Ecological Flexibility of the Southern Bamboo Lemur (*Hapalemur meridionalis*) in Southeast Madagascar

DISSERTATION

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Summary

Organisms that are adapted to a narrow range of habitat types and/or dietary resources are often referred to as specialist species, and are thus thought of as unable to survive in different environments or those devoid of their specialized dietary niche. In contrast, a generalist species typically has a large dietary breadth and is able to adapt to various habitats, exploiting new resources. This ability to adjust can therefore be defined as a degree of ecological flexibility. Among the most well-known textbook examples of a mammalian specialist is the giant panda (*Ailuropda melanoleuca*), a species that survives almost entirely on a diet of bamboo. Similar to this species, bamboo lemurs (*Hapalemur* spp. / *Prolemur simus*) are also known for their dietary predilection for bamboo; they are typically categorized as habitat and dietary specialists, and are thus regarded as the textbook example of a primate specialist. Lac Alaotran gentle lemurs (*Hapalemur alaotrensis*) have adapted in an area without bamboo, but their diet is almost entirely comprised of four food species. Due to their extremely low dietary breadth, this species is believed to be inflexible in terms of behavioral and ecological adaptability. On the other hand, recent observations of a close congener, the southern bamboo lemur *H. meridionalis*, indicate that it is an exception within the genus, as a population within a fragmented littoral forest devoid of bamboo displays an unusually diverse diet. While previous reports have observed this species feeding in stands of bamboo at other locations, the unique matrix of littoral forest, swamp, and invasive mono-dominant swamp habitats available within the Mandena area of coastal southeast Madagascar presented an excellent site model with which to explore the ecological flexibility of this species and to elucidate how they would cope without their preferred resource.

Ecological flexibility can comprise behavioral and physiological components. To examine whether the southern bamboo lemurs exhibit an ecological flexibility, I first explored their activity pattern. I then characterized the floristic diversity and structure of the disparate habitats in Mandena in an attempt to elucidate whether this species is capable of utilizing an invasive species-dominated habitat, and the potential of *Melaleuca quinquenervia* to facilitate dispersal throughout the greater fragmented landscape. In a previous study, *H. meridionalis* was recorded to spend a large proportion of time on the ground feeding on graminoids. As this dietary niche/stratum carries with it potentially increased predation risks compared to feeding in the canopy, I attempted to parse these costs from the nutritional gain provided by food items that the *Hapalemur* selected between these contrasting strata. Lastly,

prior research of *Hapalemur* congeners has described bamboo lemurs as territorial, while also occasionally utilizing latrines at some sites, and so we attempted to characterize and explicate the function of these latrine sites.

With the help of local assistants, I captured adult individuals across four separate social groups and collared them with activity data-logging tags. I then conducted both instantaneous and continuous behavioral and feeding sampling, GIS coordinate sampling, and *ad libitum* observations of behaviors and unusual interactions/situations. Utilizing this large dataset, I was able to show that southern bamboo lemurs exhibit a cathemeral activity pattern, largely influenced by lunar luminance. They were also shown to utilize disparate habitats including an invasive species mono-dominant swamp (similar to plantations) which may provide viable dispersal routes for lemurs existing in a fragmented landscape. Bamboo lemurs of Mandena were found to display the largest dietary breadth of any *Hapalemur* spp., and spent nearly half of their time feeding in the terrestrial stratum. In fact, their selection of these terrestrial foods was predicted by an increased intake of metabolizable energy. While terrestrial predation did not appear to present a greater risk than aerial predation, the lemurs did spend significantly more time in closer proximity to group individuals while using the terrestrial stratum, indicating increased anti-predator behavior. Lastly, their utilization of visually conspicuous latrine sites (regardless of habitat) was shown to provide a multimodal communicatory means for both demarcating their territory, as well as providing useful olfactory communication to neighboring and/or potentially intruding conspecifics. This ability to maintain their unique behavioral ecology in the face of fragmented and anthropogenic landscapes is evidence of their flexibility. Taken as a whole, these explorations of specific behavioral and feeding disparities among *H. meridionalis* suggest that this lemurid clade may not be as specialized as once thought, allowing potentially less conventional conservation efforts to take place in populations whose survival appears dire.

To my parents, James and Mary Anne, for their unconditional love and support

Contents

General Introduction

Ecological flexibility is loosely defined as the ability of an organism to adjust to changes, e.g., anthropogenic, gradual, stochastic, within its environment (Wieczkowski, 2003; Isaac and Cowlishaw, 2004; Nowak and Lee, 2013). In more specific terms, *flexibility* encapsulates behavioral modifications to the diet, exploitation of alternative food sources, as well as altering activity and vertical strata in response to new dietary opportunities. This ability to expand niche breadth is key to withstanding the risks of anthropogenic and/or stochastic habitat modification (Lee, 2003).

Niche partitioning can affect a species' ability to adapt to or recover from environmental changes. Specialist species, i.e., those who specialize on particular foods and/or habitats are most vulnerable to disturbances that affect their narrow dietary breadth or habitat requirements. However, many species show large intra- and inter-specific variation (Shipley et al., 2009), and so this definition is often regarded as when greater than 60% of a species' diet consists of a single, distinct genus (Dearing et al., 2000), or family of plants (Fox and Morrow, 1981). By contrast, generalist species can more easily adjust their diets or shift their ranging patterns as long as there is still some suitable habitat available nearby (Channell and Lomolino, 2000; Devictor et al., 2010).

On the other hand, flexibility in the use of habitat is equally important as dietary flexibility when understanding the ecological flexibility of a species. Essentially, if a species shows a high degree of ecological flexibility, it likely will be less affected by the degradation of habitat than one that relies on certain structural vegetation characteristics only present in specific habitat types. Specifically, habitat generalists should not exhibit large variations in their preference of micro-habitat and/or the structure of different forest types. In contrast, a habitat specialist will often be restricted to only their preferred microhabitat, unable to adjust to differing vegetation structures.

Deforestation of tropical forests is one of the primary threats to global biodiversity (Sala et al., 2000; Achard et al., 2002; Dirzo and Raven, 2003; Asner et al., 2009; Gibson et al., 2011). The destruction, fragmentation, and degradation of remaining habitats are threatening many species' ability to survive (Oates, 2013). While forest fragments typically persist after deforestation, they effectively become islands within an anthropogenic landscape, most of which are unsuitable habitat for the majority of forest species (Broadbent et al., 2008; Laurance et al., 2009). The majority of remaining habitats primarily exist in

small fragments (Pimm and Brooks, 2013); within Madagascar, for example, greater than 80% of forest area exists less than 1 kilometer from an edge (Harper et al., 2007), and thus fragmentation is of great concern for the survival of forest fauna and flora species (Hannah et al., 2008; Ganzhorn et al., 2014). Population extinctions can occur rapidly with most species ultimately disappearing due to any number of non-mutually exclusive factors (Prugh et al., 2008; Laurance et al., 2011). This can be further complicated by invasions by exotic species that threaten the preservation of endemic biodiversity as well as ecosystem restoration efforts (Braithwaite et al., 1989; D'Antonio and Vitousek, 1992). In order to properly manage these situations and conserve primates and other species, it is imperative to understand the relationship between species and their habitats (Onderdonk and Chapman, 2000; Cristóbal-Azkarate and Arroyo-Rodríguez, 2007; Isabirye-Basuta and Lwanga, 2008).

Although fragmentation of populations may result in genetic erosion and increase extinction risk (Caro and Laurenson, 1994; Lande and Shannon, 1996), it has been shown that a mosaic of small, suitable habitat fragments may act as a single large habitat if the fragments are linked via corridors (Bevers and Flather, 1999; Haddad, 2000). In general, corridors are defined as thin strips of habitat (natural or unnatural) that connect two or more otherwise isolated habitat patches, e.g., forest fragments, with many studies validating their utilization by organisms (reviewed in Beier and Noss, 1998). In fact, numerous studies have demonstrated that corridors can facilitate and potentially increase animal movement between fragmented habitats (Haas, 1995; Sutcliffe and Thomas, 1996; Gonzalez et al., 1998; Haddad, 1999; Mech and Hallett, 2001), increase population sizes (Fahrig and Merriam, 1985; Dunning et al., 1995; Haddad and Baum, 1999), increase gene flow (Aars and Ims, 1999; Hale et al., 2001; Mech and Hallett, 2001), and maintain biodiversity (Gonzalez et al., 1998). Thus, a network of stepping stones (i.e., forest fragments) within a critical dispersal distance may act as a means to maintain biodiversity and ecological processes in fragmented, anthropogenic landscapes (da Silva and Tabarelli, 2000; Hale et al., 2001; Lens et al., 2002).

Madagascar is known for its extreme biodiversity and endemism, and often identified as one of the 'hottest' biodiversity hotspots in the world (Dumetz, 1999; Myers et al., 2000; Ganzhorn et al., 2001; Mittermeier et al., 2010). It is the fourth largest island in the world, located approximately 400 km off the southeastern coast of Africa in the Indian Ocean. More than 100 endemic strepsirrhine species are now recognized throughout Madagascar (Mittermeier et al., 2008; IUCN, 2012), and the recent reassessment by the International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC) Red List

(2012) found that 94% of lemurs are threatened, making the primates of Madagascar the most threatened mammalian taxa in the world (Schwitzer et al., 2013). Habitat loss due to slash-and-burn agriculture (*tavy*) and timber harvest, charcoal production, cattle grazing, as well as bushmeat hunting, continue to jeopardize lemurs' survival (Mittermeier et al., 2008, 2010; Golden, 2009; Jenkins et al., 2011; Schwitzer et al., 2014). As habitat destruction persists in isolating the remaining lemurs to forest fragments, the need for regenerating forests and connecting those remaining fragments is crucial to prevent extinctions (Wearn et al., 2012). As such, it is imperative to understand the responses of native plants and animals to disturbance if we are to create effective buffer zones and corridors that combine secondary and natural habitats (Ganzhorn et al., 2007; Hannah et al., 2008; Kremen et al., 2008; Irwin et al., 2010; Donati et al., 2011; Campera et al., 2014). Although the future may appear bleak for these threatened primates, systematic research may help to curb the present perils facing lemurs. Furthermore, on a global scale it has been shown that Malagasy lemurs play a much larger role in their respective ecosystems, e.g., seed dispersal, compared to primates in the Neotropics or mainland Africa that live sympatrically with other groups of animals (e.g., birds, bats, and non-primate medium-sized mammals) that contribute on a larger scale to their respective environments (Jernvall and Wright, 1998). As lemurs are essential to maintaining the unique forests of Madagascar, their demise would likely trigger extinction cascades (Jernvall and Wright, 1998; Ganzhorn et al., 1999; Razafindratsima and Dunham, 2014).

In addition to the dire situation facing many of Madagascar's remaining habitats, the island itself is considered to be one of the most seasonally harsh environments for primates (Wright, 1999). Lemurs, like many other primates living in seasonal environments, have responded with a number of unique behavioral and physiological traits that have helped them to cope with changing conditions (Wright, 1999). Fluctuations in species' circadian rhythms (Fernandez-Duque, 2003; Kappeler and Erkhart, 2003; Donati and Borgognini-Tarli, 2006; Donati et al., 2013), selection for specific food items based on availability (Milton, 1980; Foster, 1982; Hemingway and Bynum, 2005) or nutritional components (Smythe et al., 1982; Terborgh, 1986; Janson and Emmons, 1990; Hemingway and Bynum, 2005; Irwin, 2008a), and changes in ranging patterns (Charnov, 1976; Janson, 2000; Hemingway and Bynum, 2005; Irwin, 2008b) are all effective responses to seasonality influenced by phenological patterns as well as abiotic factors. With changes and having to adapt to exploit new resources, a shift from arboreal to terrestrial travel and feeding may be necessary (Campbell et al., 2005; Pozo-Montuy and Serio-Silva, 2006; Mourthe et al., 2007). For many lemur species, habitat

use and behavioral ecology are determined by the distribution of critical resources (Ganzhorn et al., 1997). As habitats disappear, it has been postulated that primates that are habitat specialists will be affected more than habitat generalists (Emmons et al., 1983; Peres, 1993). However, high dietary diversity has been proposed to buffer primates against extinction (Harcourt et al., 2002).

Many lemurs exhibit disparate behavioral ecologies dependent on their available resources, habitat, and sympatric species, thus making them an excellent taxon with which to understand the extent of their ecological flexibility. It has also been shown that within a selectively logged rainforest and/or forest remnants in an agricultural landscape, grey bamboo lemurs *H. griseus* were generally less susceptible to habitat degradation than more frugivorous species, i.e., *Propithecus* spp., *Eulemur* spp., *Varecia* spp. (Grassi, 2001; Dehgan, 2003; Arrigo-Nelson, 2006; Schwitzer et al., 2007; Martinez, 2008; Irwin et al., 2010). Diademed sifaka *P. diadema* in degraded and fragmented habitats displayed lower mass, smaller home ranges, consumed less fruit, and showed reduced scent marking, aggression and play behavior than in pristine forest (Irwin, 2006, 2008a,b). However, while bamboo lemurs did show some dietary differences and smaller ranges, overall they showed no sign of reduced health. Even considering these small variations, there appear to be large differences among congeners. The great bamboo lemur *Prolemur simus* is able to survive in heavily disturbed forest fragments, whereas the golden bamboo lemur *H. aureus* is completely absent from fragments (Wright et al., 2008). While most site-specific research often touts their main findings as the rule, we are becoming more acutely aware that these so-called specializations are the result of ecological constraints due to that specific habitat available to the species. Instead, by looking at the entire species or genus as a whole, we are better able to understand the site variations and behavioural flexibilities that are displayed. It has been suggested that "specialization" is a local population phenomenon, rather than a species intrinsic trait (Fox and Morrow, 1981). Furthermore, the classification of species as either specialists or generalists may be beside the point, for they may represent temporary states as a (possibly fine-tuned) response to local abiotic and biotic conditions (Nowak and Lee, 2013).

On occasion, it has been observed that when there are alternative habitats adjacent to the degraded habitat (e.g., mangrove swamp, mono-dominant plantation), even dietary specialists can adapt and exploit them (Grimes and Paterson, 2000; Galat-Luong and Galat, 2005; Nowak, 2008). It has been recently suggested that the occasional use of wetland habitat

by primates may become obligate if preferred upland habitat becomes increasingly disturbed (Nowak, 2008, 2013; Quinten et al., 2009). However, when species are highly selective within their habitat, the loss of key resources may result in their ultimate demise (Lee and Hauser, 1998). In contrast, low selectivity may enhance a species' chances for survival, even in heavily disturbed habitats (Guo et al., 2008).

Among the most ecologically diverse areas of Madagascar is the Anosy region along the southeast coast (Barthlott et al., 1996; Ramanamanjato et al., 2002). Nearly 90% of the original littoral forest of Madagascar has already been lost. Preceding human colonization, littoral forests covered approximately 465,100 ha of the total land surface of Madagascar. Today, only about 47,900 ha remain, with only 695 ha (1.5%) existing within the protected-areas network (Consiglio et al. 2006). Within the Tolagnaro region, approximately 3,128 ha are all that remains, with much of this degraded and/or fragmented throughout the coastal landscape (Bollen and Donati, 2006; Rabenantoandro et al. 2007). This region provides a complex mosaic of heavily fragmented upland and swamp forest habitats, old and new plantations, and mono-dominant invasive species, thus presents itself as an excellent model with which to explore the behavioral and feeding ecological flexibilities amongst the lemurs who inhabit it.

Bamboo lemurs (*Hapalemur* spp. / *Prolemur simus*)

Often considered the most specialized of the Malagasy primates are the gentle lemurs (or bamboo lemurs as they are more commonly known), genera *Hapalemur*/*Prolemur* (Geoffroy 1851), Order Primates, family Lemuridae. They are small-bodied primates, albeit medium-sized lemurid strepsirrhines, weighing on average between 800 – 1300 g (Tan, 2006). Their distribution is not entirely known, as the genera are cryptic, leading to difficulties in attaining true population density estimates, and in some remote sites, lack of indicators of presence. The general distribution of the genera includes the eastern humid forests as well as the more arid deciduous forests of north and north-western Madagascar (Figure 1).

Figure 1. Distribution of *Hapalemur* spp. throughout Madagascar (Mittermeier et al., 2010)

Bamboo lemur activity rhythms remain a subject of debate, with anecdotal observations from captivity describing a cathemeral activity pattern for *H. griseus* and *P. simus* (Santini-Palka, 1994); however, only Mutschler (1999) has attempted to elucidate this in the field. While *H. alaotrensis* were shown to be seasonally active at night, these data are based on one night/month sampling (Mutschler, 1999), and thus cannot be considered conclusive of a cathemeral activity pattern. Previous studies on *Hapalemur* spp. at Ranomafana National Park in southeast Madagascar alluded to the possibility of nocturnal activity by bamboo lemurs through seasonally reduced diurnal activity (Overdorff et al., 1997), but later research noted that they displayed a strict diurnal activity pattern with no long periods of rest during the day (Tan, 1999; Grassi, 2001).

As small-bodied folivores, this genus is peculiar as they display a dietary predilection for bamboo (family Poaceae, subfamily Bambusoideae) (Wright, 1986; Overdorff et al., 1997; Tan 1999; Grassi, 2006), a subfamily of grasses that contain highly toxic cyanogenic properties (Glander et al., 1989; Ballhorn et al., 2009). Despite this preference, bamboo lemurs are capable of subsisting on diets consisting of non-bamboo food items and in habitats that are highly degraded (Mutschler et al., 1998; Mutschler, 1999; Grassi, 2001, 2006; Eppley

and Donati, 2009; Eppley et al., 2011). In Ranomafana NP, there are three sympatric bamboo lemurs (Tan, 1999); however, there may be additional subspecies here (Rabarivola et al., 2007). Although they all preferentially feed on bamboo species, they maintain disparate dietary niches by selecting for different food items/parts from these plant species (Tan, 1999).

Bamboo is often known for its low nutrient and low caloric content, yet many species have evolved a suite of adaptations in order to utilize this often-abundant resource. Perhaps the most well-known is the giant panda *Ailuropoda melanoleuca* (Dierenfeld et al., 1982; Schaller et al., 1985), which was recently discovered to shift its habitat use in order to access the most nutritious bamboo shoots (Nie et al., 2015). Other mammals have also adapted strategies to utilize bamboo, such as the red panda *Ailurus fulgens* (Johnson et al., 1988) and numerous primate species, including the Bale monkey *Chlorocebus djamdjamensis* of Ethiopia (Mekonnen et al., 2010), the golden monkey *Cercopithecus mitis kandti* in Uganda (Twinomugisha et al., 2006; Twinomugisha and Chapman, 2008), snub-nosed monkeys *Rhinopithecus bieti* (Yang and Zhao, 2001; Xiang et al., 2007), and a population of owl-faced monkey *C. hamlyni* in Rwanda that is entirely restricted to bamboo forests (Easton et al., 2011). Furthermore, mountain gorillas *Gorilla beringei beringei* (Grueter et al., 2014) and muriquis *Brachyteles arachnoides* (Strier, 1991) also feed on bamboo.

Bamboo is abundant throughout Madagascar (Dransfield 2000); however, while bamboo lemurs may specialize in their ability to digest the potentially toxic parts of bamboo, they can also be flexible in their diet, activity, and ranging (Grassi, 2001). Furthermore, not all *Hapalemur* species feed on bamboo, most notably the Alaotran gentle lemur, *H. alaotrensis*, which is confined to the few remaining reed/papyrus beds and forest habitats surrounding Lac Alaotra (Mutschler and Feistner 1995; Mutschler et al. 1998, 2001). This Critically Endangered lemur spends more than 95% of feeding time selecting four different plant species (Mutschler et al. 2001; Mutschler 2002), substituting bamboo with sedges, e.g. papyrus (*Cyperus* spp.), and plants belonging to the grass family, e.g. reeds (*Phragmites*), southern cut grass (*Leersia*), and millet (*Echinochloa*) (Pollock 1986; Mutschler et al. 1998; Mutschler 1999). Similarly, the southern gentle lemur, *H. meridionalis* (Warter et al. 1987; Warter and Tattersall 1994), is known to inhabit an area devoid of woody bamboo.

Southern bamboo lemur *Hapalemur meridionalis*

The southern bamboo lemur or southern gentle lemur (*H. meridionalis*), locally referred to as *halo*, was first identified as a subspecies of *H. griseus* (Warter et al., 1987) and

later formally described in 1994 (Warter and Tattersall, 1994). It was not until fifteen years later that genetic studies were able to upgrade these lemurs to full species status based on their mitochondrial DNA sequence (Fausser et al. 2002; Pastorini et al. 2002; Rabarivola et al. 2007).

The full distribution of *H. meridionalis* is not fully known but it is estimated that their remaining habitat is less than 20,000 km^2 (IUCN 2012). Due to increased fragmentation of remaining forest within southeast Madagascar, this species is listed as Vulnerable (VU B1ab (iii,v)) (IUCN, 2012). Among areas in which this species is known to occur, low densities have been recorded in Ambatotsirongorongo Conservation Zone (Ramanamanjato et al., 2002), Andohahela National Park (Feistner and Schmid 1999; Fausser et al. 2002; O'Connor et al. 1986; Rabarivola et al. 2007; Raharivololona and Ranaivosoa 2000), Midongy du Sud National Park (Mittermeier et al. 2010), and Tsitongambarika Nouvelle Aire Protégée (Birdlife International, 2011; Nguyen et al., 2013). Unlike other species of *Hapalemur* spp., they are not known to live sympatrically with congeners. Their distribution may extend further north than previously thought: a possible hybrid between *H. meridionalis* and *H. g. ranomafanensis* has been recently discovered in the region close to Atsimo near Ranomafana National Park (Rabarivola et al. 2007). With the exception of Mandena and some sections of Tsitongambarika, woody bamboo is known to occur at these locations and is fed on by *H. meridionalis* (O'Connor et al. 1986; Feistner and Schmid 1999). With this, a number of interesting questions arise as to the behavioral, ecological, and physiological plasticity of these small-bodied folivorous primates.

It appears *H. meridionalis* employ a behavioral plasticity and dietary flexibility to subsist in a littoral forest that is devoid of woody bamboo and has considerable marsh/swamp areas (Eppley and Donati 2009; Eppley et al. 2011). Over the course of the preliminary study at Mandena, *H. meridionalis* was observed to spend near equal amounts of time resting and feeding, while spending minimal amounts traveling and other activities (Eppley *et al*. 2011). Compared to congeners at Ranomafana National Park (Tan 2000, 2006), *H. meridionalis* was found to exhibit a similar activity budget. Dissimilar from other bamboo lemurs, the southern gentle lemur displayed a significant portion of time feeding from a terrestrial stratum. The diet of *H. meridionalis* consisted of a mixture of graminoids (terrestrial grasses, reeds, and sedges), lianas and their leaves, flowers, fruits, and fungi. When compared to congeners that spend a majority of their time feeding on woody bamboo, it appeared that the southern gentle lemur replaced feeding on woody bamboo with that of terrestrial herbaceous grass.

Preliminary study of this species within Mandena, however, only allowed us a glimpse of their behavioral ecology during the austral winter, at a time when phenological productivity was at its lowest. This indicates that they may be responding both behaviorally and ecologically to cope within a fragmented habitat without woody bamboo, feeding on myriad grass species in open-canopy areas as well as extending their activity cycle over the full 24-hours (i.e., cathemerality) (Engqvist and Richard 1991). Altogether, these unique adaptations make this population of *H. meridionalis* important for the study of lemur responses to human-altered landscapes.

It was also during this time that *H. meridionalis* were observed to descend to the ground to defecate in succession either near or under a high-rooted tree, i.e., a *Uapaca* spp. Accumulations of hardened fecal matter were identified in these sites, and so it was postulated that, similar to scent-marking (Mertl-Millhollen 1979; Lewis 2005), latrines may act as a means of demarcating home range boundaries (Irwin et al., 2004; Eppley and Donati, 2010). In fact, the latrine sites we observed *H. meridionalis* utilize were in areas of home range overlap with neighboring conspecifics' groups.

This preliminary study of *H. meridionalis* resulted in an expansion of our knowledge of this relatively unknown species, but also led to many questions about the mechanisms by which this species adapts within disparate environments. Understanding these localized strategies employed by supposedly dietary specialists would greatly assist in our understanding of how species cope within fragmented and seasonal anthropogenic landscapes. Growing knowledge of the ecological flexibility of bamboo lemurs (Mutschler, 1999; Grassi, 2006; Eppley et al., 2011), as well as the unique habitat matrix that Mandena provides, make this species and site an excellent model to examine the ability of a small-bodied lemur to utilize distinct habitats, and potentially corridors, within the anthropogenic landscape.

