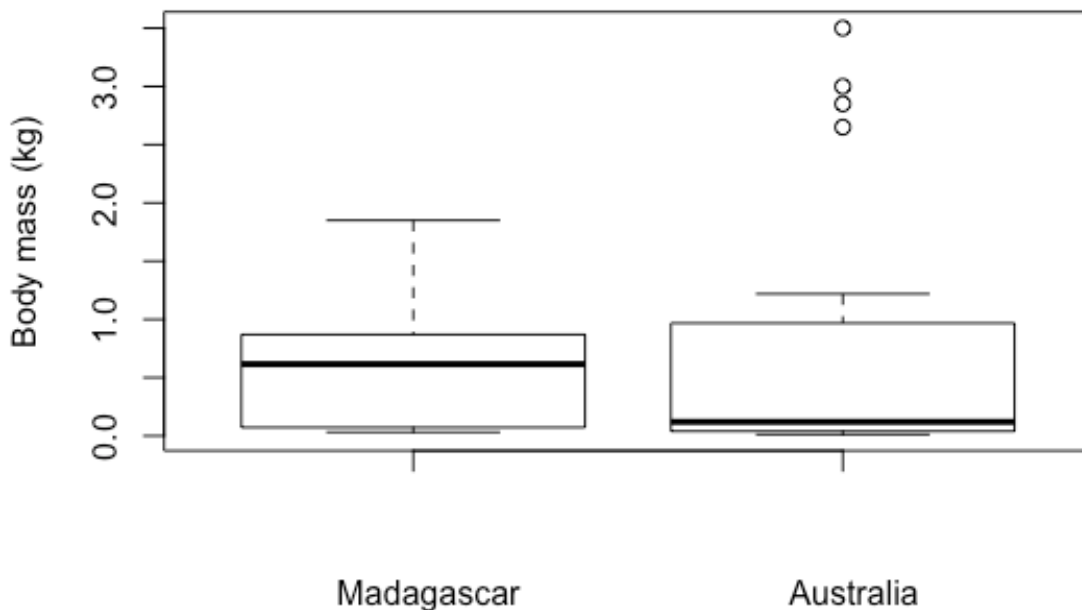


Figure 10: Mean body mass did not significantly differ between tree hollow inhabitants in Madagascar and Australia (minimum, first quartile, median, third quartile, maximum; dots represent outliers).

APPENDIX

Sleep site selection, body mass, and habitat characteristics of arboreal mammals of Madagascar and Australia.

Species	Tree Hollow Inhabitant *	Body Mass (Kg) **	Weather Station ***	Mean Rainfall (mm)	Mean Temperature (Celcius)	Mean Rainfall Driest Month (mm)	Mean Rainfall Wettest Month (mm)	Minimum Temperature (Celcius)	Maximum Temperature (Celcius)	Mean Temperature Coldest Month (Celcius)	Mean Temperature Hottest Month (Celcius)
<i>Allocebus trichotis</i>	Yes [1]	0.08 [1]	Ambatoharanana	1984.0	26.2	21.0	470.0	18.1	32.5	23.8	32.5
<i>Avahi betsileo</i>	Yes [2]	1.09 [2]	Fandriana	1495.0	17.0	27.0	292.0	7.4	25.6	12.9	19.8
<i>Avahi cleesei</i>	Data Deficient										
<i>Avahi laniger</i>	No [3]	1.18 [3]	Vavatenina	2349.0	23.4	82.0	370.0	16.3	30.4	20.3	26.2
<i>Avahi meridionalis</i>	No [4]	1.08 [4]	Ranomafana	1737.0	23.0	59.0	268.0	13.2	31.2	19.1	26.2
<i>Avahi mooreorum</i>	No [5]	0.92 [5]	Ambanizana	2939.0	24.0	83.0	396.0	17.8	30.5	21.1	26.5
<i>Avahi occidentalis</i>	No [6]	0.89 [6]	Tsaramandroso	1529.0	26.8	1.0	445.0	17.5	33.8	24.6	28.3
<i>Avahi peyrierasi</i>	No [7]	1.08 [5]	Ambalavao	1351.0	17.7	9.0	284.0	8.5	25.7	14.0	20.3
<i>Avahi ramanantsoavani</i>	Data Deficient										
<i>Avahi unicolor</i>	Data Deficient										
<i>Cheirogaleus andysabini</i>	Data Deficient										
<i>Cheirogaleus crossleyi</i>	Yes [8]	0.46 [7]	Ambanja, Amparafaravola, Ampondra, Andapa, Antsiranana, Fianarantsoa, Moramanga	1555.7	22.1	29.3	333.1	13.8	29.5	18.9	24.3
<i>Cheirogaleus grovesi</i>	Data Deficient										
<i>Cheirogaleus lavoensis</i>	Data Deficient										
<i>Cheirogaleus major</i>	Yes [9]	0.51 [8]	Aambohimahasina	1349.0	18.9	30.0	292.0	10.0	26.8	14.8	21.7
<i>Cheirogaleus medius</i>	Yes [10]	0.28 [8]	Belo sur Tsiribihina	959.0	26.1	1.0	303.0	14.4	34.0	22.1	28.3

<i>Cheirogaleus shethi</i>	Data Deficient										
<i>Cheirogaleus sibreei</i>	Yes [11]	0.26 [9]	Antanifotsy, Fianarantsoa	1336.5	17.6	17.5	301.5	7.8	26.2	13.4	20.4
<i>Cheirogaleus thomasi</i>	Data Deficient										
<i>Daubentonia madagascariensis</i>	No [12]	2.59 [10]	Anosibe an'ala, Besalampy	1739.5	24.0	26.0	423.0	14.8	31.7	20.8	26.4
<i>Eulemur albifrons</i>	No [13]	2.18 [11]	Maroantsetra	32.8	23.8	79.0	442.0	17.6	30.5	20.8	26.4
<i>Eulemur cinereiceps</i>	Data Deficient										
<i>Eulemur collaris</i>	No [14]	2.14 [12]	Befotaka	1710.0	26.7	6.0	444.0	18.7	33.4	24.7	27.8
<i>Eulemur coronatus</i>	No [15]	1.18 [13]	Marivorahona	1759.0	26.7	14.0	451.0	18.6	33.4	24.4	28.1
<i>Eulemur flavifrons</i>	No [16]	1.87 [14]	Befotaka	1710.0	26.7	6.0	444.0	18.7	33.4	24.7	27.8
<i>Eulemur fulvus</i>	No [17]	1.82 [15]	Ambatondrazaka	1103.0	21.1	5.0	262.0	11.0	29.9	17.3	23.7
<i>Eulemur macaco</i>	No [18]	2.13 [16]	Djangoa	2043.0	26.1	20.0	499.0	18.0	31.9	23.7	27.4
<i>Eulemur mongoz</i>	No [19]	1.21 [17]	Mitsinjo, Miringoni	1665.0	26.0	27.5	212.5	18.8	31.5	23.9	27.4
<i>Eulemur rubriventer</i>	No [20]	2.01 [3]	Moramanga	1638.0	19.4	40.0	319.0	10.5	27.9	15.4	22.5
<i>Eulemur rufifrons</i>	No [20]	2.21 [3]	Nosy Ambositra, Fianarantsoa	976.5	22.0	10.0	250.0	11.2	30.6	17.6	24.8
<i>Eulemur rufus</i>	Data Deficient										
<i>Eulemur sanfordi</i>	No [15]	1.85 [13]	Sadjoavato	1349.0	25.0	19.0	336.0	18.2	30.9	23.0	26.4
<i>Hapalemur alaotrensis</i>	No [21]	1.24 [18]	Vohitsara	1168.0	21.0	6.0	278.0	11.5	29.4	17.2	23.5
<i>Hapalemur aureus</i>	No [22]	1.43 [19]	Fianarantsoa	1240.0	18.7	18.0	314.0	9.4	27.2	14.4	21.4
<i>Hapalemur griseus</i>	No [23]	0.91 [20]	Belampy, Moramanga	1204.0	19.9	12.0	296.0	10.5	28.3	15.8	22.5
<i>Hapalemur meridionalis</i>	No [24]	0.85 [21]	Betroka	854.0	21.8	6.0	212.0	10.6	31.7	17.2	24.6
<i>Hapalemur occidentalis</i>	Data Deficient										
<i>Indri indri</i>	No [25]	7.75 [22]	Vavatenina	2349.0	23.4	82.0	370.0	16.3	30.4	20.3	26.2
<i>Lemur catta</i>	No [26]	2.19 [23]	Sakaraha	724.0	23.4	4.0	149.0	9.0	34.6	18.2	26.5
<i>Lepilemur aecclis</i>	Yes [27]	0.89 [24]	Mitsinjo	1404.0	26.7	1.0	439.0	18.4	32.8	24.5	28.0
<i>Lepilemur ahmansonorum</i>	Data Deficient										