Study site

I investigated the behavioral and ecological adaptability of *Hapalemur meridionalis* within a seasonal, fragmented littoral environment in southeast Madagascar. The Mandena littoral forest (24°95'S, 46°99'E; Figure 2), approximately 12 km north of Tolagnaro (Fort-Dauphin), was the focus of my study as the site provides an excellent model for understanding how the supposedly inflexible *Hapalemur* spp. subsist within an environment devoid of bamboo. The site encompasses an area of 148 ha of upland littoral forest, including

approximately 82 ha of interspersed swamp and *Melaleuca* swamp that segregate the two largest fragments (Ganzhorn et al., 2007), thus it allows us to explore the species' ecological flexibility within a fragmented habitat matrix. While there are many excellent models of continuous environments within the Anosy region that could have supported a comparative aspect to my study, namely Parcel 1 of Andohahela National Park (24°42'S, 46°11'E) and/or the Ampasy valley of northern Tsitongambarika Nouvelle Aire Protégée (24°34'S, 47°09'E: Nguyen et al., 2013), I chose to solely focus on bamboo lemurs of Mandena.
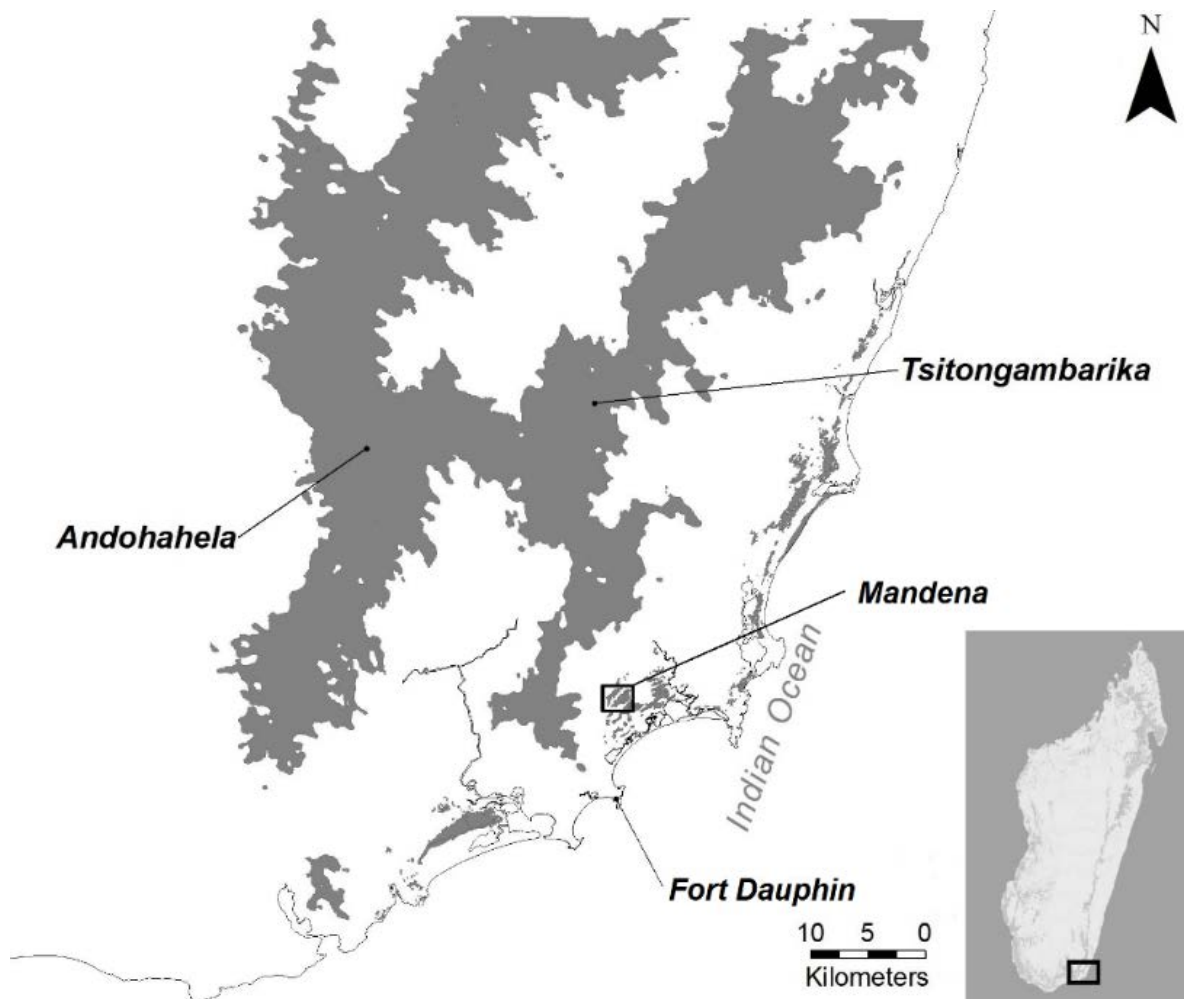

Figure 2. Location of Mandena littoral forest in southeast Madagascar, relative to the larger, continuous forests of Andohahela National Park and Tsitongambarika.

Aims of the study

The aims of the study were:

1: To investigate the proximate and ultimate control of cathemerality using a small, folivorous primate as a model (**Chapter 1**).

2: To investigate the role of an invasive species habitat on the behavioral ecology of a small-bodied folivore, (**Chapter 2**).

3: To investigate the costs and benefits that are associated with expansion to a terrestrial dietary niche by a small, arboreal primate (**Chapter 3**).

4: To investigate the functional role of terrestrial latrine sites utilized by an arboreal primate (**Chapter 4**).

While the aims provide a broad scope from which I investigated the ecological flexibility of *H. meridionalis*, the specific questions and empirical data contributing to this dissertation were:

Chapter 1

(1) Do *H. meridionalis* exhibit a cathemeral activity pattern?

(2) Which proximate factors, including photoperiodic variations and lunar luminosity, influence the activity profile of southern bamboo lemurs?

Chapter 2

(1) Are there floristic diversity and structural characterization differences between each of the habitats (i.e., upland littoral forest, littoral swamp, and *Melaleuca* swamp) within Mandena?

(2) What is the distribution of the activities of this folivorous primate model within each of the habitats, and do their home ranges constitute similar proportions of each habitat?

(3) Can *Melaleuca* (i.e., an invasive mono-dominant tree species) facilitate movement between upland forest fragments and/or natural littoral swamp, and if this invasive habitat provides additional services, e.g., suitable feeding and resting locations, could it potentially be used as dispersal corridors?

Chapter 3

(1) Is the expansion to the terrestrial dietary niche seasonal, specifically in relation to precipitation and temperature?

(2) Does daily nutritional intake of terrestrial food items represent a markedly higher dietary quality than arboreal food items (i.e., protein/fiber ratio and metabolizable

energy), thus providing justification for their increased utilization of a potentially risky stratum?

(3) With potentially increased canopy exposure while feeding on the ground, do bamboo lemurs maintain closer proximities to group members as compared to when they feed arboreally, in order to offset possible predation risks?

Chapter 4

(1) Are latrine sites situated more in the non-core area of bamboo lemur home ranges, thus acting as a territorial marker? Additionally, are visually conspicuous latrine sites or discreet sites used more frequently?

(2) Do females scent-mark more frequently during the strict breeding season, potentially advertising their sexual cycle?

(3) Do bamboo lemurs overmark the scent-marks of group mates, and if so, does this occur more during the breeding or non-breeding periods of the year?

CHAPTER 1

Cathemerality in a small, folivorous primate: proximate control of diel activity in
Hapalemur meridionalis

With Jörg U. Ganzhorn and Giuseppe Donati

Abstract

A non-adherence to a strict diurnal or nocturnal activity cycle is prevalent among mammals, including taxa of Lemuridae, but rare among other primates. While non-mutually exclusive ecological hypotheses attempted to explain the evolution of this activity, termed cathemerality, as either an old or a recent phenomenon, the scarcity of systematic data collected over 24-hours limits our potential to explore its proximate and ultimate determinants. Among strepsirrhines, systematic studies involving only two lemurid genera (*Eulemur* and *Lemur*) have recorded this activity pattern, while fewer quantitative observations are available for other taxa. If cathemerality could be shown in most members of Lemuridae despite their different ecological adaptations, this would support the hypothesis that this trait is basal and appeared early during lemurid evolution. Here we investigated whether the folivorous southern bamboo lemur (*Hapalemur meridionalis*) exhibits cathemeral activity, and determine which environmental factors influence its pattern. We deployed ten archival tags across four social groups to continuously record activity data over a 15-month period. This allowed us to generate a diurnal/nocturnal (DN) ratio for each 24-h period and assess their diel activity. Our data suggest that southern bamboo lemurs are cathemeral within Mandena; while climatic factors showed no influence, nocturnal activity increased with greater nocturnal luminance. Despite contrasting dietary niches, visual morphologies, and body sizes between *Hapalemur*, *Eulemur* and *Lemur*, all three exhibit cathemerality and lunarphilia. The close phylogenetic proximity of these lemurids supports this flexible activity pattern as an ancestral trait that likely dates to the origin of the Lemuridae radiation.

Introduction

Activity cycles are historically recognized as being either strictly diurnal or nocturnal (Ashby 1972); however, these can vary widely within and across mammalian taxonomic groups (Curtis and Rasmussen 2006). Given the significant sensorial contrasts within each of these two activity segments, the temporal organization of behaviour would have been significant at the commencement of each taxonomic radiation (Charles-Dominique 1975; Aschoff et al. 1982; Halle 2006). Many mammals display an ability to shift their activity

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across the 24-hour period, including large numbers of Artiodactyla, Carnivora, Perissodactyla, Rodentia, and Xenarthra (Hall et al., 2012). This behavioural trait, known as 'cathemerality', is a non-adherence to a strict diurnal or nocturnal activity, often showing several peaks over the diel (i.e., 24 hours) day (Tattersall 1987, 2006).

Activity patterns result from a multi-factorial interaction including the species' endogenous (i.e., circadian) rhythm, entrainment mechanisms, and masking effects of specific environmental cues (Aschoff et al. 1982). Among mammals, photoperiodic change (e.g., the alternation of light to dark, or day length) is the most frequently demonstrated entrainment (synchronizing) agent, also referred to as a Zeitgeber (Aschoff et al. 1982; Heldmaier et al. 1989; Curtis et al. 1999; Kappeler and Erkert 2003; Fernandez-Duque and Erkert 2006). Masking factors (e.g., lunar luminance or environmental variables), can override endogenous circadian rhythms by inhibiting or enhancing activity (Erkert 1989; Chiesa et al. 2010). Decreasing activity with increasing lunar illumination (lunarphobia) is common in many mammals (Penteriani et al. 2011; Prugh and Golden 2014), including carnivores (Halle 2000; Packer et al. 2011), bats (Erkert 1974, 1976; Saldaña-Vásquez and Munguía-Rosas 2013), rodents (O'Farrell 1974; Kaufman and Kaufman 1982; Corsini et al. 1995; Upham and Hafner 2013), and primates (Bearder et al. 2006; Starr et al. 2012; Rode-Margono and Nekaris 2014). Conversely, relatively few mammals display lunarphilia, i.e., increasing nocturnal activity with increasing nocturnal luminosity (Horning and Trillmich 1999; Prugh and Golden 2014). Interestingly, however, many nocturnal primates display lunarphilia (Nash 1986, 2007; Bearder et al. 2001; Gursky 2003), a strategy especially common among cathemeral primates (Erkert 1974, 1976; Charles-Dominique et al. 1980; Wright 1989; Colquhoun 1998; Curtis et al. 1999; Donati et al. 1999, 2001, 2009, 2013; Kappeler and Erkert 2003; Fernandez-Duque 2003; Donati and Borgognini-Tarli 2006; Fernandez-Duque and Erkert 2006; Schwitzer et al. 2007; Fernandez-Duque et al. 2010). This phenomenon has been explained by primates' high reliance on visual cues, resulting in increased foraging efficiency and detection of potential predators (Gursky 2003; Bearder et al. 2006). This argument would predict that primates with visual adaptations better suited for nocturnal vision, e.g. the presence of a *tapetum lucidum*, would rely less on moon luminosity.

The only monophyletic primate radiation that displays diurnal, nocturnal, and cathemeral genera are the lemurs of Madagascar and as such they represent an ideal model to study determinants of activity pattern in our Order. Among these strepsirrhines, cathemerality is almost exclusively reported in the family Lemuridae, most conclusively from two genera:

Eulemur (Overdorff 1988; Wilson et al. 1989; Andrews and Birkinshaw 1998; Colquhoun 1998; Curtis et al. 1999; Donati et al. 1999, 2009; Kappeler and Erkert 2003; Rasmussen 2005; Donati and Borgognini-Tarli 2006; Schwitzer et al. 2007) and *Lemur* (Parga 2011; Donati et al. 2013; LaFleur et al. 2014; Rea et al. 2014).

The evolution of cathemerality in lemurs remains a topic of debate largely dominated by two competing views. The first hypothesis is based on stable adaptations, arguing that cathemeral activity represents an ancestral behavioural strategy in the lemurids, potentially driven by non-mutually exclusive ecological determinants (Wright 1999; Curtis and Rasmussen 2002; Donati et al. 2007, 2009, 2013). In contrast, the evolutionary disequilibrium hypothesis states that cathemerality represents a transitional state in a current shift from a nocturnal to a diurnal activity phase, potentially due to the recent demise of certain predators (i.e., large diurnal raptors) and competitors (i.e., large-bodied diurnal lemurs) in Madagascar (Martin 1972; van Schaik and Kappeler 1993, 1996; Kappeler and Erkert, 2003). This faunal extinction (Goodman et al. 1994a, 1994b; Simons et al. 1995; Dewar 1997) occurred shortly after humans arrived to Madagascar approximately 4,000 – 2,300 years ago (Tofanelli et al. 2009; Dewar et al. 2013). The latter argument suggests that the loss of these strong selection pressures was enough to transition an entire guild of lemurs from a nocturnal to diurnal lifestyle, resulting in the intermediate phase we see today (van Schaik and Kappeler 1993, 1996; Kappeler and Erkert 2003). While the non-adaptive nature of this hypothesis makes it is inherently difficult to test, this idea would predict that all lemurs above a body size that would make them less vulnerable to current diurnal predators would have shifted to diurnality.

In terms of proximate factors regulating activity rhythms, seasonal activity variations controlled by photoperiodic changes and low nocturnal luminosity levels have been observed in most cathemeral lemurs (Colquhoun 1998; Curtis et al. 1999; Donati et al. 1999, 2001; Kappeler and Erkert 2003; but see Rasmussen 1999; Tarnaud 2006), while others in less seasonal habitats were less influenced by these factors (Overdorff 1988; Overdorff and Rasmussen 1995; Andrews and Birkinshaw 1998; Vasey 2000; but see Donati and Borgognini-Tarli 2006; Donati et al. 2009, 2013). A further conflicting trait among lemurids is their disparate retinal morphologies, which clearly distinguish them from strictly nocturnal lemurs like Cheirogaleidae (Kirk 2004, 2006). Many nocturnal birds and mammals, including nocturnal primates, maintain a *tapetum lucidum* (i.e., a reflective, specialized layer of cells behind the retina) that allows the taxon to make use of minimal available light (Ollivier et al.

2004; Ankel-Simons and Rasmussen 2008). By contrast, the *area centralis* is a common retinal adaptation for diurnal vision (Curtis and Rasmussen 2002; Peichl 2005; Dyer et al. 2009). Of the confirmed cathemeral lemurids, *Eulemur* seems to possess neither of these morphologies, although the presence of a *tapetum* in this genus still needs to be confirmed (Kirk 2006). This observation has led some authors to suggest that their nocturnality may potentially be constrained by moon phase (Colquhoun 1998; Kappeler and Erkert 2003; Donati and Borgognini-Tarli 2006; Donati et al. 2009; but see: Overdorff and Rasmussen 1995; Curtis et al. 1999). Conversely, the *Hapalemur*/*Lemur*-clade seem to possess both retinal traits (Pariente 1979; Curtis and Rasmussen 2002). In terms of eye morphometrics measured as relative cornea size, however, cathemeral birds and lemurs have been shown to possess intermediate traits between diurnal (high visual acuity) and nocturnal (high visual sensitivity) adaptations, potentially allowing them to exhibit flexible activity patterns (Kirk 2006; Hall and Ross 2007). Although still labelled as diurnal in many reports, the clade *Hapalemur*/*Lemur* shows values of relative cornea size which are comparable with those of fully recognized cathemeral lemurs (i.e. *Eulemur*) and certainly above the upper range of diurnal primates (Kirk 2006).

However, the absence of systematic data collected over the 24-hours for most lemur species hampers our ability to understand proximate and ultimate determinants of cathemerality. As for bamboo lemurs (*Hapalemur* spp.), for example, there have only been anecdotal reports from the wild (Mutschler 1999; Tan 2006) and captivity (Santini-Palka 1994), with no systematic studies yet to verify these observations. Mutschler (1999) reported *H*. *alaotrensis* as displaying cathemerality but the limited data set (i.e., seven observation nights) does not allow for any rigorous testing of exogenous factors that may influence this pattern, nor can it explicitly confirm a cathemeral activity rhythm. Nevertheless, the proposal of bamboo lemurs as cathemeral is intriguing as they display a wholly disparate dietary niche from *Eulemur*/*Lemur*, with *Hapalemur* maintaining a folivorous diet composed largely of grasses (including bamboo) and sedges (Wright 1986; Overdorff et al. 1997; Mutschler 1999; Tan 1999, 2006; Grassi 2002, 2006; Eppley et al. 2011).

In this study we present systematic 24-h activity pattern data recorded over a period of 15 months as recorded via automatic data-logging tags deployed on southern bamboo lemurs, *Hapalemur meridionalis*. To evaluate the presence and potential proximate factors of cathemerality in this species, we analysed the temporal distribution of activity in connection

with various environmental factors (i.e., ambient temperature, precipitation, and day length) and lunar luminosity.

On the basis of the anatomical adaptations of the bamboo lemurs we predict that:

(3) They will exhibit cathemerality because of their possession of an intermediate eye morphology, i.e., visual adaptations for both diurnal and nocturnal activity

(4) Their activity rhythm will be minimally constrained by photoperiodic variations and nocturnal luminance because of the presence of specialized adaptations for nocturnal vision, i.e. the *tapetum lucidum*.

If bamboo lemurs exhibit a cathemeral activity pattern, as predicted, then the phylogenetic proximity of all confirmed cathemeral lemurids (Horvath et al. 2008) would support this activity as a basal trait for the Lemuridae (Donati et al. 2013).

Methods

Study Site and Species

The study was conducted in Mandena littoral forest (24°95'S 46°99'E) in southeast Madagascar, approximately 10 km north of Fort-Dauphin (Tolagnaro). The encompassing protected area is 148 ha of fragmented and degraded littoral upland forest with approximately 82 ha of interspersed swamp (Ganzhorn et al. 2007). Littoral forests occur within 3 km of the coast and are characterized as growing on sandy soils and typically having a low canopy (Dumetz 1999).

Southern bamboo lemurs (*Hapalemur meridionalis*) are medium-sized lemurs, characterized as folivores with a female-dominated social structure (Eppley et al. 2011, 2015; TME et al. unpublished data) similar to congeners (Waeber and Hemelrijk 2003; Tan 2006). Southern bamboo lemurs in Mandena have a diet devoid of bamboo, instead focusing their feeding on terrestrial grasses and fruit when available (Eppley et al. 2011). In addition to the southern bamboo lemurs, the cathemeral *Eulemur collaris* and nocturnal *Microcebus murinus*, *Cheirogaleus medius*, *C. major*, and *Avahi meridionalis* are all present in the Mandena area (Ganzhorn et al. 2007).

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Table 1 Group composition of habituated *H. meridionalis* in Mandena

Group	Total ind.	Ad. ♀	Ad. ♂	SA ♀	SA ♂	Juv ♀	Juv ♂	Infant
1	3-6	3	2	1		1		2
2	3-4	1	2				1	1
3	4-5		3			2		
4	8-9	2	1	1	1	1	2	2

Total individual column represents the range of animals within the social group observed each month from October 2012 – December 2013

Ten adult *H. meridionalis* across four neighbouring, habituated social groups (Table 1) were captured in October 2012 by an experienced Malagasy technician via Telinject® blow darts containing a hypnotic anaesthesia (4 mg/kg of ketamine hydrochloride or tiletamine hydrochloride). All animals recovered from anaesthesia within 1.5 hours and were not moved from the capture site. There were no injuries as a consequence of the captures and animals were followed until regaining full mobility.

Individuals were fitted with external radio-transmitters with an archival tag (ARC400, Advanced Telemetry Systems, Isanti, MN, USA). Each tag contained an activity sensor that recorded a cumulative proportional rate of activity (i.e., movement) at preselected intervals, in our case every fifteen minutes, throughout the duration of the study, October 2012 – December 2013. Tags were removed from subjects in December 2013 via recapture following the methods previously described, with activity data retrieved at the tag production site (Advanced Telemetry Systems, USA). Although we conducted full-day focal observations with these lemurs from January – December 2013, for the purposes of this paper we will only discuss the influence of abiotic factors on their cathemeral activity as recorded by the data-logging tags.
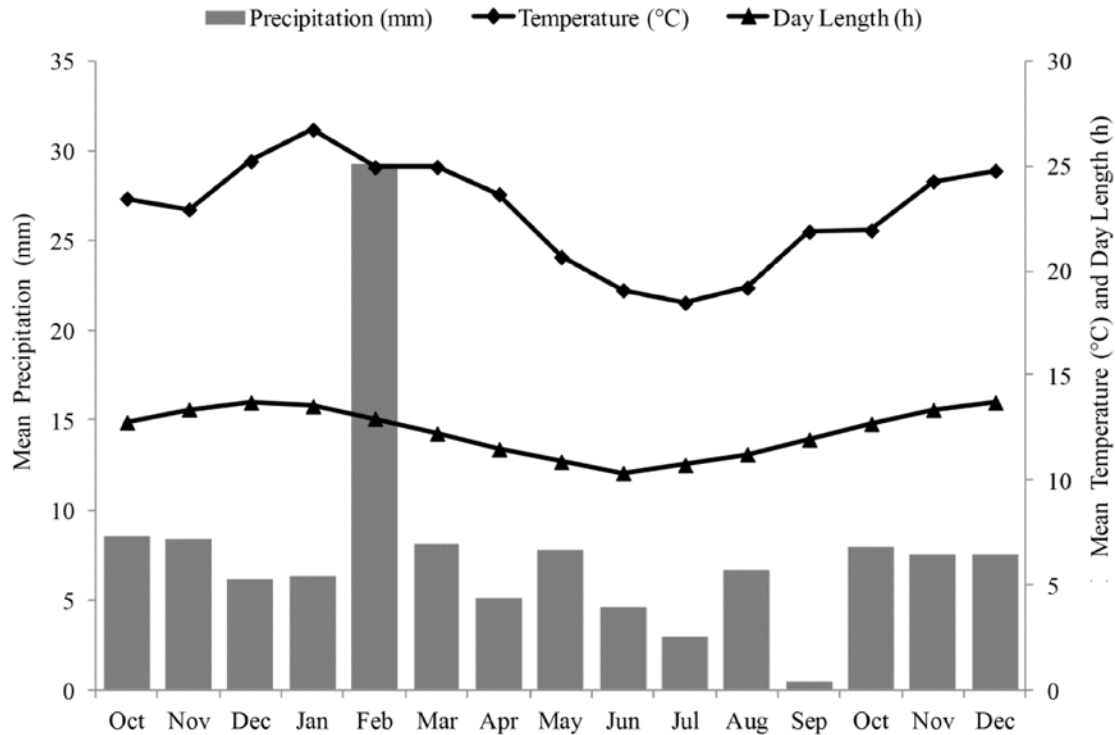
Fig. 1 Profile of monthly mean temperature (°C), mean precipitation (mm), and mean day length (h) for the Mandena littoral forest from October, 2012 through December, 2013

Temperature and Precipitation

Climatic factors can be highly variable within the littoral forests of southeast Madagascar (Bollen and Donati 2005), and as such our data do not closely reflect historical records for the area (Donati and Borgognini-Tarli 2006; Fig. 1). Temperature was recorded in 30-mins intervals with Lascar EL-USB-1 temperature data loggers (Lascar Electronics Inc., USA), operated by custom software (EasyLog USB Version 5.45, Lascar Electronics), over the course of the entire study period. Four data loggers were positioned throughout the study site in order to account for the effect of differing vegetation types (two in the upland littoral forest, two in the littoral swamp), with the monthly means (°C) calculated across all four. Precipitation (mm) was measured every day at 6:00h using a rain gauge placed in camp (which lies within the study site forest).

Astronomical Data

Sunset and sunrise, moonset and moonrise, as well as morning and evening twilight times were obtained from the US Naval Observatory Astronomical Calendar (http://aa.usno.navy.mil/data), using geographic coordinates for Mandena. As twilight times

for both dawn and dusk refer to civil twilight (-6° below horizon), we used this to calculate astronomical twilight (-18° below horizon) as animals have been shown to make use of this minimal available light (Erkert 2003; Kappeler and Erkert 2003; Donati and Borgognini-Tarli 2006). We determined that astronomical twilight corresponded to approximately 69 minutes before and after sunrise and sunset, respectively.