<i>Lepilemur ankaranensis</i>	Yes [25]	0.77 [25]	Antsakoabe	1385.0	24.0	14.0	340.0	16.9	29.9	21.8	25.4
<i>Lepilemur betsileo</i>	Data Deficient										
<i>Lepilemur dorsalis</i>	Yes [28]	0.62 [26]	Bemaneviky	2006.0	25.8	20.0	485.0	17.3	32.1	23.3	27.2
<i>Lepilemur edwardsi</i>	Yes [6]	0.93 [27]	Berivotra	1605.0	27.4	1.0	445.0	18.1	35.8	24.9	29.2
<i>Lepilemur fleuretae</i>	Data Deficient										
<i>Lepilemur grewockorum</i>	Yes [29]	0.86 [28]	Ankerika	1514.0	26.9	3.0	415.0	17.6	34.9	24.3	28.5
<i>Lepilemur hollandorum</i>	Data Deficient										
<i>Lepilemur hubbardorum</i>	Yes [30]	0.99 [26]	Mahaboboka	652.0	24.2	3.0	172.0	10.4	35.1	19.3	27.2
<i>Lepilemur jamesorum</i>	Data Deficient										
<i>Lepilemur leucopus</i>	Yes [31]	0.63 [29]	Behara	601.0	24.2	17.0	94.0	11.8	34.2	19.8	27.8
<i>Lepilemur microdon</i>	Yes [32]	0.97 [29]	Mahatsinjony	1360.0	18.7	25.0	322.0	9.5	27.0	14.5	21.5
<i>Lepilemur milanoii</i>	Data Deficient										
<i>Lepilemur mittermeieri</i>	Yes [33]	0.73 [22]	Ankaramibe	1905.0	25.6	13.0	482.0	17.6	31.4	23.3	26.9
<i>Lepilemur mustelinus</i>	Yes [34]	1.00 [5]	Moramanga	1638.0	19.4	40.0	319.0	10.5	27.9	15.4	22.5
<i>Lepilemur otto</i>	Yes [35]	0.94 [28]	Besakoa	732.0	23.0	6.0	174.0	9.8	33.4	18.4	26.3
<i>Lepilemur petteri</i>	Yes [31]	0.62 [30]	Beloha	444.0	24.1	8.0	91.0	12.3	34.1	19.5	27.8
<i>Lepilemur randrianasoloi</i>	Data Deficient										
<i>Lepilemur ruficaudatus</i>	Yes [36]	0.80 [24]	Morondava	774.0	25.2	0.0	287.0	14.0	32.6	21.0	27.9
<i>Lepilemur sahamalazensis</i>	Yes [37]	0.74 [24]	Befotaka	1710.0	26.7	6.0	444.0	18.7	33.4	24.7	27.8
<i>Lepilemur scottorum</i>	Yes [24]	0.83 [5]	Ambanizana	2939.0	24.0	83.0	396.0	17.8	30.5	21.1	30.5
<i>Lepilemur seali</i>	Data Deficient										
<i>Lepilemur septentrionalis</i>	Yes [38]	0.68 [26]	Antsiranana	1337.0	22.1	14.0	321.0	15.2	28.0	19.8	23.5
<i>Lepilemur tymerlachsoni</i>	Yes [39]	0.88 [26]	Hell-Ville	2136.0	26.5	30.0	471.0	20.1	31.5	24.2	27.8
<i>Lepilemur wrightae</i>	Yes [40]	1.85 [26]	Betroka	854.0	21.8	6.0	212.0	10.6	31.7	17.2	24.6
<i>Microcebus arnholdi</i>	Data Deficient										
<i>Microcebus berthae</i>	Yes [41]	0.03 [31,32]	Belo sur Tsiribihina	959.0	26.1	1.0	303.0	14.4	34.0	22.1	28.3
<i>Microcebus bongolavensis</i>	Data Deficient										

<i>Microcebus boraha</i>	Data Deficient										
<i>Microcebus danfossi</i>	Yes [42]	0.06 [33]	Ankerika	1514.0	26.9	3.0	415.0	17.6	34.9	24.3	28.5
<i>Microcebus ganzhorni</i>	Data Deficient										
<i>Microcebus gerpi</i>	Data Deficient										
<i>Microcebus griseorufus</i>	Yes [43]	0.05 [34]	Beloha	444.0	24.1	8.0	91.0	12.3	34.1	19.5	27.8
<i>Microcebus jollyae</i>	Yes [44]	0.05 [26, 35]	Kianjavato	2211.0	23.0	71.0	391.0	14.5	30.2	19.3	26.0
<i>Microcebus lehilahytsara</i>	Yes [44]	0.05 [36]	Andramasina	1348.0	17.4	10.0	278.0	8.0	25.4	13.4	20.1
<i>Microcebus macarthurii</i>	Data Deficient										
<i>Microcebus mamiratra</i>	Data Deficient										
<i>Microcebus manitatra</i>	Data Deficient										
<i>Microcebus margotmarshae</i>	Data Deficient										
<i>Microcebus marohita</i>	Data Deficient										
<i>Microcebus mittermeieri</i>	Data Deficient										
<i>Microcebus murinus</i>	Yes [45]	0.06 [37]	Morondava	774.0	25.2	0.0	287.0	14.0	32.6	21.0	27.9
<i>Microcebus myoxinus</i>	Yes [2]	0.05 [38]	Besalampy	1248.0	26.5	0.0	465.0	16.7	33.8	23.8	28.2
<i>Microcebus ravelobensis</i>	Yes [45]	0.09 [39]	Ambato Boeny	1437.0	26.7	2.0	414.0	17.1	35.5	24.2	28.9
<i>Microcebus rufus</i>	Yes [46]	0.04 [31]	Fianarantsoa	1240.0	18.7	18.0	314.0	9.4	27.2	14.4	21.4
<i>Microcebus sambiranensis</i>	No [45]	0.04 [40]	Ambanja	2095.0	25.9	23.0	506.0	17.5	31.9	23.4	27.3
<i>Microcebus simmonsi</i>	Data Deficient										
<i>Microcebus tanosi</i>	Yes [44]	0.05 [41]	Tolanaro	1640.0	22.6	69.0	224.0	15.1	29.4	19.5	25.5
<i>Microcebus tavaratra</i>	Data Deficient										
<i>Mirza coquereli</i>	No [47]	0.31 [36]	Belo sur Mer, Soalala	987.0	26.0	0.5	325.5	15.7	32.9	22.6	28.2
<i>Mirza zaza</i>	No [48]	0.29 [36]	Ambanja	2095.0	25.9	23.0	506.0	17.5	31.9	23.4	27.3
<i>Phaner electromontis</i>	Data Deficient										
<i>Phaner furcifer</i>	Yes [47]	0.34 [42]	Marotandrano	1314.0	23.5	11.0	346.0	15.6	31.5	20.2	25.7
<i>Phaner pallescens</i>	Yes [48]	0.34 [42]	Morondava	774.0	25.2	0.0	287.0	14.0	32.6	21.0	27.9

<i>Phaner parienti</i>	Data Deficient										
<i>Prolemur simus</i>	No [22]	2.24 [19]	Fianarantsoa, Moramanga	1439.0	19.1	29.0	316.5	10.0	27.6	14.9	22.0
<i>Propithecus candidus</i>	No [49]	6.10 [43]	Andapa	1995	21.9	61	343	13.8	29.6	18.4	24.5
<i>Propithecus coquereli</i>	Data Deficient										
<i>Propithecus coronatus</i>	No [10]	3.90 [44]	Tsiroanomandidy	1618.0	22.6	6.0	369.0	11.5	31.6	19.0	24.3
<i>Propithecus deckenii</i>	Data Deficient										
<i>Propithecus diadema</i>	No [50]	5.71 [45]	Ambatondrazaka	1103.0	21.1	5.0	262.0	11.0	29.9	17.3	23.7
<i>Propithecus edwardsi</i>	No [51]	5.60 [46]	Fianarantsoa	1240.0	18.7	18.0	314.0	9.4	27.2	14.4	21.4
<i>Propithecus perrieri</i>	No [52]	4.60 [47]	Antsakoabe	1385.0	24.0	14.0	340.0	16.9	29.9	21.8	25.4
<i>Propithecus tattersalli</i>	No [53]	3.49 [48]	Maromokotra	1479.0	26.2	22.0	329.0	18.8	32.1	23.9	27.3
<i>Propithecus verreauxi</i>	No [54]	2.99 [49]	Toliara	343.0	24.1	4.0	76.0	14.0	33.3	20.5	27.8
<i>Varecia rubra</i>	No [55]	3.51 [50]	Ambanizana	2939.0	24.0	83.0	396.0	17.8	30.5	21.1	26.5
<i>Varecia variegata</i>	No [56]	3.65 [51]	Fianarantsoa, Maroantsetra, Moramanga	970.3	20.6	45.7	358.3	12.5	28.5	16.9	23.4
<i>Acrobates pygmaeus</i>	Yes [57]	0.02 [52]	Toowoomba	895.0	35.0	127.0	16.9	3.7	28.5	10.2	22.3
<i>Antechinus agilis</i>	Yes [57]	0.02 [53]	Albury	744.0	32.0	95.0	15.1	2.9	30.5	7.5	22.8
<i>Antechinus bellus</i>	Yes [57]	0.02 [53]	Jabiru	1469.0	1.0	338.0	27.9	17.7	37.1	24.5	30.5
<i>Antechinus flavipes</i>	Yes [57]	0.05 [54]	Dubbo, Boyup Brook	676.5	33.5	111.0	16.0	3.3	29.5	8.9	22.6
<i>Antechinus leo</i>	Yes [57]	0.04 [55]	Coen	1195.0	3.0	307.0	25.5	16.6	33.6	22.2	28.1
<i>Antechinus stuartii</i>	Yes [57]	0.04 [55]	Maitland	932.0	42.0	119.0	17.9	5.8	28.6	11.6	23.3
<i>Antechinus swainsonii</i>	Yes [57]	0.03 [55]	Lithgow	908.0	49.0	113.0	12.2	0.8	24.8	5.4	18.4
<i>Cercartetus caudatus</i>	Yes [57]	0.01 [55]	Cairns	2386.0	37.0	486.0	24.7	16.4	31.5	20.8	27.5
<i>Cercartetus concinnus</i>	Yes [57]	0.08 [55]	Penong	334.0	9.0	49.0	17.4	6.0	29.4	11.8	22.5
<i>Cercartetus lepidus</i>	Yes [57]	0.04 [55]	Patchewollock	361.0	22.0	39.0	16.0	3.7	31.8	9.1	23.1
<i>Cercartetus nanus</i>	Yes [57]	0.41 [55]	Cooma	572.0	27.0	68.0	11.3	-2.0	25.8	4.3	17.9
<i>Dactylopsila trivirgata</i>	Yes [57]	1.10 [55]	Cairns	2386.0	37.0	486.0	24.7	16.4	31.5	20.8	27.5

<i>Dasyurus geoffroi</i>	Yes [57]	2.65 [55]	Perth	807.0	7.0	175.0	18.7	9.1	31.0	13.6	24.8
<i>Dasyurus maculatus</i>	Yes [57]	0.07 [55]	Sydney	1309.0	60.0	155.0	17.6	7.1	26.3	12.0	22.3
<i>Gymnobelideus leadbeateri</i>	Yes [57]	0.12 [56]	Healesville	958.0	51.0	102.0	14.3	4.2	27.2	8.4	20.2
<i>Hemibelideus lemuroides</i>	Yes [57]	0.93 [55]	Ravenshoe	1496.0	33.0	305.0	19.9	9.4	28.8	15.2	23.1
<i>Myrmecobius fasciatus</i>	Yes [57]	0.53 [55]	Darkan	548.0	12.0	107.0	15.3	4.7	30.5	9.8	21.9
<i>Petauroides volans</i>	Yes [57]	1.22 [57]	Ipswich	964.0	32.0	133.0	20.1	6.4	31.2	13.7	25.3
<i>Petaurus australis</i>	Yes [57]	0.59 [55]	Toowoomba	895.0	35.0	127.0	16.9	3.7	28.5	10.2	22.3
<i>Petaurus breviceps</i>	Yes [57]	0.11 [55]	Townsville	1111.0	9.0	275.0	24.1	13.2	31.7	19.0	27.6
<i>Petaurus gracilis</i>	Yes [57]	0.41 [58]	Cardwell	2217.0	28.0	488.0	24.1	14.0	31.8	19.5	27.4
<i>Petaurus norfolcensis</i>	Yes [57]	0.23 [58]	Toowoomba	895.0	35.0	127.0	16.9	3.7	28.5	10.2	22.3
<i>Phascogale calura</i>	Yes [57]	0.04 [55]	Narrogin	479.0	13.0	88.0	15.9	5.2	30.9	10.1	22.7
<i>Phascogale tapoatafa</i>	Yes [57]	0.21 [55]	Boonah, Cairns, Manjimup, Ballarat, Kallumburu	1233.4	26.2	237.4	19.7	9.5	30.1	14.6	24.2
<i>Pseudocheirus archeri</i>	Yes [57]	1.01 [55]	Cairns	2386.0	37.0	486.0	24.7	16.4	31.5	20.8	27.5
<i>Pseudocheirus herbertensis</i>	Yes [57]	1.05 [55]	Ravenshoe	1496.0	33.0	305.0	19.9	9.4	28.8	15.2	23.1
<i>Pseudocheirus occidentalis</i>	Yes [57]	0.70 [59]	Manjimup	981.0	21.0	172.0	14.7	6.0	27.1	10.1	20.2
<i>Pseudocheirus peregrinus</i>	Yes [57]	1.17 [55]	Toowoomba	895.0	35.0	127.0	16.9	3.7	28.5	10.2	22.3
<i>Sminthopsis dolichura</i>	Yes [57]	0.01 [53]	Merredin	324.0	13.0	52.0	17.7	5.2	33.2	10.6	25.3
<i>Sminthopsis leucopus</i>	Yes [57]	0.02 [53]	Warragul	1032.0	49.0	109.0	13.5	3.7	25.7	8.1	18.9
<i>Sminthopsis murina</i>	Yes [57]	0.02 [54]	Moree	584.0	27.0	72.0	19.1	3.7	33.5	10.6	26.6
<i>Tarsipes rostratus</i>	Yes [57]	0.01 [55]	Manjimup	981.0	21.0	172.0	14.7	6.0	27.1	10.1	20.2
<i>Trichosurus arnhemensis</i>	Yes [57]	3.50 [56]	Karratha	258.0	0.0	57.0	26.6	13.0	37.5	19.8	31.7
<i>Trichosurus caninus</i>	Yes [57]	2.85 [59]	Toowoomba	895.0	35.0	127.0	16.9	3.7	28.5	10.2	22.3
<i>Trichosurus vulpecula</i>	Yes [57]	3.00 [55]	Brewarrina, Manjimup, Kununurra	714.0	14.0	138.7	21.2	8.9	33.9	14.9	26.9