Nocturnal luminosity (NL) is difficult to record in a tropical rainforest, and simply accounting for moon phase does not accurately provide for the amount of light that may have been available on any given night due to shifting moon transit times. To partly circumvent this issue, indirect evaluations of nocturnal luminosity levels were obtained by using an ad hoc program, Moon v.2.0 software (Curtis et al. 1999), which accounts for moon phase and transit time for specific geographic coordinates. This allowed us to evaluate precisely the influence of nightly luminance by way of a nocturnal luminosity index (I), which is calculated with lunar phase (P) and sunrise, sunset, moonrise and moonset times as shown in the following formula:

$$I = \int_{a}^{b} P\, dt$$

where $a < b$ ($dt = 0.24$ h); when sunset precedes moonset, 'a' corresponds to sunset time; when sunset precedes moonrise, 'a' corresponds to moonrise time; when moonset precedes sunrise, 'b' corresponds to moonset time, and when sunrise precedes moonset, 'b' corresponds to sunrise time (Donati and Borgognini-Tarli 2006). The above index ranges between 0.000 – 0.600, although given the geographic coordinates of Mandena, our observed NL index ranged from 0.000 – 0.539. Although moon luminosity has been shown to have the largest effect on activity of other lemurids, the NL only allows for an indirect estimate of nightly nocturnal luminance, and other factors such as rainfall and cloud cover may affect animal activity (Donati and Borgognini-Tarli 2006).

Data Analyses

Ten archival tags were deployed, with data successfully recovered from seven. We calculated hourly and daily mean activity proportions for individual southern bamboo lemurs and further pooled data of individuals from the same social group. Data were used to generate monthly activity means from which we calculated daily and monthly diurnal/nocturnal (DN) activity ratios (Kappeler and Erkert 2003; Donati et al. 2013). We utilized these ratios to

allow comparisons across studies since the absolute values of activity data recorded by tags differ substantially from what would have been recorded via observational focal sampling. In particular, using 137 days of direct observations as a response variable in a regression analysis, we determined that tag activity strongly predicted observed activity ($F = 19.51$, $P < 0.001$) following the equation "observed activity" = 0.718 "tag activity" + 45.20. This comparison resulted in the tag data consistently underestimating the observed data by a factor of three throughout the study.

Although astronomical twilight was used to mark the transition between diurnal and nocturnal activity, *Hapalemur* spp. have well-adapted eyes for detecting minimal amounts of light (Pariente 1979) and are often fully active during these times. As such, we pooled twilight and diurnal data to remain consistent with previous literature (Donati and Borgonini-Tarli 2006; Donati et al. 2013).

To evaluate the influence of abiotic factors on monthly variation of activity balance, we conducted a one-way ANCOVA where monthly DN ratio was used as response variable, while the four social groups were added as fixed factor. Monthly mean temperature (°C), mean precipitation (mm) and mean day length (h) were used as continuous covariates in the model.

In order to determine the influence of lunar luminosity on diel activity profiles, we divided activity data into eight three-hour time-block intervals beginning at 06:00. Twilight time-blocks are conservative estimates as astronomical twilight time changed significantly over the course of a year. We then separated nocturnal luminosity indices into near equal categorical blocks (low luminosity: $I < 0.1$; intermediate luminosity: $0.1 < I < 0.3$; high luminosity: $I > 0.3$). A two-way repeated measures ANOVA was used to analyze the effect of nocturnal luminance index on hourly differences in activity patterns between the four lemur groups in Mandena, with two time-blocks used for nocturnal activity (21:00 – 00:00; 00:00 - 03:00), two time-blocks for twilight (03:00 – 06:00; 18:00 - 21:00), and four time-blocks corresponding with diurnal activity starting at 06:00 and ending at 18:00. Within-subjects factors were time-blocks and nocturnal luminosity categories, with groups acting as the between-subjects factor.

Data for the ANCOVA and repeated-measures ANOVA were first tested for normality using the Kolmogorov-Smirnov test and entered the parametric analyses after log or square-root transformations, respectively, as they were not normally distributed. All analyses were performed using PASW v. 21.0 and significance was set at $P < 0.05$.

Results

Southern bamboo lemurs exhibited cathemeral activity throughout the 15-month study period, displaying a typical bimodal diel activity distribution with activity peaks immediately following sunrise and preceding sunset (Fig. 2). They exhibited a monthly DN ratio (mean ± SE) of 3.98 ± 0.35:1 ($N = 7$) with fluctuations over the course of the study (Fig. 3). Appreciable differences of monthly DN ratio were observed between *H. meridionalis* groups (ANCOVA group effect: $F_{3,51} = 3.458$, $P = 0.023$; Table 2).
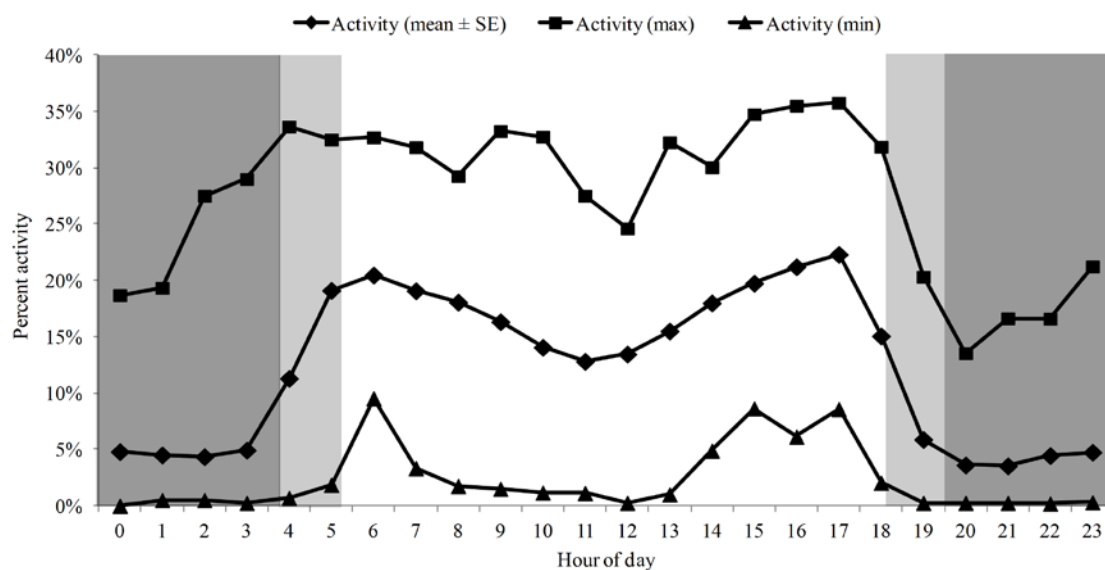

Fig. 2 Hourly activity percentages (mean ± SE) across *H. meridionalis* groups ($N = 4$). Maximum and minimum averages are provided to illustrate the activity percentage range for each hour ($N = 450$ days). Dark shaded areas represent the approximate nocturnal hours, while the lighter shaded areas represent the approximate astronomical twilights.

Effect of Environmental Factors

The activity balance of southern bamboo lemurs was not considerably affected by any abiotic factor tested. Precipitation peaked in February with a mean rainfall of 29.29mm and showed a minimal average of 0.45mm for September 2013, yet there was no significant effect on diurnality ratio (ANCOVA: $F_{3,51} = 0.096$, $P = 0.758$). The same was also true of the monthly mean temperature (ANCOVA: $F_{3,51} = 2.446$, $P = 0.124$) which ranged from 26.74°C in January to 18.49°C in July 2013. Monthly mean day length (h) ranged from 10.34 h in June 2013 to 13.70 h in December 2013, and did not influence the DN ratio (ANCOVA: $F_{3,51} = 0.492$, $P = 0.486$).
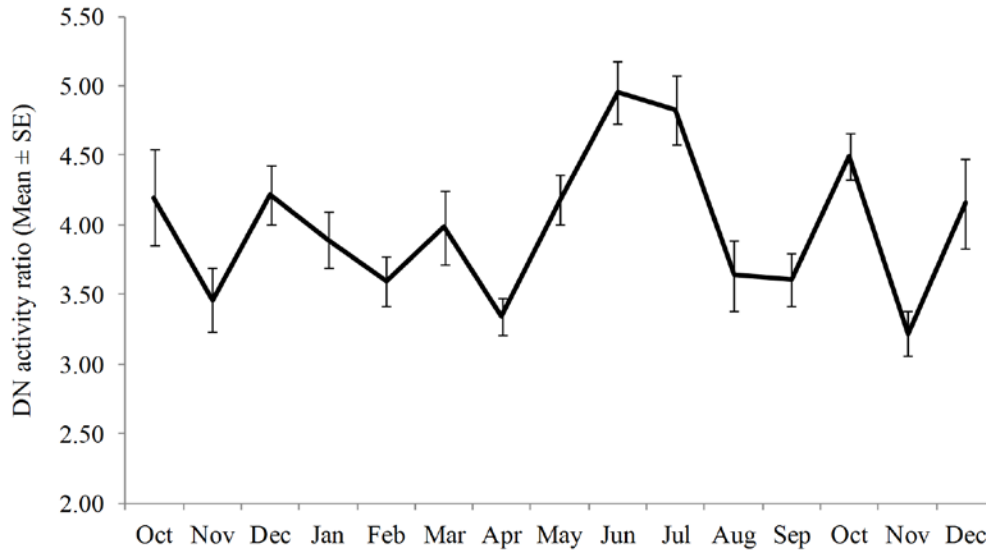
Fig. 3 Monthly DN ratio (mean ± SE) for *H. meridionalis* (*N* = 7) from October 2012 - December 2013

Table 2 DN activity ratio recorded for *H. meridionalis* from October 2012 - December 2013

Group	N tags	days	Monthly DN ratio mean ± SE	Daily DN ratio range min-max
1	2	444	4.36 ± 0.33	1.17 – 14.14
2	2	435	3.92 ± 0.18	1.12 – 63.06
3	1	432	5.27 ± 0.38	0.92 – 46.67
4	2	375	4.60 ± 0.32	1.11 – 12.94
Combined	7	450	3.98 ± 0.35	1.78 – 9.56

Effect of Nocturnal Luminosity

To assess the influence of nocturnal luminosity index, we conducted a time-block analysis that revealed activity peaks in the early morning between 06:00-09:00 and in the evening between 15:00-18:00, as expected (Fig. 4). There were significant differences between all time-blocks (percentages of activity) recorded among the four groups.
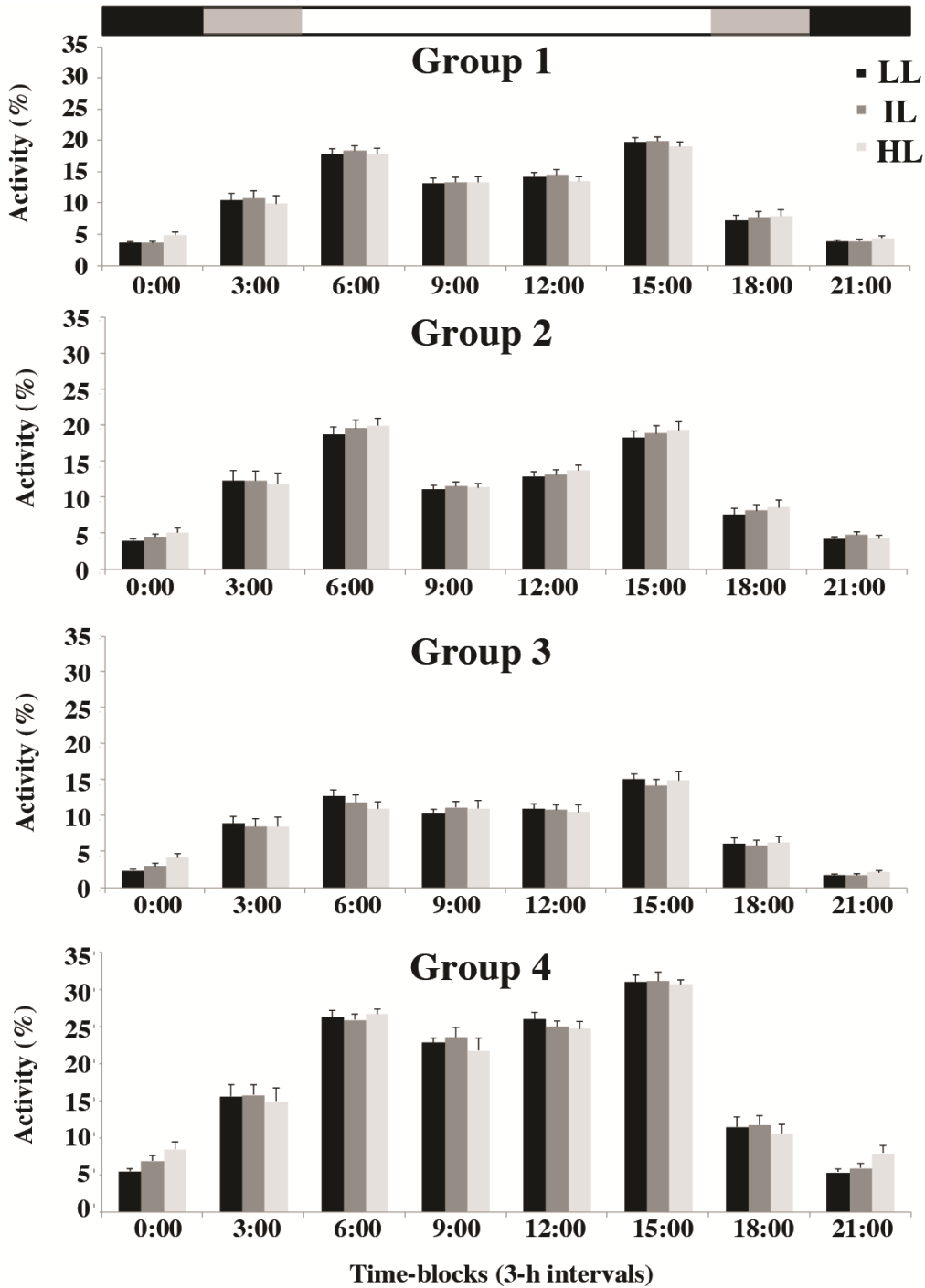
Fig. 4 Comparison of lunar luminance categories (LL = low luminance, IL = intermediate luminance, HL = high luminance) in 3-h time blocks across *H. meridionalis* groups ($N = 4$). Diurnal (white), twilight (gray), and nocturnal (black) time-blocks are indicated by the horizontal bar across the top. Error bars are standard errors.

Concerning diurnal activity, the main effect of time-block was influential ($F_{3,159} = 168.475$, $P < 0.001$), while time-block and group provided the only significant interaction ($F_{9,159} = 9.502$, $P < 0.001$). Furthermore, the between-subjects factor of group was found to

be significant ($F_{3,53} = 69.195$, $P < 0.001$). Post-hoc analyses of diurnal time-blocks (06:00 – 09:00, 09:00 – 12:00, 12:00 – 15:00, 15:00 – 18:00) revealed a significant effect between intermediate and high lunar luminance ($P = 0.024$). Pairwise comparisons of between-subjects groups showed that groups 1 & 2 behaved similarly in their use of diurnal activity ($P = 0.448$) while all other group comparisons displayed appreciable differences (1 & 3: $P < 0.001$; 1 & 4: $P < 0.001$; 2 & 3: $P < 0.001$; 2 & 4: $P < 0.001$; 3 & 4: $P < 0.001$).

When considering the influence of nocturnal luminosity on nocturnal activity, both the main effects of moon-phase ($F_{2,106} = 30.094$, $P < 0.001$) and time-block ($F_{1,53} = 10.299$, $P = 0.002$) were significant. Within-subjects factors revealed significant interactions between moon-phase and group ($F_{6,106} = 2.593$, $P = 0.022$), time-block and group ($F_{3,53} = 5.847$, $P = 0.002$), and moon-phase and time-block ($F_{2,106} = 6.923$, $P = 0.001$), while the between-subject factor of group was also significant ($F_{3,53} = 26.436$, $P < 0.001$). Post-hoc analyses of the two nocturnal time-blocks (21:00 – 00:00, 00:00 – 03:00) revealed a significant influence of lunar luminosity on nocturnal activity, with increased activity during each successive period of increased lunar luminance (LL-IL: $P = 0.001$; IL-HL: $P < 0.001$; LL-HL: $P < 0.001$). While groups 1 & 2 were shown to behave similarly ($P = 0.481$), all other pairwise comparisons of groups displayed appreciable differences (1 & 3: $P < 0.001$; 1 & 4: $P < 0.001$; 2 & 3: $P < 0.001$; 2 & 4: $P < 0.001$; 3 & 4: $P < 0.001$).

Lastly, activity during twilight was influenced by the main effect of time-block ($F_{2,106} = 82.365$, $P < 0.001$), while moon-phase and time-block provided a significant interaction ($F_{2,106} = 7.321$, $P < 0.001$). Additionally, the between-subjects factor of group was significant in twilight ($F_{3,53} = 5.012$, $P = 0.004$). Post-hoc analyses showed no discernible effects of lunar luminosity on activity during twilight blocks (03:00 – 06:00, 18:00 – 21:00); however, all pairwise comparisons between groups displayed appreciable differences (1 & 2: $P < 0.001$; 1 & 3: $P < 0.001$; 1 & 4: $P < 0.001$; 2 & 3: $P < 0.001$; 2 & 4: $P < 0.001$; 3 & 4: $P < 0.001$).

To further illustrate influence of lunar phase on cathemeral activity, an actigram of daily and hourly activity for group 4 from September 2013 is provided in Fig. 5. As nocturnal luminosity increases with the percentage of visible lunar disk (new moon, first quarter, full moon), so does corresponding nocturnal activity. Likewise, nocturnal activity decreases with diminishing nocturnal luminosity (full moon, last quarter, new moon).
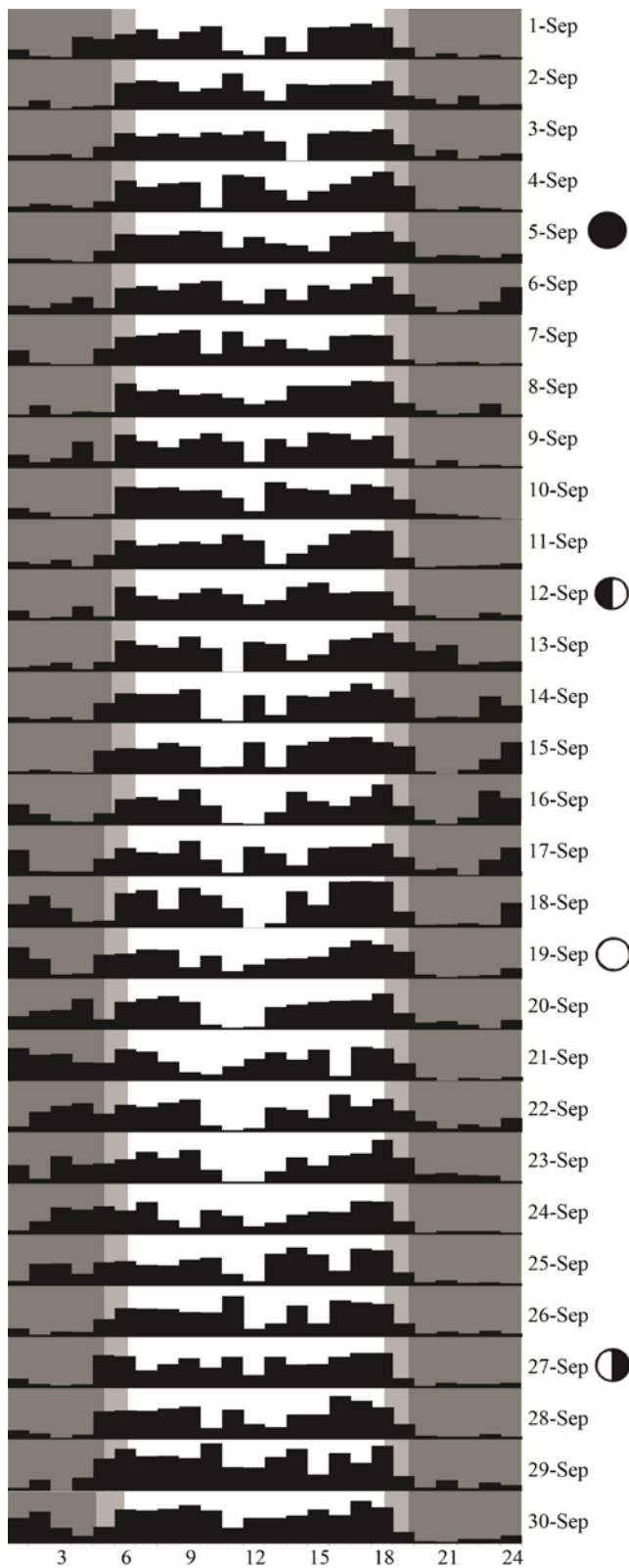
Fig. 5 Mean daily 24-h activity recorded in group 4 for the month of September, 2013. Note the increased nocturnal activity occurs mainly around the full moon portion of the month (unfilled circle represents full moon, filled circle represents new moon, and half-filled circles represent intermediate moon phases).

Discussion

As predicted, southern bamboo lemurs exhibited a cathemeral activity year-round. Overall, they displayed a mean monthly DN ratio of 3.98:1 throughout the study, a result similar to activity ratios observed in other cathemeral lemurids such as *E. collaris* (3.5:1, Donati et al. 2009), *E. collaris* x *E. rufifrons* hybrids (2.4:1, Donati et al. 2009), *E. rufifrons* (3.4:1, Kappeler and Erkert 2003), and *L. catta* (4.8:1, Donati et al. 2013). When considering the daily DN ratio variance throughout the 15-month study, *H. meridionalis* ranged from 1.78:1 (similar portions of diurnal and nocturnal activity) to 9.56:1 (entirely diurnal). This upper limit is similar to what has been found in the diurnal *P. verreauxi* (8.2:1) from the seasonal deciduous forest (Erkert and Kappeler 2004) and *L. catta* (9.3:1) from anthropogenically-disturbed gallery/spiny forests (Donati et al. 2013). The seven-night study of *H. alaotrensis* at Lac Alaotra resulted in an average DN of 11.4:1, a ratio also congruent with diurnal lemurs; however, this species was capable of displaying a daily DN range of 2.9:1 to 55.9:1 (Mutschler 1999). These results indicate an extreme flexibility of this genus consistent with our hypothesis based on their intermediate eye morphology, measured as relative cornea size (Kirk 2006), as well as the presence of both nocturnal and diurnal retinal traits (Pariente 1979; Curtis and Rasmussen 2002). While we based our prediction on the eye morphology of a congeneric species, *H. griseus*, as no measurements are available for *H. meridionalis*, we consider this approximation reasonable as intragroup variation appears limited in other genera (Kirk 2006) and *meridionalis* was considered a sub-species of *griseus* until recently (Fausser et al. 2002).

Unlike some cathemeral *Eulemur* spp. for which nocturnal activity is influenced by photoperiodic variation (Engqvist and Richard 1991; Curtis et al. 1999; Donati and Borgognini-Tarli 2006; Donati et al. 2009; but see: Overdorff and Rasmussen 1995; Andrew and Birkinshaw 1998; Colquhoun 1998), *H. meridionalis* showed no considerable association between photoperiodic changes and activity balance. Southern bamboo lemur activity was principally bimodal, exhibiting peaks around dawn and dusk. This is similar to what has been observed in other cathemeral primates (Aschoff et al. 1982; Curtis et al. 1999; Kappeler and Erkert 2003; Fernandez-Duque 2003; Donati and Borgognini-Tarli 2006; Schwitzer et al. 2007; Donati et al. 2009, 2013; Fernandez-Duque et al. 2010). The lack of a tight dependence of these lemurs to annual variations in day-length may also be explained by the presence of flexible visual structures that allow these animals to navigate from full daylight to night without major impairments, in contrast to strictly diurnal (Agetsuma and Nakagawa 1998;

Hill et al. 2003) or strictly nocturnal primates (Bearder et al. 2006). A substantial lack of photoperiodic effects on activity balance was also found in *L. catta* (Donati et al. 2013), which has visual adaptations similar to those of bamboo lemurs (Curtis and Rasmussen 2002; Kirk 2006).

Unlike photoperiodic variation, nocturnal luminosity index did have a considerable influence on the cathemeral activity of *H. meridionalis*, with animals displaying a strong lunarphilia. As observed in other fine-grained studies on cathemeral primates (*E. collaris*, Donati and Borgognini-Tarli 2006; *E. rufifrons*, Kappeler and Erkert 2003; *Aotus azarai*, Fernandez-Duque and Erkert 2006), the nocturnal activity is strongly influenced by the presence of the lunar disc in the sky. A shift to the right is in fact evident in the nocturnal phase (Fig. 5) due to changing moon-rise and moon-set times with animal activity concentrated during the last hours of the night during waning moon and during the first hours of the night during waxing moon.

The lunarphilia that we observed in these bamboo lemurs is similar to what has been observed in some cathemeral and nocturnal primates (e.g., *Aotus azarai*, Fernandez-Duque et al. 2010; *E. collaris*, Donati and Borgognini-Tarli 2006; *E. collaris* x *rufifrons*, Donati et al. 2009; *E. flavifrons*, Schwitzer et al. 2007; *E. mongoz*, Curtis et al. 1999; *E. rufifrons*, Donati et al. 2001, Kappeler and Erkert 2003; *L. catta*, Donati et al. 2013), while this is in contrast to many cathemeral and nocturnal mammals, which typically reduce their activity on nights of increased luminance (Prugh and Golden 2014; e.g., *Arctictis binturong*, Grassman et al. 2005; *Arctocephalus galapagoensis*, Horning and Trillmich 1999; *Artibeus jamaicensis*, Morrison 1978; *Caluromys philander*, Julien-Laferriere 1997; *Dipodomys* sp., Upham and Haffner 2013; *Meles meles*, Cresswell and Harris 1988; *Nycticebus javanicus*, Rode-Margono and Nekaris 2014; *Panthera leo*, Packer et al. 2011; *Peromyscas polionotus,* Wolfe and Summerlin 1989). Given their continuous cathemeral activity and contrasting retinal morphologies, it seems that the presence of *tapeta* in *Hapalemur* does not counter lunarphilia as would have been supposed if only *Eulemur* were lunarphilic. This is similar to recent data from *L. catta*, a lemurid that maintains *tapeta* and is also capable of cathemerality (Donati et al. 2013). Furthermore, this appears to parallel nightjars (family Caprimulgidae), a nocturnal insectivorous bird which maintains a *tapetum lucidum* but is similarly constrained by lunar phase (Mills 1986; Jetz et al. 2003), although this may allow them to target specific insects that are also constrained by nocturnal luminance (Kerfoot 1967; Jahn 1982). This suggests that lunarphilia may not be linked to the lack of *tapeta*; rather, other benefits are likely to

explain this phenomenon. It has been hypothesized, for example, that lunarphilia improves foraging efficiency and predator detection for species that rely on visual acuity (Prugh and Golden 2014). Some night-active lemur predators are known to exist in the evergreen littoral forest of Mandena, including boas (Rakotondravony et al. 1998) and periodically fossas (*Cryptoprocta ferox*) (Donati et al. 2007b). With an intermediate visual acuity, it may be that bamboo lemurs only extend their activity to night when the cost of foraging efficiently while maintaining vigilance for potential predators outweighs the risk. It has been shown that nocturnal predators often rely on darkness to successfully attack prey (Horning and Trillmich 1999; Lang et al. 2006; Packer et al. 2011; Prugh and Golden 2014), thus the exhibition of lunarphilia may allow bamboo lemurs to maintain vigilance while countering potential lunarphobic predators. However, testing the last hypothesis is beyond the scope of the present work.

Our data on *H. meridionalis* may help to elucidate some of the potential ultimate factors which have been proposed to determine cathemeral activity. Despite the lack of giant bamboo in Mandena, a preferential food source in other areas, the diet of *H. meridionalis* remains mainly folivorous and they seem to base a large part of their diet on grass (Eppley et al. 2011; TME et al. unpublished data). So far only frugivorous and/or omnivorous primates have been observed to exhibit a cathemeral activity rhythm, and several studies have linked activity and cathemerality to dietary changes and fibrous food in lemurids lacking gastrointestinal adaptations to efficiently digest cellulose (Enqvist and Richard 1991; Ganzhorn and Wright 1994; Tarnaud 2006; Donati et al. 2007a). The evidence of this activity rhythm in a year-round folivore makes it reasonable to hypothesize that spreading feeding bouts over the 24-hours may be used to maximize extractive abilities and thus energy intake even in species with adaptations for a folivorous diet (Mutschler 1999). Despite their caeco-colon adaptations for folivory (Overdorff and Rasmussen 1995), southern bamboo lemurs are relatively small animals averaging ($\pm$ SD) 1.072 ± 0.107 kg (Eppley et al. 2015) for which it may still be advantageous to spread activity over the 24-hour to maximize energy extraction from herbaceous food (Mutschler 1999). A relationship between cathemeral or ultradian activities and cellulose-rich food with low energy content has been well documented in small, energy-demanding mammals such as voles (Halle 2006). Gut constraints in small mammals with unstructured fermentation chambers may require more or less permanent foraging activity to meet energy requirements (Daan and Slopsema 1978).

Activity profiles of *H. meridionalis* were generated from conspecific social groups sharing territorial borders, yet each of the four lemur groups exhibited appreciable differences of monthly DN ratio and time-blocks. This difference illustrates a strong behavioural flexibility and suggests that inter-group variability for biotic factors, e.g., habitat variability and dietary quality, may have a strong, non-mutually exclusive role as influential as nocturnal luminosity. It is also possible that the variable social structure of each group (Table 1) may contribute to explain the differences in DN ratio. While group 2 consisted of a 1:1 sex ratio through the vast majority of the study, both groups 1 and 4 had multiple adult females with one adult male. These compositions are in contrast to group 3, which did not have any adult females but rather had three adult males and two juveniles. Regardless of the circumstances surrounding the disappearance of female(s) from this group (e.g., predation, senescence), the lack of females within an otherwise female dominated society (Nievergelt et al. 1998; Waeber and Hemelrijk 2003; Tan 2006) may have contributed to the overall higher DN ratio of this group. Although both sexes defend their territory, males have been shown to play a larger role via increased visual monitoring, scent-marking (including substrate, conspecific female(s), and themselves), and inter-group agonistic interactions, e.g., vocalizing, chasing, and biting intruding conspecifics (Nievergelt et al. 1998; Waeber and Hemelrijk 2003; TME unpublished data). It is possible that in the absence of females, males could devote less energy towards territorial defence (i.e., scent-marking, inter-group agonism). If we are to consider their seasonal reproduction, infants were first observed in mid-November, providing an approximate conception date in early July (Wright 1990; Tan 2006; TME unpublished data). The monthly DN ratio for group 3 during this period was 9.30:1, the highest monthly average recorded ($N = 58$ months). Though a fine-grained analysis would be necessary to support our conclusions, these observations suggest that certain social aspects, such as the energetic cost of mate-guarding female(s), may potentially drive cathemeral activity rhythms in males.

Cathemerality has been proposed as an ancestral condition for *Eulemur* (Tattersall 1982; Colquhoun 1998) or as a stable adaptation within all lemurids (Donati et al. 2013). Our data showing stable cathemeral activity in bamboo lemurs add to the recent finding demonstrating a similar activity at some sites in the previously 'diurnal' *L. catta* (Donati et al. 2013; LaFleur et al. 2014). The close phylogenetic proximity of these cathemeral genera (Horvath et al. 2008) coupled with the variable retinal morphologies (Pariente 1979; Kirk 2006) and considerable dietary differences (Enqvist and Richard 1991; Donati et al. 2009;

Eppley et al. 2011) substantiate the idea of this behavioural trait to potentially pre-date the phylogenetic node distinguishing the true lemur radiation (Donati et al. 2013). If cathemerality is a transitional state due to the extinction of large diurnal competitors and predators, as evolutionary disequilibrium hypothesis suggests, then we would not necessarily expect a phylogenetic signal on this trait.

Ethical Standards

This study complies with Malagasy and German regulations regarding the ethical treatment of research subjects. All research was carried out under the Accord de Collaboration among the University of Antananarivo and the University of Hamburg. Research protocols were approved and permits authorized by Commission Tripartite of the Direction des Eaux et Forêts de Madagascar (Autorisation de recherché N° 240/12/MEF/SG/DGF/DCB.SAP/SCB du 17/09/2012), adhering to the legal requirements of Madagascar.

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CHAPTER 2

The use of an invasive species habitat by a small folivorous primate:
implications for conservation

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Abstract

The lemurs of Madagascar are among the most threatened mammalian taxa in the world, with habitat loss due to slash-and-burn agriculture and timber harvest heavily contributing to their precarious state. Deforestation often leads to fragmentation, resulting in mixed-habitat matrices throughout a landscape where disturbed areas are prone to invasion by exotics. Within Madagascar, the exotic *Melaleuca quinquenervia* has invaded many wetland ecosystems, creating mono-dominant habitats that in some cases currently provide the only potential habitat corridors between forest fragments. We sought to determine whether an invasive species could provide suitable habitat for a threatened lemur population. Our study site, the Mandena Conservation Zone (southeast Madagascar), is a matrix of upland littoral forest, littoral swamp, and *Melaleuca* swamp habitats. In view of this habitat amalgam, we sought to understand the role of an invasive species habitat (*Melaleuca* swamp) on the behavioural ecology of a threatened, small-bodied folivore, the southern bamboo lemur (*Hapalemur meridionalis*). Behavioural and botanical data were collected monthly from January-December 2013. Our results demonstrate that while lemurs seasonally limited activities to certain habitats, all groups were capable of utilising this invasive habitat for feeding and resting, confirming *Melaleuca* as an integral part of their home range. That *Hapalemur* use an invasive plant species as a dispersal corridor increases our knowledge of their ecological flexibility, and may be useful in the conservation management of remaining threatened populations.

Key words: bamboo lemurs; corridors; fragmentation; *Hapalemur meridionalis*; invasive species; primates; Madagascar; *Melaleuca quinqueneriva*

Introduction

Deforestation of tropical forests is one of the primary threats to global biodiversity (Asner et al., 2009; Gibson et al., 2011). Forest fragments typically persist after deforestation, most of which are unsuitable habitat for the majority of forest species (Broadbent et al., 2008; Laurance et al., 2009). Forest edge areas are often considered entirely distinct ecosystems from forest interiors (Laurance et al., 2000). Within Madagascar, greater than 80% of forest area exists less than 1 kilometre from an edge (Harper et al., 2007), thus fragmentation is of great concern for the survival of forest fauna and flora species (Hannah et al., 2008;

Ganzhorn et al., 2014). Decreasing deforestation rates and reforesting fragmented landscapes would help prevent extinctions (Wearn et al., 2012).

Although fragmentation of populations may result in genetic erosion and increase extinction risk (Caro & Laurenson, 1994), it has been shown that a mosaic of small, suitable habitat fragments may act as a single large habitat if the fragments are linked via corridors (Bevers & Flather, 1999; Haddad, 2000). In general, corridors are defined as thin strips of habitat (natural or unnatural) that connect two or more otherwise isolated forest fragments, with many studies validating their utilization by organisms (reviewed in Beier & Noss, 1998). In fact, numerous studies have demonstrated that corridors can mitigate the negative effects of fragmentation (Gonzalez et al., 1998; Haddad, 1999; Mech & Hallett, 2001). Thus, a network of forest fragments within a critical dispersal distance may act as a means to maintain biodiversity and ecological processes in anthropogenic landscapes (Hale et al., 2001; Lens et al., 2002).

The primates of Madagascar are the most threatened mammalian taxa in the world (Schwitzer et al., 2014). Habitat loss due to slash-and-burn agriculture and timber harvest, as well as bushmeat hunting, continue to jeopardize lemurs' survival (Golden, 2009; Schwitzer et al., 2014). As habitat destruction persists in isolating the remaining lemurs to forest fragments, the need for regenerating forests and connecting those remaining fragments is crucial. As such, it is imperative to understand the responses of native plants and animals to disturbance if we are to create effective buffer zones and corridors that combine secondary and natural habitats (Hannah et al., 2008; Kremen et al., 2008; Irwin et al., 2010; Campera et al., 2014).

Invasions by exotic species present a critical hindrance to the preservation of endemic biodiversity as well as ecosystem restoration efforts (Braithwaite et al. 1989; D'Antonio & Vitousek, 1992). In south-east Madagascar, the Mandena littoral upland forest matrix exists within a seasonally-inundated flood plain that consists of natural littoral swamp and mahampy (*Lepironia mucronata*) wetlands, the latter of which maintains some inundation throughout the year. It is here, and in similarly inundated areas (Dray et al., 2006), that the broad-leaved paperbark tree *Melaleuca quinquenervia* (Family Myrtaceae), native to Australia, has been an aggressive disperser (Miandrimanana et al., 2014). While the viability of non-native tree plantations has been examined to potentially assist in both dispersal and fulfilment of partial habitat requirements for the conservation of lemurs (Ganzhorn, 1985, 1987; Ganzhorn & Abraham, 1991), the role of an invasive tree species has only been

minimally examined (Ramanamanjato & Ganzhorn, 2001). This is of exceptional interest as littoral forest fragments represent critical refuge for the survival and maintenance of biodiversity in the extremes of climatic variability (Virah-Sawmy et al., 2009). Riparian habitats often serve as corridors for multiple taxa (Ganzhorn & Sorg, 1996), so the conservation of these and isolated forest blocks within dispersal distance are critical to maintaining genetic resilience.

In view of this conflicting situation, we sought to understand the role of an invasive species habitat (*Melaleuca* swamp) on the behavioural ecology of a small-bodied folivore, the southern bamboo lemur (*Hapalemur meridionalis*). Growing knowledge of the ecological flexibility of bamboo lemurs (Grassi, 2006; Eppley et al., 2011) make this species an excellent model with which to examine its ability to utilize distinct habitats, and potentially corridors, within the anthropogenic landscape. We first characterize the floristic diversity and structure of each of the habitats (i.e., upland littoral forest, littoral swamp, and *Melaleuca* swamp) within Mandena. We sought to understand the distribution of the activities of this folivorous primate model within each of the habitats, as well as their exact home ranges, by conducting behavioural sampling and GIS analyses from daily follows. Furthermore, we attempt to explicate whether *Melaleuca* facilitates movement between upland forest fragments and/or natural littoral swamp, and also whether this invasive habitat provides additional services, e.g., suitable feeding and resting locations.

Methods

Study site

Our study was conducted in the Mandena littoral forest (24°95'S, 46°99'E) in southeast Madagascar (Fig. 1), a protected area approximately 10 km north of Fort-Dauphin (Tolagnaro). The encompassing area is 148 ha of fragmented and degraded littoral upland forest, which is characterized as occurring within 3 km of the coast and growing on sandy substrates with a typically low canopy (Dumetz, 1999), and approximately 82 ha of interspersed natural littoral swamp and invasive *Melaleuca*-dominated swamp that segregates the two upland forest fragments (Eppley et al., 2011). Littoral forests are among the most threatened habitats in Madagascar (Ganzhorn et al., 2001; Bollen & Donati, 2006).
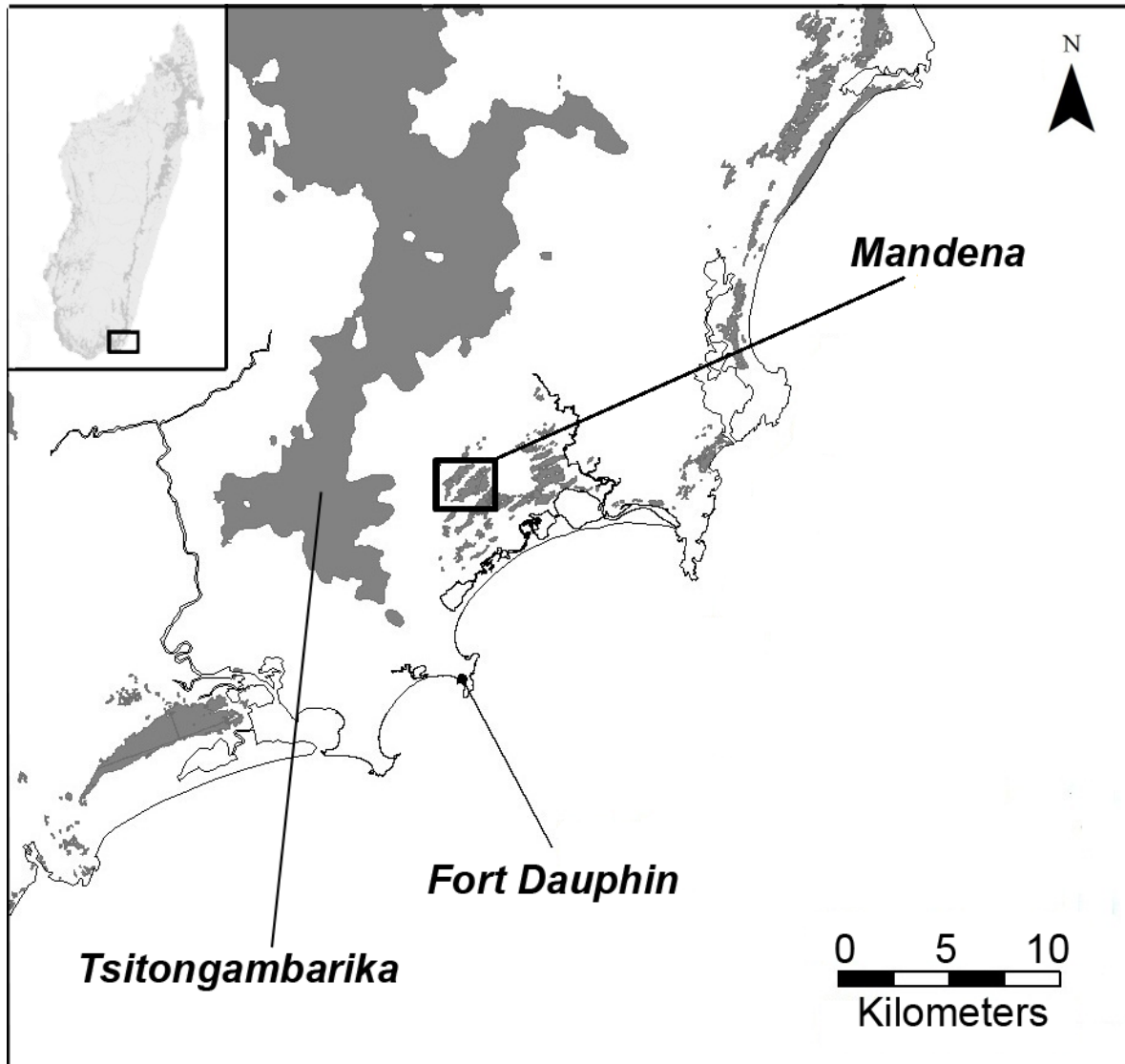
Fig. 1. Location of Mandena littoral forest in southeast Madagascar, relative to the larger, continuous forest of Tsitongambarika.

Monthly climatic factors within the littoral forests of southeast Madagascar can be highly variable (Bollen & Donati, 2005), with our data not closely reflecting historical records for the area (Fig. 2). Temperature (°C) was recorded in 30-mins intervals throughout the study using Lascar EL-USB-1 data loggers, operated by custom software (EasyLog USB Version 5.45, Lascar Electronics). Precipitation (mm) was measured daily at 6:00h using a rain gauge placed within the study site. Day length (a proxy for season) was calculated as the time between sunrise and sunset, as obtained from the US Naval Observatory Astronomical Calendar (http://aa.usno.navy.mil/data), using geographic coordinates for Mandena.
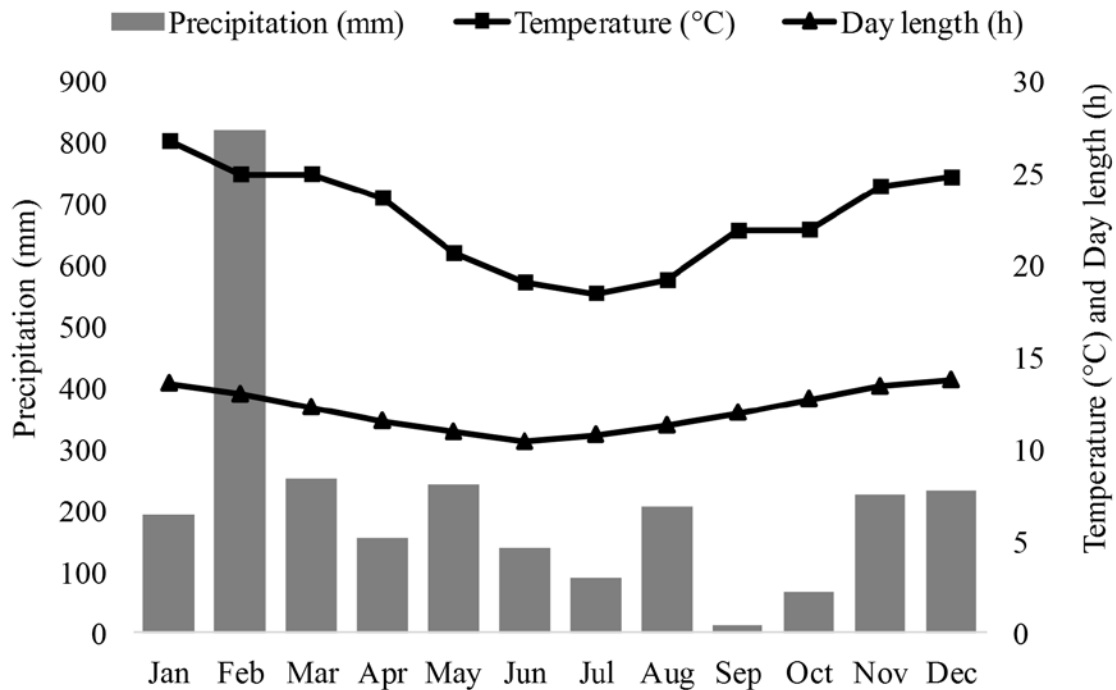
Fig. 2. Monthly total precipitation (mm), mean temperature (°C), and mean day length (h) at Mandena in 2013.

Study species

Southern bamboo lemurs (*Hapalemur meridionalis*) are relatively small-bodied cathemeral folivores with a mean body mass of 1.072 ± 0.107 kg ($X \pm$ SD; $N = 15$) (Eppley et al., 2011, 2015). This species is currently listed as Vulnerable (VU B1ab(iii,v)) by the IUCN (2012), mainly as a result of their geographically restricted range and continual loss of habitat. They live in small social groups with one or two breeding females and typically one breeding male. Within Mandena, southern bamboo lemur groups average 5.6 ± 1.5 individuals ($X \pm$ SD; $N = 5$). In addition to *H. meridionalis*, the cathemeral *Eulemur collaris* and nocturnal *Microcebus murinus*, *Cheirogaleus medius*, *C. major*, and *Avahi meridionalis* are present within Mandena.

Ten adult *H. meridionalis* across four habituated, neighbouring social groups were captured between October - December 2012 by an experienced Malagasy technician via Telinject® blow darts containing a hypnotic anaesthesia (4 mg/kg of ketamine hydrochloride or tiletamine hydrochloride), so that the animals neither suffered nor recalled the capturing process. All animals recovered from anaesthesia within 1.5 hours at the capture site, and there were no injuries as a consequence of the captures and animals were followed until regaining full mobility. As bamboo lemurs are highly cryptic, individuals were fitted with external

radio-transmitters with an archival tag (ARC400, Advanced Telemetry Systems, Isanti, USA) that allowed us to follow groups more easily. This process was repeated at the end of the study in December 2013 to remove the radio-collars from the bamboo lemurs.

Habitat characterization

To characterize each distinct habitat, we conducted 25 x 100m² botanical plots, i.e., 10 in both the upland forest and swamp, and five in the *Melaleuca*-dominated swamp, the latter requiring fewer plots due to its floristic homogeneity. Within each plot we included all trees with a diameter at breast height (DBH) ≥ 5cm, recording scientific species and family names of each so as to detail tree species diversity, in addition to their height (m) and crown volume (m³). The latter was estimated as an ellipsoid via the crown height and two crown diameters, i.e., maximum and perpendicular widths. We further conducted vertical-line transects within each plot, so as to detail the structure and canopy cover for each these three habitats (Gautier et al., 1994). Lastly, to determine the species diversity of each habitat, we calculated the Shannon index (*H'*) via the following formula:

$$H' = \sum_{i=1}^{s} Pi \ln Pi$$

where *s* is the number of individuals per species, p_i is the relative abundance of each species in the habitat. The Mandena upland littoral forest and littoral swamp that our focal *H. meridionalis* groups inhabit are legally protected forests; however, much of the *Melaleuca*-dominated swamp falls outside of this demarcation. As such, locals access these unprotected areas daily to harvest wood. To measure the degree to which this occurs, we included felled trees in our botanical plots. Lastly, it should be noted that in order for lemurs to access the *Melaleuca* swamps around Mandena, they must descend and traverse a barren, sandy area that would make them visually conspicuous to any potential predators as they leave the canopy cover of the upland forest. To examine these crossing sites, we measured the distance (m) traversed where lemurs accessed the *Melaleuca* swamp.

Behavioural sampling

From January to December 2013, we conducted full-day focal follows (sunrise to sunset) with the aim of acquiring 50hrs/month per group for three of the social groups, i.e.,

specifically groups 1, 2, and 4, while group 3 was used exclusively for home range data. Identification of individuals was made using radio-tracking tags with unique-coloured pendants. Behavioural data were collected via instantaneous focal sampling (Altmann, 1974) at 5-min intervals on broad-level activities (resting, feeding, moving, social and other) and noting the habitat (upland, swamp, and *Melaleuca*-swamp). In addition, we collected continuous feeding data each time a focal individual fed, recording the specific food item of the species, and duration of consumption measured to the second. All adult individuals in each group were sampled at least once each month. We further noted each occurrence in which the focal utilized the *Melaleuca*-swamp corridors connecting the upland forest fragments.