*References: [1] Biebow et al. 2009; [2] Razafimandimby pers. obs.; [3] Ganzhorn et al. 1985; [4] Norscia pers. obs.; [5] Sawyer pers. obs.; [6] Hakan et al. 2018; [7] Harcourt 1991; [8] Blanco & Rahalinarivo 2010; [9] Petter et al. 1977; [10] Muller 1999; [11] Blanco pers. obs.; [12] Sterling 1993; [13] Toborowsky 2006; [14] Donati et al. 2007; [15] Freed 1996; [16] Schwitzer et al. 2007; [17] Rasmussen 1999; [18] Colquhoun 2007; [19] Curtis 1997; [20] Overdorff pers. obs.; [21] Ratsimbazafy pers. obs.; [22] Wright et al. 2012; [23] Tongaso pers. obs.; [24] Eppley pers. obs.; [25] Mittermeier et al. 2010; [26] Jolly 1966; [27] Roos pers. obs.; [28] Andrews et al. 1998; [29] Gardner 2016; [30] Rowe pers. obs.; [31] Nash 1998; [32] Porter 1998; [33] Wilmet et al. 2015; [34] Rasoloharijaona et al. 2008; [35] Craul et al. 2007; [36] Hilgartner 2006; [37] Seiler et al. 2013; [38] Ratsiraron & Rumpler 1988; [39] Clark pers. obs.; [40] Irwin et al. 2004; [41] Dammhahn & Kappeler 2005; [42] Olivieri pers. obs.; [43] Genin 2008 [44] Narindra pers. obs.; [45] Radespiel et al. 2003; [46] Atsalis 2008; [47] Petter et al. 1977; [48] Schulke 2003; [49] Patel 2011; [50] Powzyk 1997; [51] Wright et al. 1987; [52] Banks pers. obs.; [53] Myers 1993; [54] Lewis pers. obs.; [55] Rigamonti 1993; [56] Balko 1998; [57] Gibbons & Lindenmayer 2002. **References: [1] Biebow et al. 2009; [2] Andriantompohavana et al. 2007; [3] Glander et al. 1992; [4] Zaramody et al. 2006; [5] Lei et al. 2008; [6] Thalmann 2001; [7] Blanco & Rahalinarivo 2010; [8] Kappeler 1990; [9] Blanco 2010; [10] Feistner & Sterling 1995; [11] Toborowsky pers. obs.; [12] Donati et al. 2007; [13] Terranova & Coffman 1997; [14] Koenders et al. 1985; [15] Rasmussen 1999; [16] Bayart & Simmen 2005; [17] Pastorini et al. 1998; [18] Mutschler et al. 2000; [19] Tan 2000; [20] Tan pers. obs.; [21] Rabarivola et al. 2007; [22] Louis pers. obs.; [23] Sussman pers. obs.; [24] Andriaholinirina et al. 2006; [25] Mittermeier et al. 2010; [26] Louis et al. 2006; [27] Rasoloharijaona et al. 2003; [28] Craul et al. 2007; [29] Charles-Dominique & Haladik 1971; [30] Nash pers. obs.; [31] Atsalis et al. 1996; [32] Dammhahn & Kappeler 2005; [33] Olivieri et al. 2007; [34] Genin 2008; [35] Louis et al. 2008; [36] Kappeler et al. 2005; [37] Schmid & Kappeler 1994; [38] Rasoloarison et al. 2000; [39] Randrianambinina et al. 2003; [40] Hending 2015; [41] Rasoloarison et al. 2013; [42] Schulke et al. 2004; [43] Patel pers. obs.; [44] Mittermeier et al. 1994; [45] Glander & Powzyk 1998; [46] King et al. 2011; [47] Ranaivoarisoa et al. 2006; [48] Ravosa et al. 1993; [49] Lewis pers. obs.; [50] Kappeler 1991; [51] Baden et al. 2008; [52] Harris 2015; [53] Parr et al. 2014; [54] Geiser 1994; [55] Myers et al. 2018; [56] Lindenmayer et al. 1991; [57] Harris & Maloney 2010; [58] Jackson 2011; [59] Inions et al. 1989. ***Climate data obtained from en.climatedata.org.

REFERENCES

- Aitken, K., & Martin, K. (2008). Resource selection plasticity and community responses to experimental reduction of a critical resource. *Ecology*, 89, 971-980.
- Alerstam, T., & Hogstedt, G. (1981). Evolution of hole-nesting in birds. *Ornis Scandinavica*, 12, 188-193.
- Andrews, J., Antilahimena, P., & Birkinshaw, C. (1998). Use of a day resting box by a wild sportive lemur, *Lepilemur dorsalis*, on Nosy Be, north-western Madagascar. *Folia Primatologica*, 69, 18-21.
- Archer, M., Hand, S.J., & Godthelp, H. (1991). Back to the future: the contribution of paleontology to the conservation of Australian forest faunas. In *Conservation of Australia's Forest Fauna*, Royal Zoological Society of NSW, Sydney.
- Bannar-Martin, K. (2015). Scale and process: primate and non-primate mammal community composition and diversity in Madagascar. Dissertation, University of Texas at Austin.
- Baumgartner, L. (1939). Fox squirrel dens. *Journal of Mammalogy*, 20, 456-465.
- Beyer, G.L., & Goldingay, R.L. (2006). The value of nest boxes in the research and management of Australian hollow-using arboreal marsupials. *Wildlife Research*, 33, 161-174.
- Blanco, M., Dausmann, K., Ranaivoarisoa, J., & Yoder, A. (2013). Underground hibernation in a primate. *Scientific Reports*, 3, 1768.
- Blanco, M., Rahalinarivo, V. (2010). First direct evidence of hibernation in an eastern dwarf lemur species (*Cheirogaleus crossleyi*) from the high-altitude for of Tsinjoarivo, central-eastern Madagascar. *Naturwissenschaften*, 97, 945-950.
- Carey, A., & Sanderson, H. (1981). Routine to accelerate tree cavity formation. *Wildlife Society Bulletin*, 9, 14-21.
- Carritt, R. (1999). *Natural Tree Hollows*. Hurstville: National Parks and Wildlife Service.
- Cawthen, L., Munks, S., Richardson, A., & Stewart, N. (2009). The use of temperature loggers to monitor tree hollow use by mammals. *Ecological Management and Restoration*, 10, 153-155.
- Chen-Krauss, C. (2019). Pers. comm.
- Clark, V. (2019) Pers. comm.
- Crowley, B. (2010). A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quaternary Science Reviews*, 29, 2591-2603.

- Engstrom, R., Brennan, L., Neel, W., Farrar, R., Lindenman, S., Moser, W., et al. (1996). Sivicultural practices and red-cockaded woodpecker management: a reply to Rudolph and Conner. *Wildlife Society Bulletin*, 24, 334-338.
- Florence, R. (1996). *Ecology and siviculture of eucalypt forests*. Melbourne: Csiro.
- Ganzhorn, J., Wilmé, L., & Mercier, J. (2014). Explaining Madagascar's biodiversity. In Scales, I.R. (Ed.). *Conservation and Environmental Management in Madagascar*. New York: Routledge.
- Gibbons, P., & Lindenmayer, D. (2002). *Tree Hollows and Wildlife Conservation in Australia*. Victoria: Csiro.
- Goodman, S., & Benstead, J. (2005). Updated estimates of biotic diversity and endemism for Madagascar. *Oryx*, 39, 73-77.
- Harper, G., Steininger, M., Tucker, C., Juhn, D., & Hawkins, F. (2007). Fifty years of deforestation and fragmentation in Madagascar. *Environmental Conservation*, 34, 325-333.
- Hausfater, G., & Meade, J. (1982). Alternation of sleeping groves by yellow baboons (*Papio cynocephalus*) as a strategy for parasite avoidance. *Primates*, 23, 287-297.
- Hokan, M., Zimmerman, E., Radespiel, U., Andriatsitohaina, B., Rasoloharijaona, S., & Strube, C. (2018). Are sleeping site ecology and season linked to intestinal helminth prevalence and diversity in two sympatric, nocturnal and arboreal primate hosts (*Lepilemur edwardsi* and *Avahi occidentalis*)? *BMC Ecology*, 18, 22-32.
- Holt, B., Lessard, J., Borregaard, M., Fritz, S., Araujo, M., Dimitrov, D., et al. (2013). An update of Wallace's zoogeographic regions of the world. *Science*, 339, 74-78.
- Isaac, J., Gabriel, J., & Goodman, B. (2008). Microclimate of daytime den sites in a tropical possum: implications for the conservation of tropical arboreal marsupials. *Animal Conservation*, 11, 281-287.
- Itoh, K., Ide, K., Kojima, Y., & Terada, M. (2010). Hibernation exhibit for Japanese black bear *Ursus thibetanus japonicus* at Ueno Zoological Gardens. *International Zoo Yearbook*, 44, 55-64.
- IUCN. (2019). *The IUCN Red List of Threatened Species*. <https://www.iucnredlist.org>. Downloaded October 2019.
- Jacobs, M. (1955). *Growth habits of the eucalypts*. Forest Timber Bureau Australia, Canberra.
- Justa, P., Kumar, S., Talukdar, G., Sinha, A. (2019). Sharing from the same bowl: resource partitioning between sympatric macaque species in the western Himalaya, India. *International Journal of Primatology*, 40, 356-373.

- Kappeler, P. (1998). Nests, tree holes, and the evolution of primate life histories. *American Journal of Primatology*, 46, 7-33.
- Kappeler, P. (2000). Lemur origins: Rafting by groups of hibernators? *Folia Primatologica*, 71, 422-425.
- Kazhan, S., Bright, E., & Beyer, J. (2015). Land management impacts on tree hole invertebrate communities in a neotropical rainforest. *Journal of Insect Conservation*, 4, 681-690.
- Lehtinen, R., Ramanamanjato, J., & Raveloarison, J. (2003). Edge effects and extinction proneness in a herpetofauna from Madagascar. *Biodiversity and Conservation*, 12, 1357-1370.
- Lindenmayer, D., Blanchard, W., Blair, D., McBurney, L., & Banks, S. (2017). Relationships between tree size and occupancy by cavity dependent arboreal marsupials. *Forest Ecology and Management*, 391, 221-229.
- Lopez-Baucells, A., Rocha, R., Andriatafika, Z., Tojoso, T., Kemp, J., Forbes, K., et al. (2017). Roost selection by synanthropic bats in rural Madagascar: what makes non-traditional structures so tempting? *HYSTRIX - the Italian Journal of Mammalogy*, 28, 28-35.
- Lowry, P., Schatz, G., & Phillipson, P. (1997). *The classification of natural and anthropogenic vegetation in Madagascar*. Washington DC: Smithsonian Institution Press.
- Lutermann, H., Verburt, L., & Rendigs, A. (2010). Resting and nesting in a small mammal: sleeping sites as a limiting resource for female grey mouse lemurs. *Animal Behaviour*, 79, 1211-1219.
- Manning, A., Gibbons, P., Fischer, J., Oliver, D., & Lindenmayer, D. (2013). Hollow futures? Tree decline, lag effects and hollow-dependent species. *Animal Conservation*, 16, 395-403.
- Marsden, S., & Pilgrim, J. (2002). Factors influencing the abundance of parrots and hornbills in pristine and disturbed forests on New Britain, PNG. *International Journal of Avian Science*, 145, 45-53.
- Mawson, P., & Long, J. (1994). Size and age parameters of nest trees used by four species of parrot and one species of cockatoo in south-west Australia. *Emu*, 94, 149-155.
- Moat, J., Smith, P. (2007). *Atlas of the Vegetation of Madagascar*. London: Kew Publishing.
- Muldoon, K., & Goodman, S. (2015). Primates as predictors of mammal community diversity in the forest ecosystems of Madagascar. *PLoS One*, 10, 1-19.

- Mavume, A., Rydberg, L., Rouault, M., & Luteharms, J. (2010). Climatology and landfall of tropical cyclones in the south-west Indian ocean. *Western Indian Ocean Journal of Marine Science*, 8, 15-36.
- Maziarz, M., Broughton, R., & Wesolowski, T. (2017). Microclimate in tree cavities and nest-boxes: Implications for hole-nesting birds. *Forest Ecology and Management*, 389, 306-313.
- Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds – a review. *Biological Conservation*, 70, 265-276.
- Nilsson, S. (1984). The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. *Ornis Scandinavica*, 15, 167-175.
- Nowak, R. (2005). Walker's marsupials of the world. Baltimore: *Johns Hopkins University Press*.
- O'Connell, C., & Keppel, G. (2016). Deep tree hollows: important refuges from extreme temperatures. *Wildlife Biology*, 22, 305-310.
- Oldroyd, B., Lawler, S., & Crozier, R. (1994). Do feral honeybees and regent parrots compete for nest sites? *Australian Journal of Ecology*, 19, 444-450.
- Rakotomalala, E., Rakotondraparany, F., Perofsky, A., & Lewis, R. (2017). Characterization of the tree holes use by *Lepilemur ruficaudatus* in the dry, deciduous forest of Kirindy Mitea National Park. *Folia Primatologica*, 88, 28-41.
- Ranius, T., Niklasson, M., & Berg, N. (2009). Development of tree hollows in pedunculate oak (*Quercus rober*). *Forest Ecology and Management*, 257, 303-310.
- Rasoloharijaona, S., Randrianamabinina, B., & Zimmerman, E. (2008). Sleeping site ecology in a rain-forest dwelling nocturnal lemur (*Lepilemur mustelinus*): implications for sociality and conservation. *American Journal of Primatology*, 70, 247-253.
- Remm, J., & Lohmus, A. (2011). Tree cavities in forests- The broad distribution pattern of a keystone structure for biodiversity. *Forest Ecology and Management*, 262, 579-585.
- Romanello, D. (in prep). Primate tree hollow inhabitation in Madagascar.
- Salmona, J., Banks, M., Ralantoharijaona, T., Rasolondraibe, E., Zaranaina, R., Rakotonanahary, A., et al. (2015). The value of the spineless monkey orange tree (*Strychnos madagascariensis*) for conservation of northern sportive lemurs (*Lepilemur milanoii* and *L. ankaranensis*). *Madagascar Conservation and Development*, 2, 53-59.
- Saunders, D., Smith, G., & Rowley, I. (1982). The availability of tree hollows that provide nest sites for cockatoos (*Psittaciformes*) in Western Australia. *Australian Wildlife Research*, 9, 541-556.