GIS analyses

During daily focal follows of groups 1, 2, and 4, we recorded their GPS location in 15-min intervals using a Garmin GPSMAP 62S unit, noting the specific habitat type. All ranging data were entered into ArcGIS 10.2 (ESRI) using the Geospatial Modelling Environment (GME) spatial ecology interface (Beyer, 2012) with R statistical software version 3.1.2 (R Development Core Team, 2014). We determined each group territory using a 95% kernel density estimate (Worton, 1989) and further estimated the area (ha) of each habitat type.

Statistical analyses

To determine whether the characterization metrics of habitats differed, we used Kruskal-Wallis analyses for tree DBH, height, and crown volumes. We performed non-parametric tests as the data were not normally distributed, even after transformations. To determine the influence of habitat on bamboo lemur activities, a two-way repeated measures ANOVA was performed for each habitat, assessing the monthly proportion of broad-level activities (limited to rest, feed, and travel). Each habitat (upland littoral forest, littoral swamp, and *Melaleuca*-dominated swamp) was treated as the within-subjects factor, with groups acting as the between-subjects factor. Additionally, abiotic factors of total precipitation (mm), mean temperature (°C), and mean day length (h) per month were included in the model as covariates. The model errors for the repeated-measures ANOVA (via unstandardized residuals) were found to be normally distributed using the Kolmogorov-Smirnov test, allowing for the continuation of parametric analyses. Adjusted *p*-values are reported

according to the Huynh–Feldt correction when assumptions of sphericity were violated; uncorrected biases from lack of sphericity can otherwise inflate F-statistics (Quinn & Keough, 2002). All analyses were performed using PASW v. 21.0 and significance was set at $p < 0.05$.

Results

Habitats

Compared to the botanically diverse upland littoral forest and littoral swamp, the *Melaleuca* swamp was comprised of only six tree species, each from a distinct family (Table 1). While 90.02% was *M. quinquenervia*, the majority of the remaining composition consisted of *Typhondorum lindleyanum* (7.52%), *Pandanus platyphylus* (2.09%), *Barringtonia racemosa* (0.27%), *Ravenala madagascariensis* (0.05%), and *Acacia* sp. (0.05%). Tree analyses found that the three variables were significantly different between habitats (DBH (cm): Kruskal-Wallis $H = 363.70$, $df = 2$, $p < 0.001$; height (m): Kruskal-Wallis $H = 195.43$, $df = 2$, $p < 0.001$; crown volume (m^3): Kruskal-Wallis $H = 350.33$, $df = 2$, $p < 0.001$).

Table 1 Comparison of available trees (means ± SD) measured in different habitats within Mandena.

Habitat	N	Species (N)	Families (N)	DBH (cm)	Height (m)	Crown volume (m^3)	Shannon (H')
Upland Forest							
≥ 5cm (DBH)	1454	84	40	9.53 ± 5.09	7.22 ± 1.48	10.41 ± 18.31	3.54 ± 0.05
Littoral Swamp							
≥ 5cm (DBH)	2211	49	32	11.66 ± 5.95	6.47 ± 1.13	3.91 ± 6.68	2.92 ± 0.08
Melaleuca Swamp							
≥ 5cm (DBH)	2194	6	6	12.11 ± 5.89	6.76 ± 2.33	4.61 ± 7.64	0.39 ± 0.07

To account for the human impact on the *Melaleuca* habitat, we recorded 65 recently felled *M. quinquenervia* with a mean DBH ($X ± SD$) of 12.85 ± 8.89 cm within our five *Melaleuca* botanical plots. In addition to timber harvesting and significantly different tree metrics, habitats were further distinguished by their vertical structure (Fig. 3). Furthermore, the mean distance of the eight confirmed crossing sites that *Hapalemur* groups utilized in order to access the *Melaleuca* habitat from adjacent upland forest is 9.75 ± 2.71 m ($X ± SD$).
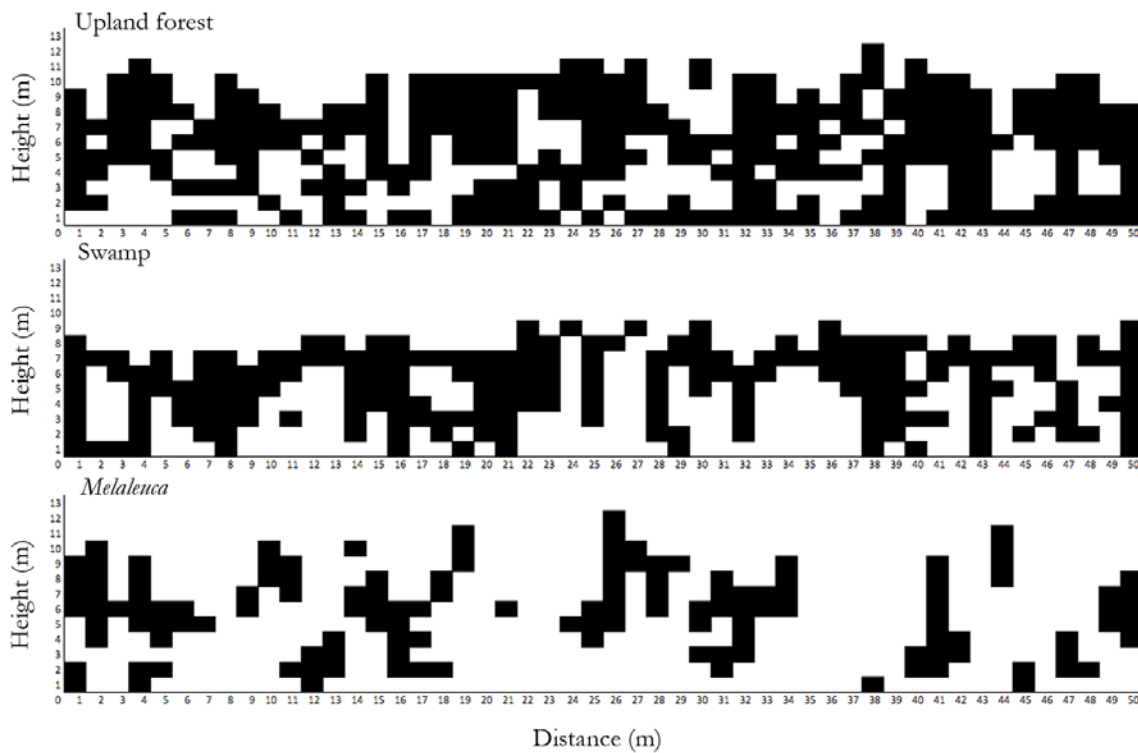
Fig. 3. Vertical structure comparison between each of the three Mandena habitats based on Gautier-transects (Gautier et al., 1994): upland littoral forest, littoral swamp forest, and *Melaleuca*-dominated swamp.

Spatial analysis

The total area (ha) of both home ranges utilized by groups 1 and 2 were even in size, while the home range of group 4 was substantially smaller (Table 2). Considering our three focal groups, the *Melaleuca* habitat constituted large portions of the home ranges of groups 1 and 4, while it appeared to be minimal for group 2 (Fig. 4).

Table 2 Total area (ha) and area per habitat type as obtained via 95% kernel density estimate.

Group	Upland (ha)	%	Swamp (ha)	%	*Melaleuca* (ha)	%	Total (ha)
1	11.67	53.45	1.27	5.81	8.89	40.74	21.82
2	19.95	94.16	0.85	4.03	0.38	1.80	21.19
4	3.68	27.13	4.69	34.58	5.19	38.29	13.55

Group 3 habitat data were not included as they constitute a smaller dataset.
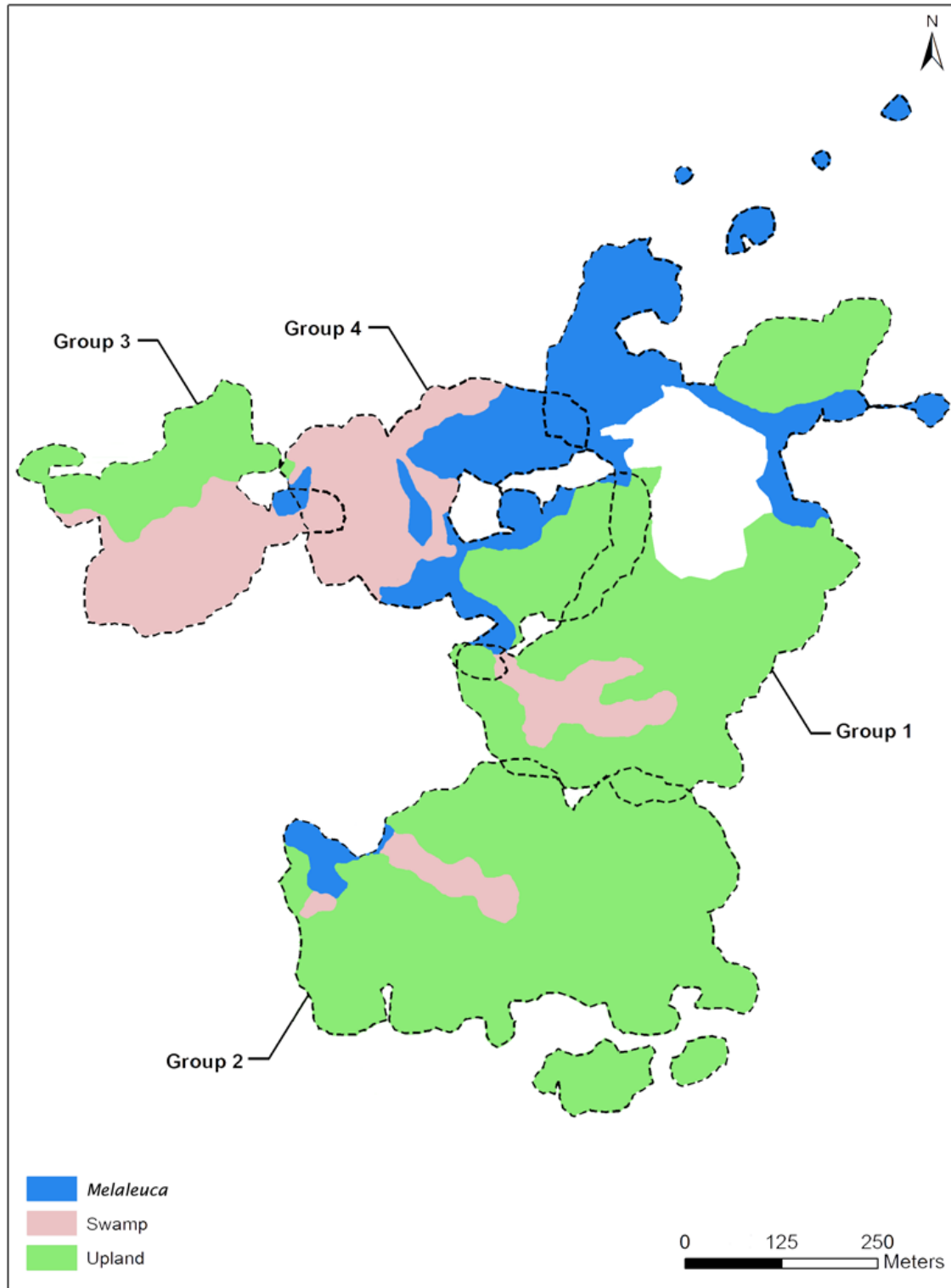
Fig. 4. Home ranges (95% kernel) of *Hapalemur meridionalis* focal groups at Mandena between January and December 2013. Areas for each habitat (i.e., upland, swamp, *Melaleuca*) are shown within each.

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Activity and Habitat

We observed *H. meridionalis* for 1,762 hours from January - December, 2013 across 194 focal days. Groups differed in the amount of time spent resting in each habitat (Upland = 27.99 ± 2.21; Swamp = 7.23 ± 1.35; *Melaleuca* = 4.76 ± 1.02 ($X \pm$ SE; $N = 36$)), but there were no differences in overall rates of resting between the habitat types (Table 3). Significant interactions were found between temperature and habitat, day length and habitat, as well as group and habitat. Considering the covariates, resting is significantly affected by temperature, but not affected by seasons (i.e., day length). Post-hoc analyses of groups revealed a significant difference between groups 1 & 4 ($p = 0.004$), while groups 1 & 2, and 2 & 4 were similar in the proportion of time and location they chose to rest.

When considering feeding activity, there was no appreciable difference in the mean proportion of time each group fed; however, there were significant differences in the average proportion of feeding between the habitats (Upland = 25.52 ± 2.75; Swamp = 5.72 ± 1.09; *Melaleuca* = 11.35 ± 2.31 ($X \pm$ SE; $N = 36$)). Significant interactions were revealed between temperature and habitat, day length and habitat, and group and habitat (Table 3). Furthermore, feeding activity is affected by both temperature and day length, varying seasonally. Post-hoc analyses showed no discernible effect of feeding between groups.

Table 3 Repeated measures analysis of variance for effects of habitat type on activity of *H. meridionalis* at Mandena, January-December, 2013. Significant differences indicated in bold.

Activity	Source of variation	*df*	*F*-ratio	*p*
Rest	*Within-subjects*			
	Habitat	1.786	1.303	0.278
	Temperature x Habitat	1.786	3.521	**0.041**
	Precipitation x Habitat	1.786	2.170	0.129
	Day length x Habitat	1.786	3.756	**0.034**
	Group x Habitat	3.573	23.713	**<0.001**
	Covariates			
	Temperature	1	7.144	**0.012**
	Precipitation	1	1.330	0.258
	Day length	1	3.271	0.081
	Between-subjects			
	Group	2	4.848	**0.015**
Feed	*Within-subjects*			
	Habitat	1.995	3.523	**0.036**
	Temperature x Habitat	1.995	3.868	**0.026**
	Precipitation x Habitat	1.995	0.991	0.377
	Day length x Habitat	1.995	6.249	**0.003**
	Group x Habitat	3.990	25.583	**<0.001**
	Covariates			
	Temperature	1	24.282	**<0.001**
	Precipitation	1	1.431	0.241
	Day length	1	10.154	**0.003**
	Between-subjects			
	Group	2	0.473	0.628
Travel	*Within-subjects*			
	Habitat	1.995	1.396	0.256
	Temperature x Habitat	1.995	1.309	0.278
	Precipitation x Habitat	1.995	3.454	**0.038**
	Day length x Habitat	1.995	2.108	0.131
	Group x Habitat	3.991	27.393	**<0.001**
	Covariates			
	Temperature	1	15.279	**<0.001**
	Precipitation	1	1.619	0.213
	Day length	1	5.504	**0.026**
	Between-subjects			
	Group	2	0.107	0.899

Traveling showed no differences in means between the groups (Table 3), while the main effect of habitat was revealed to have no influence (Upland = 6.69 ± 0.51; Swamp = 2.02 ± 0.37; *Melaleuca* = 1.41 ± 0.21 (*X* ± SE; *N* = 36)). There were significant interaction effects between precipitation and habitat, and group and habitat. Considering the covariates,

traveling is affected by both temperature and day length, varying seasonally. Post-hoc analyses showed no discernible effect of feeding between groups.

Melaleuca habitat use

Considering individual focal days, southern bamboo lemurs were observed to access *Melaleuca* habitat on 54.12% of days, although this only constituted 18.55% of our total observation record (Table 4). Despite this, both groups 1 and 4 accessed this invasive habitat often, while the minimal proportion of *Melaleuca* available to group 2 was still utilized on greater than 20% of observation days. In terms of monthly percentage of time, however, group 2 utilized *Melaleuca* minimally compared to the other lemur groups (Fig. 5).

Table 4 Role of *Melaleuca*-dominated habitat on daily activity budget of *H. meridionalis*.

	Observ. days	Accessed *Melaleuca*		
		Number of days	% of days	% of observation record
Group 1	65	37	56.92	24.22
Group 2	63	13	20.63	1.70
Group 4	66	55	83.33	30.97
Overall	**194**	**105**	**54.12**	**18.55**

Furthermore, we found two of our three focal groups feed regularly on the flowers of this invasive species when available. Group 1 was observed to feed on the flowers of *M. quinquenervia* for 110.65mins, constituting 0.79% of the annual diet (although this was only fed on in January). While group 2 never fed on these flowers, group 4 spent a substantial 2.43% of their annual total feeding record (316.32mins) selecting for it.
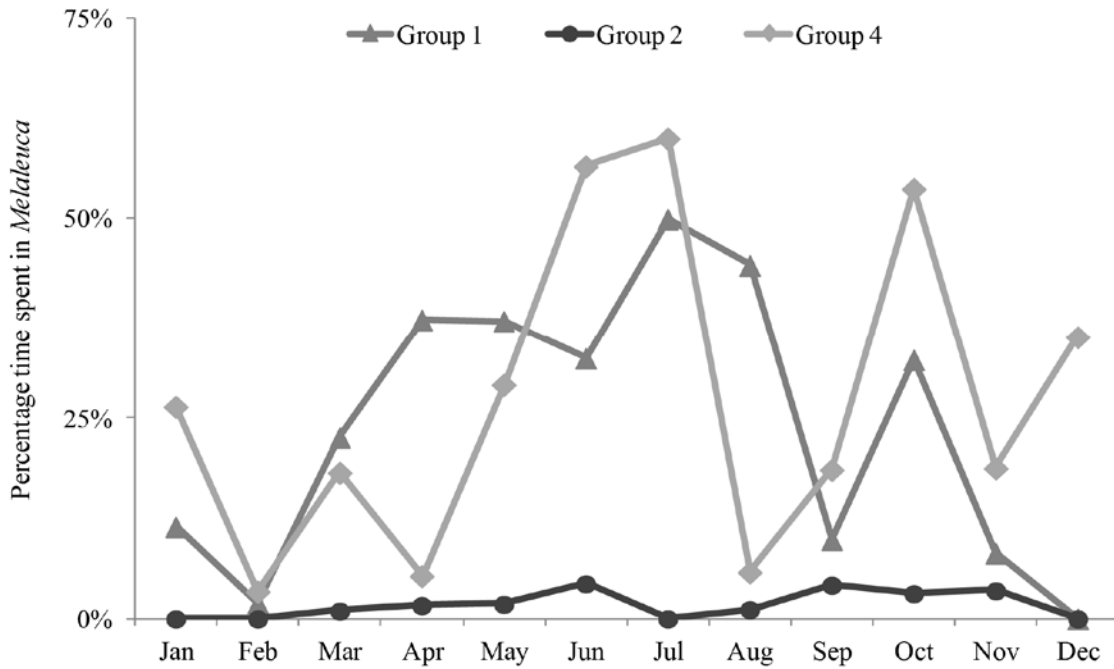
Fig. 5. Monthly percentage of time spent by *H*. *meridionalis* groups in the *Melaleuca* habitat from January-December, 2013.

Discussion

Our results confirmed that all three *H. meridionalis* focal groups differed in terms of proportional time they spent for each activity in the three habitats. In general, the monthly time-budget of bamboo lemur activities is significantly affected by seasonality (i.e., day length) and temperature. *Melaleuca* and swamp habitats were often inundated by water during the warm/wet austral summer, which may have been responsible for restricting their use of these habitats by lemurs to the cooler/drier months. However, examination of the monthly use of *Melaleuca* habitat by each group shows that while they spend less time here in the warmer months, they are capable of accessing this habitat when inundated. In fact, it is during this inundated period (Oct-Apr) when *M*. *quinquenervia* flowers in short, frequent bursts, but availability of this confirmed food item does not appear to influence the proportion of time bamboo lemurs spend in this habitat. This is especially true of groups 1 and 4 which spent considerable time feeding on these exotic flowers when available, something that *E. collaris*, *C. medius* and *M. murinus* have also been observed to exploit (Bollen, 2003).

There were larger proportional areas of *Melaleuca* habitat in the territories of groups 1 and 4, thus they spent more time resting, feeding, and travelling in this habitat compared to

group 2. Furthermore, these social groups were occasionally found sleeping in a *Melaleuca* tree before sunrise, typically huddled together at an approximate height of 7m. The overall difference in time-budget between the groups (when controlling for the effect of habitat and the covariates) was similar for feeding or travelling activity categories, but displayed appreciable differences for resting. Interestingly, precipitation was not influential, except in the case of travelling. Additionally, we observed *E. collaris A. meridionalis*, and *M. murinus* travelling and sleeping in the *Melaleuca* habitat (see also Andriamandimbiarisoa et al., in press).

Indigenous and/or exotic tree species can provide benefits to both locals and primates (Bicca-Marques & Calegaro-Marques, 1994; Grimes and Paterson, 2000); the presence of *Melaleuca* in Mandena has value as habitat and as timber. Locals have begun to harvest these trees daily with the recent legal protection status of the Mandena upland forest. Gaps in the canopy would allow for continued growth of terrestrial swamp vegetation, specifically graminoid species, which constitute a large portion of the *H. meridionalis* diet (Eppley et al., 2011). *Melaleuca* may have value as a temporary, fast-acting solution to connecting fragments while more long-term conservation solutions are being put in place, e.g., the Mandena nursery/reforestation efforts (Andriamandimbiarisoa et al., in press). In the case of Mandena, the exotic *Melaleuca* acts similar to a plantation forest for native fauna; while not as ideal as natural upland littoral forest, it provides valuable habitat and may possibly contribute to the conservation of endemic fauna (Brockerhoff et al., 2008). Thus, the continued harvesting of these exotic trees may assist in the effective management of its geographic spread and would be essential for successful long-term conservation efforts.

Many studies from various countries have documented that exotic plantation forests can provide habitat for numerous native forest fauna (Gascon et al., 1999; Barbaro et al., 2005, 2008). As an example, threatened bird species such as *Apteryx mantelli*, *Casuarius casuarius*, and *Upupa epops* have been known to occur in substantial populations in some exotic plantation habitats (Kleinpaste, 1990; Keenan et al., 1997; Barbaro et al., 2008; but see Watson et al., 2005). Furthermore, primates such as black howler monkeys (*Alouatta pigra*) have been reported to thrive in *Eucalyptus* spp. plantations (Bonilla-Sánchez et al., 2012), mantled howler monkeys (*A. palliata*) are able to use shade-grown coffee (*Coffea arabica*) as the core of their habitat range (Williams- Guillén et al., 2006), while siamang (*Hylobates syndactylus*) are known to occur in rubber (*Hevea brasiliensis*) and dammar gum (*Shorea javanica*) tree plantations (Michon & de Foresta, 1995). Bamboo lemurs are no different in

their use of an exotic species habitat and appear to be relatively adaptable within anthropogenic landscapes, being noted to frequent agricultural fields and crop-raid at some sites (Grassi, 2006; Martinez, 2008).

That the lemurs utilized invasive *Melaleuca* for behavioural activities demonstrates its potential role as a riparian corridor to facilitate dispersal. From October 2012 – December 2013 we confirmed three separate *Hapalemur* dispersals that utilized *Melaleuca* corridors to emigrate from their natal group, while a fourth dispersal remains unconfirmed. While our data indicate that *H. meridionalis* are tolerant to habitat degradation and fragmentation, habitat matrix composition and connectivity have been shown to influence dispersal in various birds and mammals (Wethered & Lawes, 2003; Pardini, 2004), e.g., hazel grouse *Bonasa bonasia* (Aberg et al., 1995), barred antshrikes *Thamnophilus doliatus* (Gillies & St. Clair, 2008), Angola black-and-white colobus *Colobus angolensis palliatus* (Anderson et al., 2007), and various marsupials (Laurance & Laurance, 1999). Furthermore, exotic tree plantations/forests have been demonstrated to facilitate dispersal for a wide range of taxa (Ferreras, 2001; Wethered & Lawes, 2005), for example, dispersal of the chucao tapaculo (*Scelorchilus rubecula*) is facilitated by the vertical structure rather than plant species composition of the corridor, in this case shrub fields dominated by 1-2 m tall invasive *Baccharis magellanica* (Castellón & Sieving, 2006).

While instances of successful dispersal provide a glimmer of hope, the further fragmentation of remaining forests is of great concern if forest species of Madagascar are to persist (Ganzhorn et al., 2014). Lemurs fulfil important ecological roles, e.g., they are the primary seed dispersers and pollinators, and are essential for maintaining the island's unique forests; their loss would likely trigger extinction cascades (Ganzhorn et al., 1999; Razafindratsima & Dunham, 2014). Although the fate of all lemur species should be considered precarious due to increasing habitat destruction, the knowledge that some lemurs are able to cope with this degradation (to a certain degree) should be seen as positive. Recent studies have begun to alter our view of *Hapalemur* as dietary specialists, demonstrating dietary flexibility and ability to subsist on items other than bamboo in some populations (Mutschler, 1999; Grassi, 2006; Eppley et al., 2011). Some primate species adapted to narrow ecological specializations may be sensitive to natural or anthropogenic habitat perturbations (Harcourt et al., 2005; Kamilar & Paciulli, 2008), whereas others have been shown to adjust to these ever-changing environments (Anderson et al., 2007; Nowak & Lee, 2013).