- Sedgeley, J. A. (2001). Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied Ecology*, 38, 425-438.
- Sharma, N., Huffman, M., Gupta, S., Nautiyal, H., Mendonca, R., Morino, L., et al. (2016). Watering holes: the use of arboreal sources of drinking water by Old World monkeys and apes. *Behavioural Processes*, 129, 18-26.
- Smith, A.P., & Ganzhorn, J.U. (1996). Convergence in community structure and dietary adaptation in Australian possums and gliders and Malagasy lemurs. *Australian Journal of Ecology*, 21, 31-46.
- Strahan, R. (1983). *The complete book of Australian mammals*. Sydney: Angus and Robertson.
- Svensson, M., Nekaris, K., Bearder, S., Bettridge, C., Butynski, T., Cheyne, S., et al. (2018). Sleep patterns, daytime predation, and the evolution of diurnal sleep site selection in lorisiforms. *American Journal of Physical Anthropology*, 116, 563-577.
- Tews J., Brose, U., Grimm V., Tielborger K., Wichmann M., Schwager M., et al. (2003). Animal species diversity driven by habitat heterogeneity / diversity: the importance of keystone structures. *Journal of Biogeography*, 31, 79-92.
- Vences, M., Raxworthy, C., Nussbaum, R., & Glaw, F. (2019). New microhylid frog (Plethodontohyla) from Madagascar, with semiarboreal habits and possible parental care. *Journal of Herpetology*, 37, 629-636.
- Vieilledent, G., Grinand, C., Rakotomalala, F., Ranaivosoa, R., Rakotoarijaona, J., Allnut, T. et al. (2018). Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation*, 222, 189-197.
- Waeber, P., Wilme, L., Ramamonjisoa, B., Garcia, C., Rakotomalala, D., Rabemananjara, et al. (2015). Dry forests in Madagascar: neglected and under pressure. *International Forestry Review*, 17, 127-148.
- Webb, J., & Shine, R. (1997) Out on a limb- conservation implications of tree-hollow use by a threatened snake species (*Hoplocephalus bungaroides*, *Serpentes*, *Elapidae*). *Biological Conservation*, 81, 21-33.
- White, M. (1990). *The Flowering of Gondwana*. New Jersey: Princeton University Press.
- Whitford, K. (2002). Hollows in jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) trees: I. Hollow sizes, tree attributes and ages. *Forest Ecology and Management*, 1, 201-214.

APPENDIX REFERENCES

- Andrews, J., Antilahimena, P., & Birkinshaw, C. (1998). Use of a day resting box by a wild sportive lemur, *Lepilemur dorsalis*, on Nosy Be, north-western Madagascar. *Folia Primatologica*, 69, 18-21.
- Andriaholinirina, N., Fausser, J., Roos, C., Zinner, D., Thalmann, U., & Rabarivola, C., et al. (2006). Molecular phylogeny and taxonomic revision of the sportive lemurs. *BMC Evolutionary Biology*, 6, 1471-1484.
- Andriantompohavana, R., Lei, R., & Zaonarivelo, J. (2007). Molecular phylogeny and taxonomic revision of the woolly lemurs, genus *Avahi* (Primates: *Lemuriformes*). *Special Publications of the Museum of Texas Tech University*, 51.
- Atsalis, S. (2008). *A Natural History of the Brown Mouse Lemur*. New Jersey: Prentice Hall.
- Atsalis, S., Schmid, J., & Kappeler, P. (1996). Metrical comparisons of three species of mouse lemur. *Journal of Human Evolution*, 31, 61-68.
- Baden, A., Brenneman, R., & Louis, E. (2008). Morphometrics of wild black-and-white ruffed lemurs (*Varecia variegata*; Kerr, 1792). *American Journal of Primatology*, 70, 913-926.
- Balko, E. (1998). A behaviorally plastic response to forest composition and logging disturbance by *Varecia variegata* in Ranomafana National Park, Madagascar. Dissertation, State University of New York, Syracuse.
- Banks, M. (2011). Pers. obs.
- Bayart, F., & Simmen, B. (2005). Demography, range use, and behavior in black lemurs (*Eulemur macaco macaco*) at Ampasikely, northwest Madagascar. *American Journal of Primatology*, 67, 299-312.
- Biebouw, K. (2009). Home range size and use in *Allocebus trichotis* in Analamazaotra Special Reserve, central eastern Madagascar. *International Journal of Primatology*, 30, 367-386.
- Blanco, M. (2010). Reproductive biology of mouse and dwarf lemurs of eastern Madagascar, with an emphasis on brown mouse lemurs (*Microcebus rufus*) at Ranomafana National Park, a southeastern rainforest. Dissertation, University of Massachusetts, Amherst.
- Blanco, M. (2011). Pers. obs.
- Blanco, M., & Rahalinarivo, V. (2010). First direct evidence of hibernation in an eastern dwarf lemur species (*Cheirogaleus crossleyi*) from the high-altitude forest of Tsinjoarivo, central-eastern Madagascar. *Naturwissenschaften*, 97, 945-950.
- Charles-Dominique, P., & Hladik, C. (1971). Le *Lepilemur* du sud de Madagascar: ecologie, aliementation et vie sociale. *Revue D Ecologie-La Terre Et La Vie*, 25, 3-66.

Clark, V. (2016). Pers. obs.

Colquhoun, I. (2007). Anti-predator strategies of the cathemeral primates: dealing with the predators of the day and the night. In Gursky, S., & Nekaris, N. (2007), 146-172.

Craul, M., Zimmerman, E., Rasoloharijoana, S., Randrianambinina, B., & Radespiel, U. (2007). Unexpected species diversity of Malagasy primates (*Lepilemur* spp.) in the same biogeographical zone: a morphological and molecular approach with a description of two new species. *BMC Evolutionary Biology*, 7, 15.

Curtis, D. (1997). The mongoose lemur (*Eulemur mongoz*): a study in behaviour and ecology. Dissertation, University of Zurich.

Dammhahn, M., & Kappeler, P. (2005). Social system of *Microcebus berthae*, the world's smallest primate. *International Journal of Primatology*, 26, 407-435.

Donati, G. (2007). Pers. obs.