Though bamboo lemurs display an ecological flexibility, we will soon be at the point that bold decisions need to be made if we are to see some of their congeners survive. Among the most threatened within the genus is the Lac Alaotran gentle lemur (*H. alaotrensis*), assessed by the IUCN (2012) as Critically Endangered (CR B1ab(iii,v)), due to its greatly restricted range that is becoming increasingly populated while the remaining viable habitat continues to shrink (Bakoariniaina et al., 2006). Interestingly, they subsist on a dietary niche limited to sedges and non-bamboo grasses (Mutschler, 1999), similar to *H. meridionalis* when it is in the *Melaleuca* habitat. In captivity, however, *H. alaotrensis* regularly display a preference for bamboo (Beattie & Feistner, 1998), suggesting they are no different from congeners, with a flexibility that may allow them to persist in habitats outside of Lac Alaotra. It is because of this ecological flexibility that perhaps conservationists need to rethink their strategy when considering how to save this species. While perhaps a little "outside the box", it may be time to consider the translocation of some individuals to geographically nearby protected lake/wetland and forest areas with either similar vegetation and/or bamboo present. Ultimately, conservation plans thereafter can focus on the development of protected corridors between the two respective populations to link these habitats within a larger framework so that we offset the requirements for this threatened species within a larger habitat range. This would potentially allow the species to retreat into suitable habitats and maintain viable populations while buffering against extinction, as they are threatened by small remaining population sizes and species genetic erosion (Anderson et al., 2007; Hannah et al., 2008; Kremen et al., 2008; Irwin et al., 2010).

Building on this, once the most geographically widespread lemur (Godfrey & Vuillaume-Randriamanantena, 1986; Godfrey et al., 2004), the greater bamboo lemur *Prolemur simus* is now listed as Critically Endangered (CR C1+2a(i)) by the IUCN (2012), yet congruent with other bamboo lemurs appears to show considerable flexibility. Their preferred food source is large-culmed bamboo *Cathariostachys madagascariensis*, and while this food item may act as a limiting factor to the current distribution of *P. simus* (Wright et al., 2008), they exploit canopy gaps and areas of anthropogenic disturbance (Olsen et al., 2013). Though the *P. simus* population of Ankeniheny-Zahamena displays preferences for primary forest and little anthropogenic disturbance (Olson et al., 2013), a separate population is able to survive within a coffee plantation with interspersed stands of *C. madagascariensis* at Kianjavato (Wright et al., 2008). Exotic, though not invasive, plant species might provide fast growing alternatives to native species (Bicca-Marques & Calegaro-Marques, 1994;

Grimes & Paterson, 2000; Andriamandimbiarisoa et al., in press), of which woody bamboos may present a viable option.

Conclusion

The exhibited group differences in habitat utilization indicate that *H. meridionalis* are highly adaptable, displaying an ecological flexibility that allows them to persist across a mosaic of distinct habitats. More specifically, their use of an invasive species-dominant habitat, one that acts as a riparian corridor, appears to facilitate and maintain movement between the Mandena littoral fragments as well as the larger continuous humid forests. Non-native species have the ability to catastrophically dismantle the ecological integrity of habitats; however, their ability to facilitate dispersal within fragmented landscapes and thus potentially circumvent faunal genetic erosion should be carefully considered in tandem within future conservation management plans and native reforestation efforts.

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Biographical sketches

Timothy M. Eppley is interested in primate behavioural ecology and how certain species adapt to anthropogenic landscapes. Giuseppe Donati is senior lecturer who, since 1996, has been conducting research on the evolution of primate activity patterns and lemur responses to habitat disturbance. Jean-Baptiste Ramanamanjato is the superintendent of Biodiversity at Rio Tinto QIT Madagascar Minerals QMM), and an ecologist with more than 20 years' experience of fieldwork and biodiversity management in Madagascar. Faly Randriatafika is a botanist who leads RTQMM's flora and rehabilitation team. Laza N. Andriamandimbiarisoa oversees the Biodiversity Conservation at RTQMM, with experience in conservation issues throughout Madagascar. David Rabehevitra is a botanist for RTQMM who is working on a photography inventory of all littoral plant species from southeast Madagascar. Robertin Ravelomanantsoa is a fieldworker within RTQMM who has worked mainly on monitoring *Hapalemur* over the last decade. Jörg U. Ganzhorn is Professor of Animal Ecology and Conservation with over 30 years of experience conducting fieldwork in Madagascar.

CHAPTER 3

Determinants of terrestrial feeding in an arboreal primate

With Giuseppe Donati and Jörg U. Ganzhorn

in preparation for submission

Summary

1. Mammals have evolved to fill certain ecological niches, with primates maintaining either a mostly arboreal or terrestrial lifestyle. Despite the present-day ubiquity of this dichotomy, early primate radiations displayed an arboreal ancestry, and so we aim to identify the costs and benefits imposed on the transition.

2. Within a fragmented littoral forest in southeast Madagascar, a strepsirrhine population of *Hapalemur meridionalis* spends a large portion of time on the ground, providing an excellent model with which to test terrestriality costs and benefits. As such, we conducted full-day focal follows, recording continuous feeding time on all food items separated by strata (arboreal or terrestrial), and biochemical analyses on each item for dietary quality comparisons for three groups of *H. meridionalis*.

3. While diet was twice as diverse as previously recorded in this genus, all three social groups displayed varying amounts of terrestrial feeding, predicted by both seasonal factors (temperature and precipitation) as well as metabolizable energy, but not by protein/fiber ratio or by canopy exposure.

4. These results show that the southern bamboo lemurs expanded their dietary niche to increase their daily metabolizable energy intake seasonally. There were no differences in canopy exposure between the two feeding strata, showing that aerial predation was not a greater threat in one location over the other; however, focal subjects fed more closely to a conspecific when on the ground, perhaps to increase vigilance for potential predators.

5. Our study provides empirical evidence that suggests a proximate origin of terrestriality, providing a seasonal alternative to increasing metabolizable energy intake while weighing the potential predation risks associated with this new ecological niche. Coupled with the disturbance of the habitat in our study, it may be that as environments changed/evolved over time, localized populations expanding their dietary niche to the ground was a catalyst in the radiation of terrestrial species.

Key-words: anti-predator, feeding ecology, graminoids, *Hapalemur meridionalis*, nutrition, Primates, southern bamboo lemur, terrestrial grazing

Introduction

      All organisms, including mammalian taxa, often focus on exploiting specific ecological niches in order to decrease competition with sympatric species. It has been

suggested that ancestral eutherian orders, including placental mammals, are likely characterized by a terrestrial evolutionary history, with subsequent events of arboreality derived multiple times to fulfill various ecological niches (reviewed in Szalay, 2007; Ji et al., 2010). On the other hand, arboreality is the primitive condition for the Order Primates, having initially evolved in a euarchonton, i.e., ancestral mammals from which Primates radiated (Sussman, 1991; Szalay, 2007; Kirk et al., 2008).

As environments changed over time, some primates adapted and descended from the trees to extend into a more terrestrial niche. Generally the focus of this shift from arboreal to terrestrial niche expansion is shown through various morphological adaptations (e.g., limb, dental, postcranial, etc.) in the fossil record (Gebo and Sargis, 1994; Gebo, 1996; Fleagle, 2013). However, on a more proximate scale, the initial influences on expanding to a terrestrial niche are unknown. It has been hypothesized that larger-bodied, terrestrial primates tend to live in larger social groups than arboreal primates because the rate of predation is higher on the ground (van Schaik, 1983). This is not clear-cut, however, and primates with arboreal or terrestrial lifestyles may be equally susceptible to predators (Cheney and Wrangham, 1987; Isbell, 1994; Janson and Goldsmith, 1995; Hart, 2007). Despite the potential increase in predation pressure from a shift to a terrestrial niche by an arboreal species (Newell, 1998, 1999), terrestrial behavior may facilitate movement and potential dispersal throughout a landscape, evading genetic erosion and habitat fragmentation (Pahl et al., 1988; Laurance, 1990; Ancrenaz et al., 2014)

Causal to predation pressure, food distribution and dietary quality are considered to be additional ultimate ecological factors that have an influence on whether primate species live arboreally or terrestrially (Jolly, 1985; Janson, 1990; Cant, 1992; Campbell et al., 2005; Xiang et al, 2009). It is often shown that arboreal primates face the risk of descending to the ground primarily to gain access to water or to obtain micronutrients, specifically, a certain amino acid and/or minerals (Izawa, 1993; Campbell et al., 2005; Link et al., 2011a, 2011b). However, this is quite different from a dietary niche expansion, whereby animals may be seasonally supplementing their daily nutritional intake during a lean season (Grueter et al., 2009; Barnett et al., 2012). Thus, the transition of an arboreal mammal to a terrestrial dietary niche becomes a cost/benefit analysis, specifically balancing the nutritional gain of terrestrial food items compared to the potential risk of predation.

Among the strepsirrhine primates of Madagascar (i.e., lemurs), the ring-tailed lemur (*Lemur catta*) is the most terrestrial species, spending approximately 30% of its time on the

ground (Jolly, 1966; Sussman, 1974). The occurrence of terrestrial behavior by lemurids is common but the duration is often minimal. Bamboo lemurs (*Hapalemur* spp. and *Prolemur simus*) are no exception, having been observed to feed on the ground (Wright, 1986; Overdorff et al., 1997; Tan, 1999; Grassi, 2006; Eppley and Donati, 2009; Eppley et al., 2011). However, bamboo lemurs are mostly arboreal, typically exploiting the low to mid-canopy habitat niche while relying on their cryptic nature as an anti-predator strategy (Tan, 2006). Like their name indicates, they are known for their dietary preference of bamboo, a type of grass that is widespread throughout the eastern forests of Madagascar (Dransfield, 2000), and at times can make up 85-95% of their diet across a multitude of study sites (Wright, 1986; Overdorff et al., 1997; Tan, 1999; Grassi, 2002, 2006). The Alaotran gentle lemur has been the only exception within the genus clade, with its entire population living in the wetlands around Lac Alaotra, a habitat devoid of bamboo. Here, *Hapalemur* have a diet that contains reeds and sedges, yet their dietary breadth remains low (~11spp.) due to the lack of available food options (Mutschler, 1999). Contrastingly, southern bamboo lemurs (*Hapalemur meridionalis*) in Mandena, an area devoid of bamboo (Rabenantoandro et al., 2007; Eppley et al., in review), spend nearly 70% of their feeding time on the ground during the austral winter, an exceedingly large amount of time compared with congeners. (Eppley and Donati, 2009; Eppley et al., 2011). It has been previously suggested that terrestrial foraging in some arboreal species may represent a nutritional fallback strategy when more preferred food items are in seasonally low abundance in more degraded habitats (Newton, 1992; Grueter et al., 2009; Barnett et al., 2012). However, while this may be the case with *H. meridionalis*, their terrestrial grazing often takes place in an open swamp/marsh habitat, potentially increasing their susceptibility to aerial and terrestrial predation (Karpanty, 2006; Karpanty and Wright, 2007).

The southern bamboo lemurs of Mandena provide an exceptional model for exploring the proximate influences on the transition to a terrestrial niche expansion. Given previous observations, we predicted that:

- An expansion to the terrestrial dietary niche would be seasonal, specifically in response to nutritionally-deficient food availability during the austral winter.
- As such, we further predicted that the daily nutritional intake of terrestrial food items would represent a markedly higher dietary quality than arboreal food items (i.e.,

protein/fiber ratio and metabolizable energy), thus providing justification for their increased utilization of a potentially risky stratum.

- Furthermore, we predicted that terrestrial feeding would be associated with increased canopy exposure, but as a response to the increased predation risk, we predicted that bamboo lemurs would maintain closer proximities to group members as compared to when they feed arboreally.

Methods

Study site

Our study was conducted in the protected area of Mandena (24°95'S 46°99'E) in the extreme southeast of Madagascar, approximately 10 km north of Fort-Dauphin (Tolagnaro). This 230 ha area consists of fragmented and degraded littoral upland forest and interspersed, seasonally-inundated swamp (Ganzhorn et al., 2007; Eppley et al., in review). Among the most threatened habitats in Madagascar (Du Puy and Moat, 1996; Ganzhorn et al., 2001; Bollen and Donati, 2006), littoral forests occur within 3 km of the coast and are characterized as having a relatively low canopy that grows on sandy substrates (Dumetz, 1999; Consiglio et al. 2006).

Monthly climatic factors can be highly variable within the littoral zone of southeast Madagascar; our data do not closely reflect historical records for the area (Bollen and Donati, 2005; Eppley et al., 2015a). Temperature (°C) was recorded in 30-mins intervals throughout the study using Lascar EL-USB-1 data loggers, operated by custom software (EasyLog USB Version 5.45, Lascar Electronics). Precipitation (mm) was measured daily at 6:00h using a rain gauge placed within the study site.

Study species

Southern bamboo lemurs (*Hapalemur meridionalis*) are relatively small-bodied primates (1.072 ± 0.107 kg; $N = 15$) that exhibit a cathemeral activity pattern (Eppley et al., 2015a, b). They live in small social groups with one or two breeding females and typically one breeding male, with an average group size of 5.6 ± 1.5 individuals ($N = 5$) (Eppley et al., in review). Similar to congeners, they are classified as folivores (Eppley et al., 2011). Within Mandena, they live sympatrically with cathemeral *Eulemur collaris* and nocturnal *Microcebus murinus*, *Cheirogaleus medius*, *C. major*, and *Avahi meridionalis* (Ganzhorn et al., 2007).

In order to expedite the habituation process (Juarez et al., 2011) and increase our ability to locate these highly cryptic animals, we captured and collared ten adult *H. meridionalis* across four neighboring social groups between October and December 2012. Details of the capture protocol followed have been previously described in Eppley et al. (2015b).

Behavioral Data

From January to December 2013, we conducted full-day focal follows (from sunrise to sunset) for approximately five days a month with groups 1, 2, and 4 each, while group 3 was used exclusively for home range data collection. Identification of individuals was made using radio-tracking tags with colored pendants, with all adult individuals in each group sampled at least once each month. Behavioral data were collected via instantaneous focal sampling (Altmann, 1974) at 5-min intervals on broad-level activities (resting, feeding, moving, social and other), noting the height (arboreal or terrestrial) of the focal subject, as well as whether there was canopy cover directly above the individual. Continuous sampling was utilized each time the focal was observed feeding. This included the exact time spent feeding (timed to the second) per food item(s) while noting the plant species. Height, i.e., arboreal or terrestrial, was also recorded for each feeding bout. A new bout was recorded if there was a 60 second interval with no feeding.

Due to the differences in habitat and their contrasting floristic structures (Eppley et al, in review), we evaluated exposure to diurnal birds of prey by collecting instantaneous point sampling of whether the focal subject was located directly under canopy cover, or if they were exposed. Two species of hawk are present in Mandena, Madagascar harrier-hawk *Polyboroides radiatus* and Henst's goshawk *Accipiter henstii* (TME, personal observation), all of which represent a potential threat for adult bamboo lemurs (Karpanty, 2006; Karpanty and Wright, 2007). A third large aerial raptor, Madagascar buzzard *Buteo brachypterus*, is also present in Mandena, a species observed to prey on medium-sized lemurs (Wright et al., 1998). Given the various hunting strategies of these raptors (Brockman 2003) and the habitat differences, our method may not provide an accurate measure of predation risk. However, playback experiments of aerial predators have shown *Hapalemur* to descend in the canopy in response to raptor calls (Karpanty and Wright, 2007). As our main goal was a comparative measure between feeding strata (i.e., arboreal or terrestrial), we considered our canopy exposure method as an acceptable proxy.

Predation risk of *Hapalemur* spp. is not limited to aerial predators; viverrid carnivores, e.g., fossa *Cryptoprocta ferox* (Goodman and Pidgeon, 1999; Sterling and McFadden, 2000), as well as large snakes, e.g., Madagascar tree boa *Sanzinia madagascariensis* (formerly *Boa manditra*; Goodman et al., 1993; Rakotondravony et al., 1998) and Dumeril's boa *Acrantophis dumerili*, present potential arboreal and terrestrial predatory threats, respectively. Though bamboo lemurs are known for their cryptic nature, other evolutionary anti-predator strategies may include lowering predation susceptibility via group defense, dilution of risk, or increased vigilance (Hamilton, 1971; Janson, 1992). To test whether *H. meridionalis* employed these strategies, we recorded the nearest neighbor to the focal, categorizing these as *close* ($\leq$ 3m) and *far* (> 3m), allowing us to calculate a proportion for both arboreal and terrestrial feeding. In addition to this, we collected *ad libitum* observations on specific instances of potential predatory risks.

Nutritional Analyses

We collected food item samples (e.g., young and mature leaves, lianas, flowers, unripe and ripe fruits, fungi, soil etc.) directly from feeding trees and/or grazing sites on the same day or at the same time the following day. Samples were weighed with an electronic balance (fresh weight), dried in an oven at approximately 40°C for a standard period, and weighed again (dry weight) at the field site. Dry matter specimens were exported to the University of Hamburg and biochemical analyses on all food items were conducted in 2013-2014. Specimens were then ground to pass a 2 mm sieve and dried again at 50-60°C before analyses. Nitrogen was measured via the Kjeldahl method while soluble proteins were assessed via BioRad after extraction of the plant material with 0.1 N NaOH for 15 h at room temperature. Soluble carbohydrates were extracted with 50% methanol. Concentrations of soluble sugars were determined as the equivalent of galactose after hydrolization of 50% methanol extract. Specimens were analysed for neutral (NDF) and acid (ADF) detergent fibres, with NDF representing all the insoluble fibre (cellulose, hemicellulose and lignin) and ADF representing the fibre fraction containing cellulose and lignin. Lipid content was determined by extraction using petroleum ether, followed by evaporation of the solvent. Detailed reviews of the procedures and their biological relevance are provided by Ortman et al. (2006), Donati et al. (2007) and Rothman et al. (2012).

Data Analyses

Our initial examination of the southern bamboo lemur feeding ecology sought to assess dietary diversity for both annual and monthly diets in each of the three social groups via species numbers and the Simpson's diversity index (Begon et al., 1996; Irwin, 2008):

$$D = \frac{1}{\sum_{i=1}^{S} P_i^2}$$

where S = the total number of species eaten and P_i = proportion of feeding time devoted to species i. The index value increases with the species richness (S) and each species' equitability, i.e., infrequently eaten species contribute less than commonly eaten species. We also evaluated the differences between *Hapalemur* groups and their food choices by examining dyadic dietary overlap (i.e., group 1 – group 2; group 2 – group 4; and group 1 – group 4) via Schoener's index (Schoener 1968):

$$D = 1 - 0.5 \bullet \sum_{i=1}^{n} |p_{ij} - p_{ik}|$$

where p_{ij} is the proportional representation of food i in group j's diet, p_{ik} is the proportional representation of food i in group k's diet, and n is the total number of foods eaten by both groups. The index (D) varies between 0 (no overlap) and 1 (complete overlap).

Arboreal leaves and terrestrial grasses are not easily comparable; therefore we decided to focus our assessment on the dietary quality within these two feeding strata. To evaluate dietary quality of arboreal and terrestrial food items, we calculated the protein-to-fibre ratio (PF) and metabolizable energy (ME) in the daily diet at each feeding strata. We calculated the weighted proportion of dry matter per month for each nutritional compound, with the proportion of feeding records for each food item as the weighted coefficient (Kurland and Gaulin, 1987):

$$\text{Intake} : \sum (F_i \times X_i)$$

where F_i is the monthly proportion of feeding records and X_i is the percentage of dry matter of each chemical parameter for the ith item. The protein-to-fiber ratio was calculated as crude protein/acid detergent fiber (Milton 1979; Dasilva 1994; Mutschler 1999), using a conversion

factor of 6.25 to estimate crude protein from the total nitrogen present via the Kjeldahl method (Ortmann et al., 2006). This ratio is a useful indicator of whether certain species choose to consume a particular leaf species (Milton 1979, 1998; McKey et al. 1981; Davies et al. 1988; Ganzhorn 1992); however, it may only explain leaf choice for some groups but not others (Chapman and Chapman, 2002; Chapman et al., 2004) and its biological meaning has been questioned based on theoretical (Wallis et al. 2012) and empirical grounds (Gogarten et al., 2012). Nevertheless, we use this ratio as one component in our analyses to allow comparisons with previous studies.

Energy content from food was obtained by standard conversion factors such as 4 kcal g^{-1} for soluble carbohydrate, 4 kcal g^{-1} for soluble protein and 9 kcal g^{-1} for lipid. We used a fiber conversion factor of 3 kcal g^{-1} rather than 4 kcal g^{-1} usually used for carbohydrates, since the anaerobic microbes take ~1 kcal g^{-1} of fibers for their own growth during fermentation processes (Conklin-Brittain et al., 2006). Energy was then obtained via the following equation:

$$ME = (9 \times L) + (4 \times SP) + (4 \times SC) + (3 \times [NDF \times 0.709])$$

where ME is the metabolizable energy per gram (in $kcalg^{-1}$) of diet; L is the proportion of lipids; SP the proportion of soluble proteins; SC the proportion of soluble carbohydrates and [NDF $\times$ 0.709] the fraction of NDF which are digested by bamboo lemurs (Campbell et al., 2004).

Arboreal and Terrestrial Feeding

To determine which factors influenced arboreal feeding, we fitted linear mixed-effects models (LMM) in R statistical software (R Development Core Team, 2014) using the lmer function of the lme4 package (Bates et al., 2012), with the daily proportion of time spent feeding terrestrially as a continuous response variable. We only included data from days in which the focal subject was observed for ≥80% of the day length, as determined by sunrise and sunset. Included fixed effects were calculated as the differences from terrestrial and arboreal proportional values for the following variables: canopy exposure (as a proxy of exposure to birds of prey), nearest neighbor (as a proxy for group vigilance and/or sentinel behavior), as well as protein-to-fiber ratio and metabolizable energy (both as proxies for dietary quality). In addition, we included seasonal variables of daily mean temperature and

daily total precipitation as fixed effects. Groups were included as random effect to control for repeated sampling. We then used the anova function to calculate likelihood ratio tests for model comparison, allowing us to determine which model had the best explanatory power by comparing Akaike's Information Criterion (AIC) values for all possible models. *P*-values were obtained with a likelihood ratio test using the afex package (Singmann, 2014), developed for R statistical software (R Development Core Team, 2014).

Ethical Note

All data were collected in accordance with the ASAB/ABS Guidelines for Use of Animals in Research. This research was carried out under the Accord de Collaboration among the University of Antananarivo and the University of Hamburg. Research protocols were approved and permits authorized by Commission Tripartite of the Direction des Eaux et Forêts de Madagascar (Autorisation de recherché N° 240/12/MEF/SG/DGF/DCB.SAP/SCB du 17/09/2012), adhering to the legal requirements of Madagascar.

Results

We observed *H. meridionalis* for >1,762 h, resulting in 693.89h (41,633.27mins) of feeding recorded. Overall, southern bamboo lemurs selected for 86 different food items from 72 distinct species in Mandena. The top ten species in their diet (Table 1) made up just less than 76% of their total feeding record. These lemurs appear to rely heavily upon a few key liana and graminoid species for the majority of their daily food intake. Graminoids (i.e., species of the Families Poaceae and Cyperaceae) are almost exclusively eaten from a terrestrial position, and thus their selection of these items is intriguing. Bamboo lemurs in Mandena were not limited to an exclusively folivorous diet; they selected for a total of 34 different fruit species, a few of which contributed to a large proportion of their monthly diet with peaks in February, July, and December (Table 2).

Table 1. Top ten species consumed by *H. meridionalis* from Jan. – Dec. 2013

Scientific name	Vernacular	Family	TFR (%)	Part(s)
Panicum parvifolium	Ahipoly	Poaceae	16.43	grass
Aristida rufescens	Tsingirifiry	Poaceae	13.16	grass
Uapaca spp.	Voapaky	Euphorbiaceae	11.11	un/ripe fruit
Baroniella camptocarpoides	Vahihazo	Apocynaceae	10.90	yl, ml, liana
Secamone sp.	Vahigoneny	Asclepiadaceae	7.71	yl, ml, liana
Lepironia mucronata	Mahampy	Cyperaceae	4.29	pith
Brexia madagascariensis	Voakarepoky	Celastraceae	3.48	flower
Ravenala madagascariensis	Ravinala	Strelitziaceae	3.27	flower
Sarcolaena multiflora	Meramaintso	Sarcolaenaceae	2.97	flower, fruit
Stenotaphrum dimidiatum	Ahipisaka	Poaceae	2.66	grass
Total			75.99	

TFR total feeding record; *yl* young leaves; *ml* mature leaves
Liana refers to young vines, leaves not included

Table 2. Number of species eaten and overall percent by each food type selected by *H. meridionalis* groups in Mandena from Jan. – Dec. 2013

Food type	Group 1		Group 2		Group 4		Total	
	No. species	TFR (%)	No. species	TFR (%)	No. species	TFR (%)	No. species	TFR (%)
Grass	8	25.44	7	35.64	7	44.29	8	34.34
Leaves	5	10.99	5	11.32	7	4.54	7	8.75
Pith	11	18.89	8	5.22	14	15.02	14	12.75
Liana	5	15.65	5	12.27	4	6.35	5	11.17
Fruit	23	19.25	19	27.98	18	9.78	34	18.58
Flower	9	7.25	7	11.18	7	20.78	10	12.78
Fungi	4	2.32	2	0.98	3	0.72	4	1.31
Soil	Y	0.09	Y	0.20	Y	0.02	Y	0.10
Water	Y	0.11	Y	0.49	Y	0.04	Y	0.21

TFR total feeding record
Note: Species are not all limited to one category, overlap can occur.