Donati, G., Ramanamanjato, J., Ravoahangy, A., & Vincelette, M. (2007). Translocation as a conservation measure for a threatened species: the case for *Eulemur collaris* in the Mandena littoral forest, south-eastern Madagascar. In Ganzhorn, J., Goodman, S., & Vincelette, M., *Biodiversity, Ecology and Conservation of the Littoral Ecosystems of South-eastern Madagascar*, 237-246. Washington, DC: Smithsonian Institution Press.

Eppley, T. (2012). Pers. obs.

Feistner, A. & Sterling, E. (1995). Body mass and sexual dimorphism in the aye-aye. *Dodo*, 31, 73-76.

Freed, B. (1996). Co-occurrence among crowned lemurs (*Lemur coronatus*) and Sanford's lemur (*Lemur fulvus sanfordi*) of Madagascar. Dissertation, Washington University.

Ganzhorn, J., Abraham, J., & Razanahoera-Rakotomalala, M. (1985). Some aspects of the natural history and food selection of *Avahi laniger*. *Primates*, 26, 452-463.

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

Geiser, F. (1994). Hibernation and daily torpor in marsupials- a review. *Australian Journal of Zoology*, 42, 1.

Genin, F. (2008). Life in unpredictable environments: first investigation of the natural history of *Microcebus griseorufus*. *International Journal of Primatology*, 29, 303-321.

Gibbons, P., & Lindenmayer, D. (2002). *Tree Hollows and Wildlife Conservation in Australia*. Victoria: CSIRO.

Glander, K., & Powzyk, J. (1998). Morphometrics of wild *Indri indri* and *Propithecus diadema diadema*. *Folia Primatologica*, 69, 399.

Glander, K., Wright, P., Daniels, P., & Merenlender, A. (1992). Morphometrics and testicle size of rainforest lemur species from southeastern Madagascar. *Journal of Human Evolution*, 22, 1-17.

Harcourt, C. (1991). Diet and behavior of a nocturnal lemur, *Avahi laniger*, in the wild. *Journal of Zoology*, 223, 667-674.

Harris, J. (2015). *Acrobates Pygmaeus* (Diprotodontia: Acrobatidae). *Mammalian Species*, 47, 32-44.

Harris, J., & Maloney, S. (2010). *Petauroides volans* (Diprotodontia psuedocheiridae). *Mammalian Species*, 42, 207-219.

Hending, D., McCabe, G., & Holdereid, M. (2017). Sleeping and ranging behavior of the sambirano mouse lemur, *Microcebus sambiranensis*. *International Journal of Primatology*, 38, 1072-1089.

Hokan M., Zimmerman E., Radespiel U., Andriatsitohaina B., Rasoloharijaona S., & Strube C. (2018). Are sleeping site ecology and season linked to intestinal helminth prevalence and diversity in two sympatric, nocturnal and arboreal primate hosts (*Lepilemur edwardsi* and *Avahi occidentalis*)? *BMC Ecology*, 18, 22-32.

Inions, G., Tanton, M., & Davey, S. (1989). Effect of fire on the availability of hollows in trees used by the common brushtail possum, *Trichosurus vulpecula* and the Ringtail Possum, *Pseudocheirus peregrinus*. *Wildlife Research*, 16, 449-458.

Irwin, M., Samonds, K., Raharison, J., & Wright, P. (2004). Lemur latrines: observations of latrine behavior in wild primates and possible ecological significance. *Journal of Mammalogy*, 85, 420-427.

Jackson, S. (2011). *Petaurus gracilis*. *Mammalian Species*, 43, 141-148.

Jolly, A. (1966). *Lemur Behavior: A Madagascar Field Study*, Chicago: University of Chicago Press.

Kappeler, P. (1991). Patterns of sexual dimorphism in body weight among prosimian primates. *Folia Primatologica*, 57, 132-146.

Kappeler, P. (1990). The evolution of sexual size dimorphism in prosimian primates. *American Journal of Primatology*, 21, 201-214.

Kappeler, P., Rasoloarison, R., Razafimanantsoa, L., Walter, L., & Roos, C. (2005). Morphology, behaviour, and molecular evolution of giant mouse lemurs (*Mirza* spp.) Gray, 1870, with description of a new species. *Primate Report*, 71, 3-24.

King, S., Morelli, T., & Arrigo-Nelson, S. (2011). Morphometrics and pattern of growth in wild sifakas (*Propithecus edwardsi*) at Ranomafana National Park, Madagascar. *American Journal of Primatology*, 73, 155-172.

Koenders, L., Rumpler, Y., Ratsirarson, J., & Peyrieras, A. (1985). *Lemur macaco flavifrons* (Gray, 1867): a rediscovered subspecies of primates. *Folia Primatologica*, 44, 210-215.

Lei, R., Engberg, S., & Andriantompohavana, R. (2008). Nocturnal lemur diversity at Masoala National Park. *Special Publications of the Museum of Texas Tech University*, 53.

Lewis, R. (n.d.). Pers. obs.

Lindenmayer, D., Cunningham, R., Tanton, M., Smith, A., & Nix, H. (1991). Characteristics of hollow bearing trees occupied by arboreal marsupials in the montane ash forests of the central highlands of Victoria, southeast Australia. *Forest Ecology and Management*, 40, 289-308.

Louis, E., Engberg, S., & Lei, R. (2006). Molecular and morphological analyses of the sportive lemurs (family *Megalapidae*: genus *Lepilemur*) reveals 11 previously unrecognized species. *Special Publications of the Museum of Texas Tech University*, 49.

Louis, E., Engberg, S., McGuire, S., McCormick, M., Randriamampionona, R., & Ranaivoarisoa, 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.

Louis, E. (n.d.). Pers. obs.

Mittermeier, R., Louis, E., Richardson, M., Schwitzer, C., Langrand, O., Rylands, A., et al. (2010). *Lemurs of Madagascar*, Virginia: Conservation International.

Mittermeier, R., Tattersall, I., Konstant, W., Meyers, D., & Mast, R. (1994). *Lemurs of Madagascar*, Virginia: Conservation International.

Muller, A. (1999). Social organization of the fat-tailed dwarf lemur (*Cheirogaleus medius*) in northwestern Madagascar. In Rakotosamimanana, et al. (1999), 139-158.

Mutschler, T., Nievergelt, C., & Feistner, A. (2000). Social organization of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*). *American Journal of Primatology*, 50, 9-24.

Myers, P., Espinosa, R., Parr, T., Jones, G., Hammond, S., & Dewey, T. (2018). *The Animal Diversity Web*.

Nash, L. (n.d.) Pers. obs.

Nash, L. (1998). Vertical clingers and sleepers: seasonal influences on the activity and substrate use of *Lepilemur leucopus* at Beza Mahafaly Special Reserve, Madagascar. *Folia Primatologica*, 69, 204-217.

Narindra, V. (2019) Pers. obs.