Overall, dietary diversity was high for bamboo lemurs, with both groups 1 and 4 selecting for 56 distinct species while group 2 had lower diversity, selecting 47 species annually (Table 3). Group 1 had both the highest species and family diversity of selected foods. There were monthly differences in dietary diversity between the three social groups (Figure 1), but what is more intriguing is the minimal monthly dietary overlap that occurred between groups (Figure 2).

Table 3. Annual dietary diversity (via Simpson's dietary diversity index) for each of the three *H. meridionalis* social groups, including the number of species/families selected and number of species/families that contributed ≥ 1% to the overall diet.

	Species diversity			Family diversity		
Group	Selected	≥ 1%	Simpson's D	Selected	≥ 1%	Simpson's D
1	56	15	11.97	29	13	6.91
2	47	14	6.61	27	10	5.49
4	56	20	7.79	33	16	4.49
Total	72	18	12.08	37	14	6.26

Southern bamboo lemurs in Mandena were mainly graminivorous, feeding on terrestrial grasses and the soft piths of sedges and reeds (Table 2). Their selection of grasses typically included reaching for bouquets of leaf blades (both young and mature) and often included the culm (and inflourenscence, when available) as they ate approximately two-thirds of the specimen from the new growth towards the root. Although their selection for these items was quite stable throughout the year, we did observe a peak in graminoid consumption in June and July, corresponding with the austral winter. In general, terrestrial feeding was not limited to just graminoid species (and soil and water), but rather comprised 29 different items that included forbs, fungi, lianas (specifically the vine, leaves considered separate), and fallen fruit.

Table 4. Phytochemical characteristics of food items per major category: grass, piths, lianas (vine only), young leaves (YL), mature leaves (ML), unripe fruit (U. Fruit), ripe fruit (R. Fruit), flower, fungi, soil, and non-food leaves. Values are medians and quartiles.

Item	N	SP	SC	NDF	ADF	Lipid	Tannins	Phenol	Ash
Grass	**1.79**	**2.06**	**4.10**	**67.34**	**31.76**	**1.48**	**0.00**	**0.79**	**7.59**
N=10	1.67-2.16	1.83-2.68	3.47-4.39	62.88-70.62	28.32-35.00	1.08-1.81	0.00-0.00	0.59-0.92	6.75-8.44
Pith	**1.25**	**2.28**	**3.37**	**62.33**	**37.87**	**1.11**	**0.27**	**0.60**	**10.27**
N=13	1.05-1.55	2.07-3.72	2.65-3.91	59.23-66.89	35.98-46.04	0.78-1.57	0.00-0.42	0.54-0.85	7.81-11.14
Liana	**1.36**	**1.50**	**3.50**	**52.41**	**36.06**	**1.37**	**0.00**	**0.48**	**8.21**
N=7	1.23-2.83	1.23-2.38	3.18-9.90	44.64-56.36	28.40-41.25	1.22-1.60	0.00-0.00	0.36-0.86	5.96-9.31
YL	**1.82**	**1.82**	**4.25**	**37.87**	**26.92**	**1.86**	**0.00**	**0.91**	**9.38**
N=6	1.52-1.98	1.48-2.50	4.07-7.46	30.55-57.52	21.02-34.57	1.18-2.74	0.00-0.00	0.51-1.74	7.40-11.75
ML	**1.49**	**1.06**	**4.52**	**45.66**	**31.75**	**4.65**	**0.23**	**0.49**	**11.05**
N=1									
U. Fruit	**0.78**	**4.71**	**1.94**	**65.12**	**48.07**	**3.77**	**0.22**	**0.57**	**7.00**
N=3	0.76-0.98	3.34-4.82	1.34-2.71	59.72-68.77	43.19-52.31	2.14-5.21	0.11-0.26	0.47-0.69	4.89-7.42
R. Fruit	**0.69**	**2.35**	**6.83**	**56.79**	**40.50**	**3.35**	**0.00**	**0.85**	**3.67**
			4.41-10.67						
N=33	0.59-0.87	1.94-4.07	10.67	45.14-61.21	33.22-44.50	1.48-4.47	0.00-0.49	0.65-1.37	2.90-4.50
Flower	**0.86**	**4.33**	**7.39**	**36.97**	**29.80**	**1.55**	**0.29**	**1.90**	**6.27**
			5.81-10.06						
N=11	0.74-1.00	3.14-6.14	10.06	32.10-53.45	25.22-35.48	1.09-1.81	0.00-0.90	1.19-4.08	5.59-8.48
Fungi	**1.48**	**1.87**	**3.70**	**59.98**	**23.95**	**0.60**	**0.00**	**0.24**	**2.74**
N=4	1.16-1.75	1.43-3.17	3.41-5.45	55.33-64.60	19.97-33.66	0.43-0.82	0.00-0.00	0.16-0.35	2.15-3.33
Soil	**0.13**	**0.24**	**0.14**	**97.84**	**97.14**	**0.09**	**0.00**	**0.02**	**95.28**
N=1									
Non-food	**1.25**	**2.72**	**6.50**	**42.01**	**30.89**	**na**	**0.20**	**2.74**	**7.18**
N=11	1.15-1.49	2.08-4.13	4.68-9.77	38.59-51.48	26.20-34.01		0.00-0.65	1.58-3.99	5.19-9.89

N = nitrogen; SP = soluble protein; SC = soluble carbohydrates; NDF = neutral detergent fiber; ADF = acid detergent fiber.
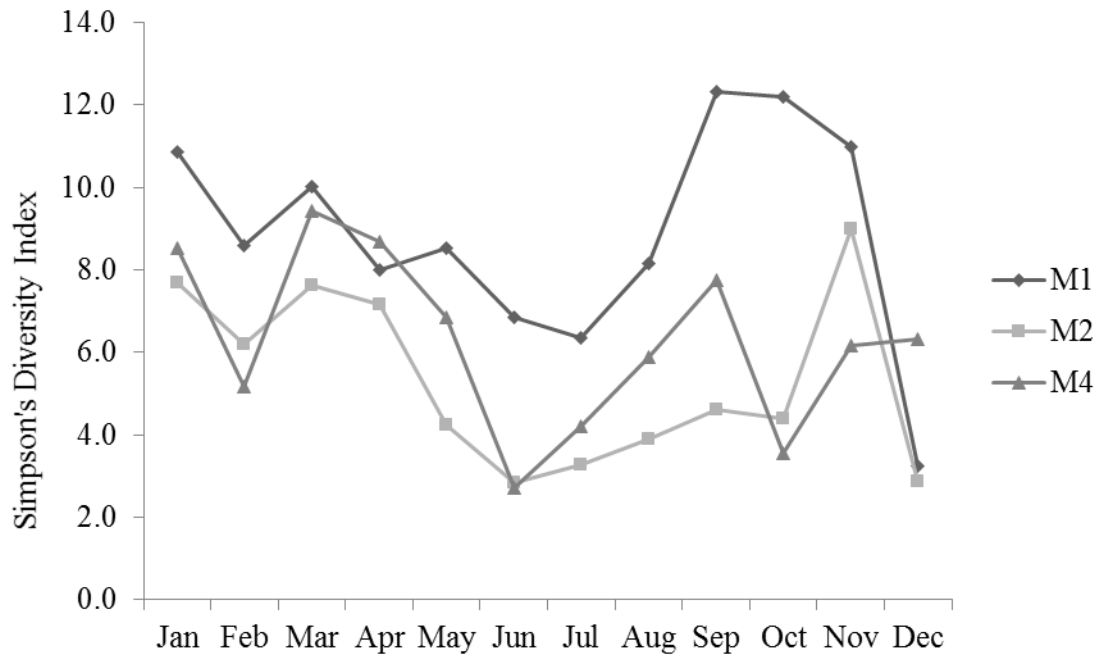
Figure 1. Monthly dietary diversity (via Simpson's dietary diversity index) for each of the three *H. meridionalis* groups
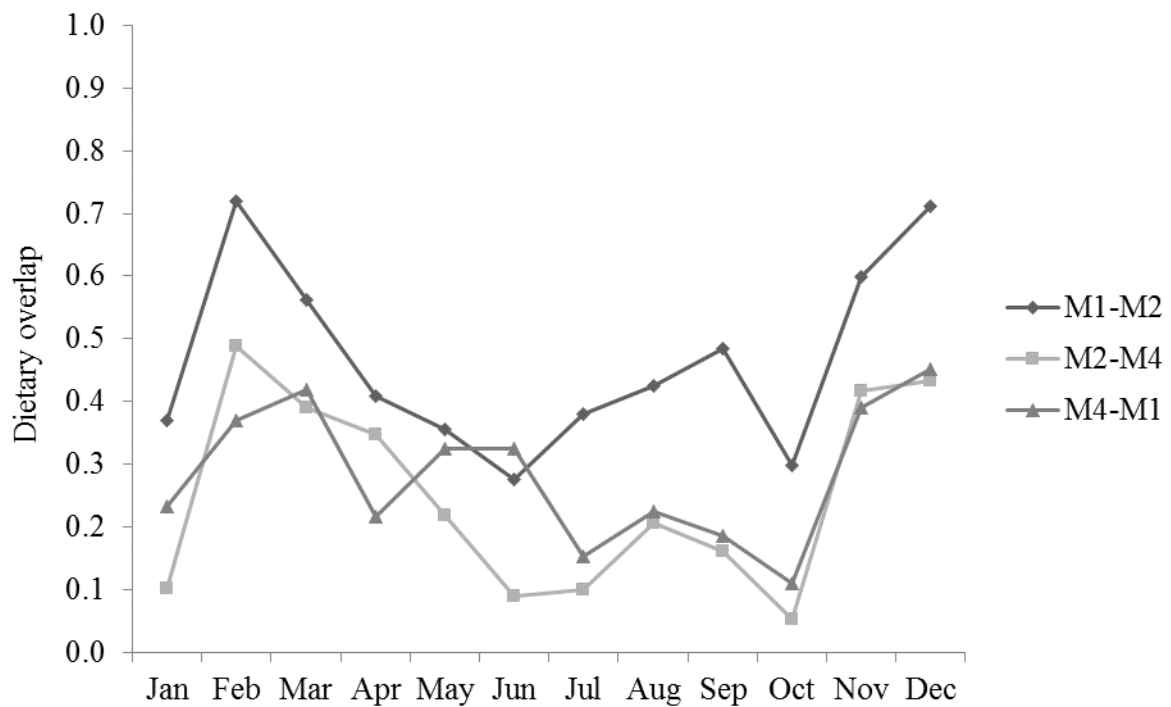

Figure 2. Schoener's dietary overlap. Monthly dyadic comparison between each of the three bamboo lemur groups.

When only considering our full-day focal follows ($N = 106$), bamboo lemurs averaged feeding terrestrially for 148.08mins and arboreal feeding for 158.99mins, daily. This was calculated from a total of 15,696.96 mins of terrestrial feeding and 16,853.15 mins of

arboreal feeding. We used a linear mixed model (LMM) to determine which factors best predicted a greater daily proportion of terrestrial feeding (Table 5). The best-fit model included significant values for nutritional proxies (metabolizable energy alone and as an interaction with protein-to-fiber ratio), and seasonal climatic influences, i.e., temperature and precipitation (AIC = -7.81, χ^2 = 9.18, df = 1, P = 0.002; Table 6).

Table 5. Daily averages and ranges of arboreal and terrestrial feeding and proximate factors.

		Dietary proxy		Predation proxy	
	Feeding (%)	PF ratio	ME	Canopy exposure	Nearest Neighbor
Arboreal					
Median	56.98	0.19	1.68	4.61	48.10
Quartiles	32.21 – 75.34	0.16 – 0.23	1.56 – 1.78	0.64 – 13.64	32.24 – 60.26
Terrestrial					
Median	43.02	0.35	1.87	6.22	66.35
Quartiles	24.66 – 67.79	0.31 – 0.38	1.84 – 1.89	0.00 – 16.75	44.80 – 81.70

N = 106 days; *PF ratio* Protein-to-Fiber ratio; *ME* Metabolizable Energy

Similar to the group differences in monthly dietary diversity, proportion of terrestrial feeding was also different between the groups. As for predictors of terrestrial feeding, the differences between terrestrial and arboreal canopy exposure and protein-fiber ratio (PF) were not significant. On the other hand, metabolizable energy (ME) did predict terrestrial feeding (Table 6). Seasonal climatic variables (i.e., temperature and precipitation) were significant predictors of terrestrial feeding. The only interaction that was included in the best-fit model was PF x ME, which was shown to be significant despite PF not influencing terrestrial feeding by itself.

Table 6. Linear mixed model predicting increased daily proportion of terrestrial feeding.

Variable	β	SE	95% CI	t	P
(Intercept)	**1.30**	**0.18**	**0.95, 1.65**	**7.15**	
Canopy Exposure	-0.10	0.10	-0.29, 0.09	-1.02	0.29
Protein-Fiber Ratio (PF)	-0.02	0.27	-0.53, 0.50	-0.07	0.94
Metabolizable Energy (ME)	**0.40**	**0.09**	**0.23, 0.56**	**4.64**	**<0.0001**
Temperature	**-0.04**	**0.01**	**-0.06, -0.03**	**-5.35**	**<0.0001**
Precipitation	**-0.01**	**0.00**	**-0.01, 0.00**	**-2.14**	**0.03**
PF * ME	**1.87**	**0.62**	**0.67, 3.06**	**2.99**	**<0.001**

N = 106 days
P-values (significant at P < 0.05, indicated in bold) were obtained using likelihood-ratio test
SE standard error, *CI* confidence interval

Given the near equal proportion of time spent feeding from an arboreal and terrestrial position by *H. meridionalis*, we tested a second proxy related to predation risk (i.e., sentinel or group vigilance). To do this, we analyzed the distance of the focal individual with a nearest neighbor via Pearson's correlation. Terrestrial feeding was significantly correlated with having a close nearest neighbor ($r(106) = 0.202$, $P = 0.038$), whereas arboreal feeding was not significantly correlated with the focal individual having a close nearest neighbor ($r(106) = 0.009$, $P = 0.929$).

Discussion

The southern bamboo lemurs of Mandena display a dietary breadth beyond what has been previously recorded for any *Hapalemur* spp. (Table 7). Furthermore, their ability to expand their dietary niche to include such a wide variety of fruits is exceptional, having selected 34 spp. over the course of the year, more than the total number of food species selected by all other congeners. This was not entirely unexpected since *H. griseus* have been recorded to eat multiple fruit species in Ranomafana (Tan, 1999; Grassi, 2001, 2006), but these are proportionally limited in comparison. Southern bamboo lemurs showed substantial peaks in fruit consumption in February, July/August, and December, the latter two periods being almost solely based upon *Uapaca* spp. fruiting. A reason for the low frequency of graminoids observed eaten in February is potentially due to the increased rainfall during that month. As the swamp areas are part of a seasonally-inundated flood plain, the water depth in these areas increased by approximately 2 meters, completely inhibiting our ability to follow animals on days when they accessed the swamps.

Table 7. Food species and families selected by bamboo lemurs (*Hapalemur* spp. / *Prolemur simus*)

Congener	Species	Families	Site	Reference
H. alaotrensis	11	8	Lac Alaotra	Mutschler 1999
H. aureus	≥21	15	Ranomafana	Tan 1999
H. griseus	≥24	12	Ranomafana	Tan 1999*
	22-31	na	Ranomafana	Grassi 2001
	12	8	Andasibe	Overdorff et al. 1997
H. meridionalis	72	37	Mandena	This study
P. simus	7	3	Ranomafana	Tan 1999

H. griseus noted as having been observed feeding on ≥40 food species (Tan, 2006);
na information not available

Our data show that terrestrial feeding did increase during the austral winter, influenced by both decreasing temperature and precipitation. Inter-group dietary diversity displayed large differences (also indicated by the low dietary overlap between groups), but our results also showed these values to decrease during the austral winter. Interestingly, dietary diversity was very low while dietary overlap was exceptionally high in December. This corresponds with a fruiting period for *Uapaca* spp., which bamboo lemurs selected for heavily during this time. Despite the diversity of fruit species selected by *H. meridionalis*, we still consider them folivores as fruits only constitute approximately 20% of their total feeding record. These data suggest that *H. meridionalis* should be considered feeding generalists, and perhaps even facultative frugivores. Regarding leaves, Tan (1999) observed that the majority of non-bamboo leaves eaten by *H. griseus* in Ranomafana were from lianas rather than trees, similar to our observations in Mandena. In fact, southern bamboo lemurs were not observed to feed on any tree species' leaves; rather, they were only seen selecting for leaves from grasses, lianas, and other terrestrial ground cover (such as Asiatic pennywort *Centella asiatica*, Apiaceae). Within each group, lianas and their leaves (mostly from *Baroniella camptocarpoides* and *Secamone* sp.) constituted a large portion of their diet, and were ubiquitous throughout the upland forest of Mandena. On the other hand, terrestrial grasses such as *Panicum parvifolium* and *Stenotaphrum dimidiatum* were distributed across both the upland forest and the swamps.

Gelada baboons (*Theropithecus gelada*) are often regarded as the only graminivorous primate and as such, an excellent model for early primates (Dunbar, 1983; Dunbar and Bose, 1991; Fashing et al., 2014). As previous bamboo lemur studies and our results showed, *Hapalemur* spp. share a niche in which they focus their dietary efforts on graminoids, similar to geladas. Despite their utilization of a similar terrestrial dietary niche, *T. gelada* are large-bodied, large social group monkeys that inhabit high-altitude grasslands with practically no forest cover whereas bamboo lemurs are much smaller-bodied, family unit-living primates. Furthermore, no extant predators (other than humans) remain in the environments where geladas live (Gippoliti and Hunter, 2008), thus the risks imposed on these two species are wholly disparate and not easily comparable.

The foods available on the ground are mostly graminoids, which are typically assumed to be of low nutritional quality with tough and abrasive properties (Jablonski, 1994; Venkataraman et al., 2014). However, as we predicted, the nutritional quality of bamboo lemur daily intake increased with terrestrial feeding. Our results showed that metabolizable

energy increased while feeding in this stratum, whereas protein-fiber ratio was not significant in predicting the expansion to the terrestrial dietary niche. Specifically, for every 0.1 unit that terrestrial ME is greater than arboreal ME when there was no difference in PF, they spend 2.3 - 5.6% more time feeding on the ground. Considering the significant interaction of PF * ME, for every unit increase in the difference of PF ratio, the slope of ME increases by 1.87. In other words, the positive relationship between ME and terrestrial feeding gets stronger the larger the difference between terrestrial and arboreal feeding. It is possible that PF ratio was not as important given the bamboo lemurs' seasonally large proportion of fruits in their diet, for which PF is not an accurate measure of dietary quality (Wallis et al., 2012).

The challenge of meeting mineral requirements is faced by many herbivores, e.g., elephants *Loxodonta africana* (Holdø et al. 2002), moose *Alces alces* (Belovsky 1981), and bison *Bison bison* (Delgiudice et al., 1994), and perhaps is even more difficult in the tropics as plants in warmer climates generally have lower nutrient values compared to temperate plants (Chiy and Phillips, 1995; McDowell, 1997). In general, sodium in plants is often associated with reduced concentrations of protein and other minerals (Masters et al., 2001), and so primates likely only consume the minimum amount necessary to meet their needs (Rode et al., 2003). The large proportion of time spent feeding on the ground by the *Hapalemur* in our study seems unlikely to be in response to reduced mineral concentrations, especially since the daily PF ratio and ME from terrestrial food items were of greater value compared to arboreal items. However, the location of our study is an intricate matrix of upland littoral forest and swamps (Eppley et al., in review), and since swamp plants are often sodium-rich (Oates, 1978; Belovsky, 1981), it is possible that terrestrial grazing in the swamp may satisfy these needs.

Bamboo lemurs maintain morphological adaptations, i.e., short arms and proportionally long legs (Jungers 1979), for vertical clinging and leaping, their primary mode of locomotion; however, congeners often move quadrupedally along branches while foraging (Mittermeier et al., 2010; Fleagle, 2013), allowing them to extend their niche to a terrestrial stratum. While Neotropical primates are well-known for their arboreality, many spend at least some time on the ground, e.g., *Alouatta* spp. (Bicca-Marques and Calegaro-Marques, 1995; Pozo-Montuy and Serio-Silva, 2007), *Ateles* spp. (Campbell et al., 2005), *Brachyteles* spp. (Dib et al., 1997; Tabacow et al., 2009; Mourthé et al., 2007), *Cebus capucinus* (Gilbert and Stouffer, 1995), and some pitheciin monkey genera (Barnett et al., 2012). These observations of terrestrial behaviour are often associated with disturbed habitats whereby animals traverse

open areas between forest fragments, exceptional exposure that may increase risk of predation (Takemoto, 2004). Unlike terrestrial feeding by the bamboo lemurs, spider monkeys appear very nervous when on the ground, continually scanning the area and taking long periods of time before fully descending (Campbell et al., 2005). Analyses of *Ateles* spp. communities across Central and South America found that sites with more intact predator communities (i.e., perceived or real high risk of predation), spider monkeys only descended to the ground in very limited conditions when nutritional returns were high. In contrast, spider monkeys descended to the ground more frequently at sites where predator populations are less intact, often for purposes beyond just nutritional gain, e.g., socializing and traversing gaps in forest cover (Campbell et al., 2005). Interestingly, *Eulemur collaris* in the nearby larger forest of Ste. Luce spend significantly less time on the ground compared to their conspecifics in Mandena (Donati, pers. observ.), perhaps lending additional evidence of relaxed predation risks in Mandena.

Similar to *Ateles* spp., snub-nosed monkeys (*Rhinopithecus* spp.) also show occasional terrestrial behavior possibly attributed to localized ecological factors, e.g., distribution and availability of food items, vegetation structure, and predation risk (Xiang et al., 2009). Interestingly, *R. bieti* have been observed to descend to the ground to feed on terrestrial grasses and bamboo shoots (Ding and Zhao, 2004; Xiang et al., 2007), possibly representing additional dietary quality during the nutritionally lean season (Grueter et al., 2009). Feeding on the ground for increased nutrition has also been suggested for the semi-terrestrial *Semnopithecus* sp. (Newton, 1992).

Ad libitum predation attempts

Our *ad libitum* records consist of instances when the individual and/or entire group of *Hapalemur* alarm called persistently, mobbed, and/or fled from the potential predator. Several instances of attempted predation occurred during focal follows, and it would appear that aerial raptors present possibly the greatest and/or most frequent risk (Karpanty, 2006; Karpanty and Wright, 2007). We observed one occasion of *Accipiter henstii* nearly capturing a juvenile bamboo lemur who was feeding on top of the canopy. Attempts by *Polyboroides radiatus* were more common, with six instances of the entire bamboo lemur group fleeing/descending from the canopy, sometimes involving dropping multiple meters to the ground. In fact, instances of aerial predation always occurred during arboreal feeding, with individuals descending from the canopy, increasing vigilance, and moving cautiously to a

new feeding location, but were never observed when the animals were feeding terrestrially. Lastly, *Buteo brachypterus* was also observed to attack (unsuccessfully) bamboo lemurs feeding both on top of the canopy (twice) and once under the canopy, a situation which led to the bamboo lemurs positioning themselves behind TME's body and moving at an angle away from the aerial predator. It is possible that our presence inhibited some predation attempts or decreased the perceived risk of predation (Isbell and Young, 1993), yet despite our presence bamboo lemurs chose to feed in significantly closer proximity to group members when on the ground.

Predation pressure on arboreal and terrestrial species likely occurs at a similar rate (Shattuck and Williams, 2010). It is apparent from our study that both feeding strata pose similar predation risks for the Mandena southern bamboo lemurs. This predation pressure, similar to predator avoidance and escape tactics, may play a significant selective role – both proximately and ultimately – in the habitat use and positional behavior of arboreal primates (Gebo et al., 1994; McGraw and Bshary, 2002). Given that *H. meridionalis* display a cathemeral activity rhythm (Eppley et al., 2015a), proximate fluctuations in predation risk may cause temporal niche shifts, such as changes in home range use and/or the vertical strata (Gautier-Hion, et al., 1983; McGraw and Bshary, 2002). Accessing the various upland and swamp habitats requires terrestrial travel to cross the open gaps (Eppley et al., in review), putting lemurs at risk from potentially both aerial and terrestrial predators. It should also be noted that while infrequently observed, crocodiles (*Crocodylus niloticus*) are present along the river where bamboo lemurs occasionally graze, which may represent an additional terrestrial predation risk.