- Norscia, I. (2019). Pers. obs.
- Olivieri, G. (n.d.) Pers. obs.
- Olivieri, G., Zimmermann, E., & Randrianambinina, B. (2007). The ever-increasing diversity in mouse lemurs: three new species in north and northwestern Madagascar. *Molecular Phylogenetics and Evolution*, 43, 309-327.
- Overdorff, D. (n.d.). Pers. obs.
- Pastorini, J., Zaramody, A., Scheffrahn, W., Clark, M., Waters, M., & Curtis, D. (1998). Body measurements from wild mongoose lemurs at Anjamena. In XVIIth Congress of the IPS, Poster Abstracts (Antananarivo, Madagascar, 1998).
- Patel, E. (2011). Diet, habitat, and ranging of the silky sifaka (*Propithecus candidus*). MS Thesis.
- Patel, E. (n.d.) Pers. obs.
- Petter, J., Albignac, R., & Rumpler, Y. (1977). *Mammifères Lemuriens (Primates Prosimiens)*, In *Faune de Madagascar*, Paris: ORSTOM/CNRS.
- Porter. (1998). Influences on the distribution of *Lepilemur microdon* in the Ranomafana National Park, Madagascar. *Folia Primatologica*, 69, 172-176.
- Powzyk, J. (1997). The socio-ecology of the two sympatric indriids, *Propithecus diadema* and the *Indri indri*: a comparison of feeding strategies and their possible repercussions on species-specific behaviors. Dissertation, Duke University.
- Rabarivola, C., Prosper, P., Zaramody, A., Andriaholinirina, N., & Hauwy, M. (2007). Cytogenetics and taxonomy of the genus *Hapalemur*. *Lemur News*, 12, 46-49.
- Radespiel, U., Ehresmann, P., & Zimmerman, E. (2003). Species specific usage of sleeping sites in two sympatric mouse lemur species (*Microcebus murinus* and *M. ravelobensis*) in northwestern Madagascar. *American Journal of Primatology*, 59, 139-151.
- Ranaivoarisoa, J., Ramanamahefa, R., Louis, E., & Brenneman, R. (2006). Range extension of Perrier's sifaka, *Propithecus perrieri*, in the Andrafiarana Classified Forest. *Lemur News*, 11, 17-21.
- Randrianambinina, B., Rakotondravony, D., Radespiel, U., & Zimmerman, E. (2003). Seasonal changes in general activity, body mass and reproduction of two small nocturnal primates: a comparison of the golden brown mouse lemur (*Microcebus ravelobensis*) in northwestern Madagascar and the brown mouse lemur (*Microcebus rufus*) in eastern Madagascar. *Primates*, 44, 321-331.
- Rasmussen, M. (1999). Ecological influences on the activity cycle in two cathemeral primates, the mongoose lemur (*Eulemur mongoz*) and the common brown lemur (*Eulemur fulvus fulvus*). Dissertation, Duke University.

- Rasoloarison, R., Goodman, S., & Ganzhorn, J. (2000). Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. *International Journal of Primatology*, 21, 963-1019.
- Rasoloarison, R., Weisrock, D., Yoder, A., Rakotondravony, D., & Kappeler, P. (2013). Two new species of mouse lemurs (*Cheirogaleidae: Microcebus*) from eastern Madagascar. *International Journal of Primatology*, 34, 455-469.
- Rasoloharijaona, S., Rakotosamimanana, B., Randrianambinina, B., & Zimmerman, E. (2003). Pair-specific usage of sleeping sites and their implications for social organization in a nocturnal Malagasy primate, the Milne Edward's sportive lemur (*Lepilemur edwardsi*). *American Journal of Physical Anthropology*, 122, 251-258.
- Rasoloharijaona, S., Randrianamabinina, B., & Zimmerman, E. (2008). Sleeping site ecology in a rain-forest dwelling nocturnal lemur (*Lepilemur mustelinus*): implications for sociality and conservation. *American Journal of Primatology*, 70, 247-253.
- Ratsimbazafy, (n.d.). Pers. obs.
- Ratsirarson, J., & Rumpler, Y. (1988). Contribution a l'étude compare de l'éco-ethologie de deux especes de lemuriens. *Lepilemur mustelinus* (Geoffrey 1850) et *Lepilemur septentrionalis* (Rumpler et Albignac 1975). In Rakotovao, L., Barre, V., & Sayer, J. L'équilibre des ecosystems forestiers a Madagascar: *Actes d'un seminaire international*, 100-102. Gland, Switzerland: IUCN.
- Ravosa, M., Meyers, D., & Glander, K. (1993). Relative growth of the limbs and trunk in sifakas: heterochronic, ecological, and functional considerations. *American Journal of Physical Anthropology*, 92, 499-520.
- Razafimandimby, D. (2019). Pers. obs.
- Rigamonti, M. (1993). Home range and diet in red ruffed lemurs (*Varecia variegata rubra*) on the Masoala peninsula, Madagascar. In Kappeler & Ganzhorn (1993), 25-39.
- Roos, C. (2019). Pers. obs.
- Rowe, N. (2011). Pers. obs.
- Sawyer, R. (2019). Pers. obs.
- Schmid, J. & Kappeler, P. (1994). Sympatric mouse lemurs (*Microcebus* spp.) in western Madagascar. *Folia Primatologica*, 63, 162-170.
- Schulke, O. (2003). To breed or not to breed? Food competition and other factors involved in female breeding decisions in the pair-living nocturnal forked marked lemur. *Behavioral Ecology and Sociobiology*, 55, 11-21.
- Schulke, O., Kappeler, P., & Zischler, H. (2004). Small testes size despite extra-pair paternity in the pair-living nocturnal primate *Phaner furcifer*. *Behavioral Ecology and Sociobiology*, 55, 293-301.

Schwitzer, N., Randriatahina, G., Kaumanns, W., Hoffmeister, D., & Schwitzer, C. (2007). Habitat utilization of blue-eyed black lemurs, *Eulemur macaco flavifrons* (Gray, 1867), in primary and altered forest fragments. *Primate Conservation*, 22, 79-87.

Seiler, M., Schwitzer, C., Gamba, M., & Holderied, M. (2013). Interspecific semantic alarm call recognition in the solitary Sahamalaza sportive lemur, *Lepilemur sahamalazensis*. *PLoS One*, 8, 6.

Sterling, E. (1993). Behavioral ecology of the aye-aye (*Daubentonia madagascariensis*) on Nosy Mangabe, Madagascar. Dissertation, Yale University.

Sussman, R. (n.d.) Pers. obs.

Tan, C. (2000). Behavior and ecology of three sympatric bamboo lemur species (genus *Hapalemur*) in Ranomafana National Park, Madagascar. Dissertation, State University of New York at Stony Brook.

Tan, C. (n.d.) Pers. obs.

Terranova, C., & Coffman, B. (1997). Body weights of wild and captive lemurs. *Zoo Biology*, 16, 17-30.

Thalmann, U. (2001). Food resource characteristics in two nocturnal lemurs with different social behavior: *Avahi occidentalis* and *Lepilemur edwardsi*. *International Journal of Primatology*, 22, 287-324.

Toborowsky, C. (2006). Ecology of the white-fronted brown lemur (*Eulemur fulvus albifrons*) in Betampona Natural Reserve, Madagascar. MS thesis, University of Missouri-St. Louis.

Toborowsky, C. (n.d.) Pers. obs.

Tongasoa, L. (2013). Pers. obs.

Wilmet, L., Schwitzer, C., Beudels-Jamar, R., Sonet, G., Devillers, P., & Vermeulen, C. (2015). Field data on the little known and endangered *Lepilemur mittermeieri*. *Journal of Primatology*, 4, 2-7.

Wright, P., Daniels, P., Meyers D., Overdorff, D., & Rabesoa, J. (1987). A census and study of *Hapalemur* and *Propithecus* in southeastern Madagascar. *Primate Conservation*, 8, 84-87.

Wright, P., Erhart, E., & Tecot, S. (2012). Long-term lemur research at Centre ValBio, Ranomafana National Park, Madagascar. In Kappeler & Watts (2012), 67-100. Berlin: Springer-Verlag.

Zaramody, A., Fausser, J., & Roos, C. (2006). Molecular phylogeny and taxonomic revision of the eastern woolly lemur (*Avahi laniger*). *Primate Report*, 74, 9-23.