Concerning potential carnivore viverrids, fossa (*Cryptoprocta ferox*) are only known to occur occasionally in Mandena (Donati et al., 2007). We recorded two instances of the entire bamboo lemur group repeatedly alarming and barking at a ring-tailed mongoose *Galidia elegans* that had terrestrially approached the group, which was foraging arboreally. A third observation was made in which *G. elegans* targeted a juvenile *Hapalemur*, trying to corner it in a tree. The mother bamboo lemur quickly positioned herself in between, alarmed, and then barked at the mongoose. The mongoose then lunged at both of the lemurs, to which they alarmed and fled the area, crossing an inundated swamp that would have been difficult for the mongoose to follow. From our observations, it would appear that *G. elegans* presents a potential arboreal and terrestrial risk to juvenile bamboo lemurs, and possibly adults too considering they have been observed to kill larger prey (Albignac, 1973). In addition, exotic

predators such as feral dogs (*Canis familiaris*) are also creating a hazardous environment to navigate and seen in and around the Mandena forest frequently. We recorded three occasions when these feral dogs chased the bamboo lemurs when they were feeding on the ground, to which they quickly ascended into the trees. These dogs were quickly deterred and fled upon noticing the human observer. Similar to our observations, it has been reported that feral dogs have harassed northern muriquis (*Brachyteles hypoxanthus*) (Melo et al., 2005). While more dire, both black-horned capuchins (*Cebus nigritus*) and brown howler monkeys (*Alouatta guariba*) have reported being killed by feral dogs (*C. familiaris*) while traversing forest gaps terrestrially (Galetti and Sazima, 2006). This appears to be common in Australia as well, with tree-kangaroos (*Dendrolagus* spp.) being vulnerable to predation by native dogs (*C. lupus dingo*) while on the ground (Newell, 1998, 1999).

In regards to large snakes, we twice observed *Sanzinia madagascariensis* resting in a tree in which the *Hapalemur* group was foraging, though no alarms were made despite hopping directly over the potential predator. Given the camouflage of the snake, it is possible that the lemurs did not see it. It was not uncommon for the lemurs to display group mobbing behavior towards a snake when one was present. This was most frequently observed in response to a foraging Madagascar hognose *Leioheterodon madagascariensis*. No reports exist of this large species preying on *Hapalemur* spp. or lemurs in general, though we did witness extensive alarm calls and barking at their presence on four occasions. It is quite possible that given their size, they may present a potential risk to juvenile and infant lemur. Additionally, we observed two instances of the lemurs alarming and barking at a large Dumeril's boa *Acrantophis dumerili*. On April 3rd, 2013 we tracked an adult female *H. meridionalis* (body mass: 1.15 kg) from group 1 to her radio-collar using telemetry, which inadvertently led us to a male Dumeril's boa (155 cm long, 2.95 kg). The large boa was located in a vast marsh/swamp area where the bamboo lemurs often feed terrestrially, thus it is likely that she was captured while on the ground. The data-logging capabilities of the collar tag indicate she became inactive at 09:45 on March 10th, 2013 and body temperature shifted to ambient temperature, thus we deduced it was around this time that the female bamboo lemur was eaten.

Additional constraints

The expansion to a terrestrial dietary niche likely imposes additional constraints on bamboo lemurs. The gastrointestinal tract of *Hapalemur* spp. certainly assists in their

elevated ability to digest fibre, allowing for leafy material to be fermented by symbiotic gut microbes (Campbell et al., 2000; Perrin, 2013). While this likely allows for digesting the large quantities of graminoids in their diet, feeding on grasses is often associated with the evolution of several dental modifications (Yamashita et al., 2009), mostly due the abrasive silicates, i.e., phytoliths, that are embedded in the epidermal layer of grass leaves (Judziewicz et al., 1999). These have the potential to increase the rate of wear on teeth through the mastication of this abrasive vegetation (Jablonski, 1994; Lucas and Teaford, 1995; Cuozzo and Yamashita, 2007; Yamashita et al., 2009), which may lead to a more rapid dental senescence.

It is also possible that increased terrestriality may increase exposure to unfamiliar pathogens (Anderson, 2000), thus increasing parasite loads compared to sympatric arboreal species (Loudon and Sauther, 2013). While we have hypothesized that this species' use of visually conspicuous latrines may act to limit the spread of feces throughout their territory, we have no true way of testing this (Eppley et al., in revision).

Conclusion

Our data present strong evidence for the ability of this species, and perhaps the entire *Hapalemur* clade, to subsist in anthropogenically disturbed environments, demonstrating that they may not be as ecologically sensitive as we once thought. In general, these lemurs are highly adaptable and do not have rigid dietary restrictions, rather they appear to cope well within a seasonal and ever-changing landscape. This observed flexibility and use of a terrestrial dietary niche is likely to be an adaptation to a habitat devoid of their preferred food resource, i.e., bamboo, which southern bamboo lemurs are often found near and feeding on at other sites, e.g., Andohahela NP (Feistner and Schmid, 1999) and Nahampoana Reserve in Tsitongambarika (TME, personal observation), the latter being an exotic botanical garden. In the absence of these foods, *H. meridionalis* have greatly expanded their dietary diversity while utilizing a terrestrial feeding niche daily, where food items represented a greater dietary quality. While there was no significant difference in predation risk from canopy exposure, bamboo lemurs displayed caution when grazing, maintaining a close proximity to conspecifics as compared to when they fed in the trees. Knowledge of their ecological flexibility can, we hope, assist in future management decisions on how to effectively implement conservation within large human-altered landscapes.

Acknowledgements

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CHAPTER 4

Latrine behaviour as a multimodal communicatory signal station in wild lemurs:
the case of *Hapalemur meridionalis*

With Jörg U. Ganzhorn and Giuseppe Donati

in review with *Animal Behaviour*

Abstract

Latrine behaviour is the non-random selection of sites for defecation/urination, and is common among most mammals, including carnivores, herbivores, marsupials, and rodents. While rare among primates, latrine use has been observed among some lemurs. Hypotheses proposed to explain their occurrence within group-living primates include maintenance of inter-group spacing (i.e., territorial defence) and female advertisement of sexual condition. To test these, we conducted focal follows of three neighbouring southern bamboo lemur (*Hapalemur meridionalis*) groups in Mandena littoral forest of southeast Madagascar. From January-December, 2013, we recorded all occurrences of latrine behaviour and characterised unique sites to determine what factors influenced returning to specific latrines. Additionally, we attempt to elucidate the functional role of scent-marking at latrines. We assessed the degree of home range overlap between neighbouring groups, and recorded inter-group aggression. Overall, latrines were almost exclusively visually conspicuous sites and located in the non-core areas of group home ranges. Best-fit models, however, indicated that multiply-visited latrines occurred more often in core areas, and are influenced by both sexes. Scent-marking at latrine sites appeared to be driven by males, which occurred more during the non-mating season. Males overmarked female scent-marks less often during mating season, and more often when younger males were likely to disperse into new groups. Thus, overmarking may potentially function as a mate-guarding strategy to deter new males. The energy frugality hypothesis proposes that lemur social systems, known for female social dominance and low rates of agonism, evolved as responses to the low productivity of Malagasy forests. Latrine use may support this paradigm, whereby the deposition of olfactory cues throughout a territory may convey information to neighbouring conspecifics, thus reducing the need for inter-group agonism. Our data appear to support the hypothesis that the

latrine behaviour of southern bamboo lemurs acts as a multimodal means of inter-group communication.

Key words: energy frugality hypothesis; *Hapalemur meridionalis*; latrines; mate defence; olfactory communication; primates; scent-marking; territorial defence

Highlights

- First systematic 12-month study of latrine behaviour in group-living primates.
- Conspicuous latrines provide a multimodal means of territorial defence.
- Male overmarking female scent-marks at latrines supports mate-guarding.
- Scent-marking at latrines does not support sexual advertisement hypothesis.
- Latrine sites convey vital information, potentially limiting inter-group agonism.

Introduction

Latrine behaviour is defined as the non-random selection of defecation/urination sites in such a way that faeces accumulate either along arboreal, terrestrial or subterranean substrates (Irwin et al., 2004). Utilisation of latrine sites is often understood as a means of olfactory communication (Kleiman, 1966, Brown & Macdonald, 1985, Gorman & Trowbridge, 1989), with recent evidence suggesting it as an ancestral communicatory strategy predating mammalian synapsids (Fiorelli et al., 2013). Today, many mammals retain this behaviour, including carnivores (Macdonald, 1980; Gorman & Mills, 1984; Gorman & Trowbridge, 1989; Roper et al., 1993; Ben-David et al., 1998; Nel & Bothma, 2002; Jordan et al., 2007; Darden et al., 2008; Kilshaw et al., 2009; Hulsman et al., 2010), herbivores (Laurie, 1982; Wronski & Plath, 2010), marsupials (Sprent et al., 2006; Ruibal et al., 2010), and

rodents (Chame, 2003), but it is rare among primates (Gilbert, 1997; Irwin et al., 2004; Gonzalez-Zamora et al., 2012; Dröscher & Kappeler, 2014).

Chemical communication (via olfaction) is the most commonly postulated function for latrine use: chemicals deposited via faeces/urine and/or scent-marking, are less temporally and/or spatially limited than other signals, e.g., vocalizations (Eisenberg & Kleiman, 1972; Dawkins & Krebs, 1978; Schilling, 1979; Dröscher & Kappeler, 2014). Adaptive reasons for latrine use include intra- and inter-specific communication (Gorman & Trowbridge, 1989; Jordan et al., 2007), improving reproductive success (Jordan, 2007; Ruibal et al., 2010), avoidance of endoparasite transmission / re-infestation (Gilbert, 1997), and avoidance of detection by predators (Boonstra et al., 1996; Jordan et al., 2007). Furthermore, latrines have been shown to play a key role in ecosystem dynamics, having a direct impact on plant populations (Dinerstein, 1991; Pigozzi, 1992; Clevenger, 1996; Ben-David et al., 1998; Quiroga-Castro & Roldan, 2001; Feeley, 2005; Neves et al., 2010; Pouvelle et al., 2009; Gonzalez-Zamora et al., 2012).

Although primates primarily rely on visual and auditory communication, olfaction also appears to be important for strepsirrhine primates, allowing individuals to receive chemical information from a conspecific signaller who may no longer be present in the immediate area (Epple, 1986; Alberts, 1992; Colquhoun, 2011). Similar to other mammals, strepsirrhine chemical signals are transmitted via secretions from scent-producing skin glands, saliva, and/or faeces/urine deposited on substrates, conspecifics, and/or self-anointed (Epple, 1986; Schilling, 1979, 1980; Nievergelt et al., 1998; Lewis, 2005; Colquhoun, 2011), and can occur in conjunction with latrine use (Irwin et al., 2004; Dröscher & Kappeler, 2014). Thus far, observations of latrine use have been recorded in four distinct strepsirrhine genera, i.e., *Cheirogaleus*, *Lepilemur*, *Hapalemur*, and *Lemur* (Charles-Dominique & Hladik, 1971; Irwin et al., 2004; Eppley & Donati, 2010; Dröscher & Kappeler, 2014).

Among the possible functions of latrine use by lemurs, four non-mutually exclusive hypotheses have been proposed (Irwin et al., 2004). The first is that they provide a system of territorial demarcation, whereby faecal/urine deposits are placed around home range boundaries to act as a delineation of the territory, i.e. inter-group spacing (Brashares & Arcese, 1999; Stewart et al., 2001), similar to scent-marking strategies observed in some lemur genera (Mertl-Millhollen, 1979, 2006). Although many mammalian species use latrines with the functional role of providing territorial defence, the deposition of glandular secretions in addition to faeces/urine can provide additional chemical information (MacDonald, 1980; Gosling, 1982; Brown & MacDonald, 1985; Gorman & Trowbridge, 1989; Gorman, 1990). As such, a second hypothesis is that latrines may strategically serve to advertise sexual condition via scent-marking (Gorman, 1990; Woodroffe et al., 1990; Asa, 2008). In fact, among meerkats (*Suricata suricatta*), evidence of male-biased scent-marking at latrines suggests that they serve a subsidiary role in mate-defence. Male meerkats not only scent-mark more than females but also preferentially overmark female scent marks (Jordan, 2007; Jordan et al., 2007). Similar behaviour has been observed in European badgers (*Meles meles*), showing distinct sex and seasonal differences (Kruuk, 1978; Roper et al., 1986, 1993; Begg et al., 2003). This 'overmark', i.e., a secondary scent marking, involves placing a scent mark directly on top of a previous mark potentially disguising the presence of females in the territory from bordering or dispersing males (Roper et al., 1986; Lewis, 2005). A third hypothesis states that advertising proximal resource use may assist intra-group spacing (Kruuk, 1992); however, this is unlikely within cohesive groups as there would be no need to signal resource use (Irwin et al., 2004). Lastly, a fourth hypothesis postulates that the repeated use of concealed defecation sites may act as an anti-predator strategy by impairing the ability of a potential predator to detect prey populations (Viitala et al., 1995; Boonstra et al., 1996). As previous reports of terrestrial latrine use among lemurs remain limited (Petter

& Peyrieras, 1970; Irwin et al., 2004; Eppley & Donati, 2010; Dröscher & Kappeler, 2014), there is little understanding of what functional role this behaviour may have for a highly cryptic group-living species, such as bamboo lemurs (*Hapalemur* spp.). As this genus displays a cathemeral activity rhythm (Eppley et al., 2015a), it makes for an excellent model with which to explore latrine behaviour. This ability to be active throughout the 24 hour cycle may potentially require them to utilise multimodal signals to maintain inter- and intra-group communication with conspecifics.

We aimed to test predictions for each of the hypotheses mentioned via the first systematic study of latrine behaviour by a group-living strepsirrhine, the southern bamboo lemur (*Hapalemur meridionalis*). Specifically, (a) if latrines and/or scent-marking are used for territorial defence, we would expect them to be located in larger proportions throughout the non-core areas rather than concentrated in the core areas of their home ranges. Conversely, it could be considered that latrine sites that do not occur in greater proportion in either the core or non-core areas of bamboo lemur home ranges may simply be a strategy by which a group increases the likelihood of neighbouring or intruding individuals locating a latrine (Gosling, 1981). As an auxiliary role of territorial defence, if the latrines are to maintain inter-group communication, we would expect that southern bamboo lemurs occasionally utilise latrines used by neighbouring conspecific groups, leading them to maintain marginal home range overlap and thus display minimal inter-group aggression. (b) If latrines and/or scent-marking are used to convey sexual advertising, we would predict an increase in these behaviours by females near or during the mating season (June-July) when southern bamboo lemur females become sexually receptive. Additionally, we would predict directional male-female overmarking to occur during the mating season so as to deter intruding males. Furthermore, Eppley & Donati (2010) previously noted *H. meridionalis* displaying a preference for utilising large stilt-rooted trees, specifically within the genus

Uapaca (Family Euphorbiaceae), as latrine sites. As such, (c) if latrine use is intended as an anti-predator strategy, we would predict a significant portion of defecations to occur under stilt-roots where waste accumulation can be obscured from the view of potential aerial predators.

Methods

Ethical Note

All data were collected in accordance with the ASAB/ABS Guidelines for Use of Animals in Research. This research was carried out under the Accord de Collaboration among the University of Antananarivo and the University of Hamburg. Research protocols were approved and permits authorized by Commission Tripartite of the Direction des Eaux et Forêts de Madagascar (Autorisation de recherché N° 240/12/MEF/SG/DGF/DCB.SAP/SCB du 17/09/2012), adhering to the legal requirements of Madagascar.

Study Site and Species

Our study was conducted in Mandena (24°95'S 46°99'E) in the extreme southeast of Madagascar (Fig. 1), approximately 10 km north of Fort-Dauphin (Tolagnaro). This protected area consists of 148 ha of fragmented and degraded littoral upland forest with approximately 82 ha of interspersed, seasonally-inundated swamp (Ganzhorn et al., 2007). Littoral forests occur within 3 km of the coast, characterised by a typically low canopy growing on sandy substrate (Dumetz, 1999).

Southern bamboo lemurs (*Hapalemur meridionalis*) are medium-sized (1.072 ± 0.107 kg) cathemeral lemurs characterised as folivores and by female dominance (Eppley et al., 2011, 2015a, 2015b, unpublished data). They maintain small social groups with one adult male and one to two breeding adult female(s) that are generally in constant daily contact with

one another. In Mandena, southern bamboo lemur groups average (±SD) 5.6 ± 1.5 individuals (*N* = 5). Most lemuriformes, including *Hapalemur* spp., exhibit seasonal reproduction which is typically entrained by photoperiod (Wright, 1999). It has been reported that close congeners, e.g., *H. griseus*, mate between June and July, experiencing a gestation length of approximately 130-140 days (Wright, 1990; Tan, 2006). Although we never observed copulation during the study period, infants in the three groups were first observed in mid-November, validating a similar gestation length. We therefore group June-July together as "mating season" as females would likely be sexually receptive at some point during this time, while all other months are allocated to "non-mating season".

Ten adult *H. meridionalis* (5 females, 5 males) across four neighbouring social groups were captured between October and December 2012 by an experienced Malagasy technician via Telinject® blow darts containing 4 mg/kg of either Ketamine® (ketamine hydrochloride) or Zoletil® (tiletamine and zolazepam), so that the animals neither suffered nor recalled the capturing process. Differences in anaesthesia sedatives used were due to the limited quantities available. Only adults without dependent infants were captured and all animals recovered from anaesthesia within 1.5 hours at the capture site and were followed until regaining full mobility, approximately one hour. There were no injuries as a consequence of the captures, nor did we observe any short-term or long-term effects as a result of these manipulations. As this species is highly cryptic, individuals were fitted with external radio-transmitters (ARC400, Advanced Telemetry Systems, Isanti, MN, USA) secured via a neoprene collar looped through pvc tubing and fastened with a small nut/bolt. The total weight per transmitter tag and collar attachments was 38g (ranging from 2.9 - 4.2% of total body mass for the heaviest and lightest individuals, respectively). These tags were slightly larger due to their data-logging abilities (see Eppley et al., 2015a), but allowed for expediting the habituation period via locating/following groups more easily (Juarez et al., 2011). In

addition, a colour-coded pendant was attached to assist in individual identification. We removed radio-collars at the end of the study in December 2013 following the same protocol.

Behavioural Data

From January to December 2013, we conducted full-day focal follows (from sunrise to sunset) for approximately five days/month for three of the social groups, i.e., specifically groups 1, 2, and 4 (Table 1). Home range data were collected via GIS coordinates recorded with a Garmin GPSMAP 62S unit every 15-mins throughout the focal follow. Conversely, group 3 was located bi-weekly for approximately two hours to exclusively collect home range data via the same waypoint sampling; however, behavioural focal sampling was not conducted on this group due to time constraints. All bamboo lemurs were categorized by age/sex class (Table 1) with all adult individuals in each group sampled at least once each month, collecting both instantaneous and continuous focal sampling data for concurrent studies (Altmann, 1974).

Table 1. Group composition of habituated *H. meridionalis* in Mandena.

Group	Total	Adult ♀	Adult ♂	Juvenile ♀	Juvenile ♂	Infant*
1	3-5	3	1	1		2
2	3-4	1	1		1	1
3	4-5		3	2		
4	8-9	2	2	1	2	2

Total column represents the number of animals within the social group observed each month from January – December 2013.
*Infant refers to dependent offspring.

During daily follows of a focal subject, all latrines sites visited (i.e., specific locations involving defecation/urination) were flagged and given a unique code in addition to recording its GIS coordinates. As bamboo lemurs travel as a cohesive group, they often arrived and departed from latrine sites at approximately the same time (+/- 15seconds). Thus, we were able to directly observe and to collect the relevant behavioural data on all individuals within

the group visiting the latrine site. We also noted whether previous faeces had accumulated here, which could range from two to greater than 50 faeces. These were easily identifiable as *Hapalemur* faeces due to their dietary reliance on grasses and lianas (Eppley et al., 2011, unpublished data); the only similarly-sized lemur in this forest (*Eulemur collaris*) do not use latrines (Donati, pers. observ.) while carnivores of similar size are also very rare in this fragmented area. It is possible that the remaining defecation/urination sites were visited less frequently and thus any accumulated faecal material may have been subject to faster degradation and decomposition, an issue that also may be due to habitat differences (i.e., swamp vs upland forest) within Mandena. Regardless, sites that had no accumulation of faeces yet that were collectively defecated/urinated at by the entire group were included in our analyses. Micro-habitat data for each of these sites was recorded by TME, specifically the dimensions of the tree from which the latrine was accessed, e.g., tree family, genus, and species, diameter at breast height (DBH), height (m), and crown volume (m^3). Crown volume was estimated as an ellipsoid via the crown height and two crown diameters, i.e., maximum and perpendicular widths. As *Uapaca* trees constitute the majority of the latrine sites across all three groups, we sought to determine whether these were characteristically different from individuals of the same species sampled in our botanical plots. As part of a larger ecology research project, we conducted $100m^2$ (20 x 50m) botanical plots ($N = 20$), using the same metrics described above so as to characterise the Mandena habitats (Henderson, 1999). Plots were then used for comparison with the latrine sites to gain an understanding of site selection preferences by the bamboo lemurs.

Though lemurs are macrosmatic (Scordato & Drea, 2007; Sacha et al., 2012), *Hapalemur* maintain a *fovea*, i.e., a retinal structure that improves visual acuity (Pariente, 1979; Kirk, 2006). Because bamboo lemurs do not rely solely on olfactory communication, they often selected visually conspicuous locations to function as their latrine sites,

specifically, stilt-rooted *Uapaca* spp. trees, large terrestrial liana tangles, and fallen/horizontal trees from which they defecated/urinated. These latrine sites maintain a distinguishable structure characterised by horizontal and/or oblique substrates along or just above the ground, and would all be readily noticed from a distance by visually-oriented mammals when traversing through the forest, and possibly enhance their detection by conspecifics (Barja & List, 2006). This is in contrast to non-descript latrine sites, which would be indistinguishable from other low branches within the forest. We thus classified latrines into these two categories: non-descript and visually conspicuous.

Furthermore, we recorded all instances of inter-group agonism, specifically noting when groups defended their home range by vocalizing, chasing, and occasionally biting intruding and/or neighbouring groups. These occurrences were analysed monthly so as to gain a greater understanding of inter-group agonism and how this may influence territorial defence.

From June 2013 – Dec 2013, we recorded two additional behaviours including the act of, and sequential order of individuals, scent-marking at latrine sites. Specifically, we recorded instances of scent-marking immediately before and/or after defecation/urination at a latrine site, i.e., on the woody substrate directly above or immediately adjacent to the latrine ($\leq$ 2m). For example, scent-marking was often observed to be deposited along the stilt-root of an *Uapaca* tree or a portion of liana within a large terrestrial liana tangle that was located directly over the accumulated faeces. Scent-marking behaviour in *H. meridionalis* is similar to what has been described for *H. alaotrensis* (Nievergelt et al., 1998), and so we employ the same definition. Bamboo lemurs damage a substrate (e.g., the bark of a stilt-root from an *Uapaca* tree) by scratching it with their lower front dentition. In the case of male individuals, they then rub their antebrachial glands against their brachial glands, followed by smearing their antebrachial glands across the damaged spot (e.g., the scrape or notch) that exists on the

woody substrate. Females have less pronounced antebrachial and brachial glands, and instead

mark the substrate with their anogenital region by sit-rubbing several times along the

substrate, while on a rare occasion depositing urine. Additionally, bamboo lemurs were

observed to overmark, occasionally referred to as counter-marking, whereby an individual

scent-marks directly on top of a previously deposited scent-mark. Although scent-marking

does occur at non-latrine sites, we did not record these and are thus unable to include them in

our analyses.

Data Analyses

All ranging and latrine data were entered into ArcGIS 10.2 (ESRI) using the

Geospatial Modelling Environment (GME) spatial ecology interface (Beyer, 2012) with R

statistical software version 3.1.2 (R Development Core Team, 2014). We determined each

group home range with a 95% kernel density estimate while prescribing a core area as having

a 50% kernel density estimate (Worton, 1989). We then assigned unique latrine sites as

within or outside of the core area of each group home range, performing a non-parametric

chi-square to test for possible asymmetry in latrine distribution, i.e., whether the frequency of

latrines in the core area (comprising 50% of the home range) and the non-core area differed

from a uniform distribution. Additionally, using the 95% kernel density estimate we

calculated the amount of home range that overlaps between all groups to understand the

degree of territoriality this species exhibits. Furthermore, to examine selection preferences for

latrine sites, we used a *t*-test to determine whether specific tree metrics differed significantly

from those obtained from botanical plots. We then used a non-parametric chi-square to test

whether the frequency of use of non-descript and visually conspicuous latrine sites differed

from a uniform distribution.

To determine which factors influenced the repeated use of latrine sites, we fitted

generalized linear mixed-effects models (GLMM) in R statistical software (R Development

Core Team, 2014) using the glmer function of the lme4 package (Bates et al., 2012), with

preferred latrines as a binomial dependent variable. We define preference latrines as those

sites that are visited multiple times (i.e., more than once) by a focal group. By creating this

dichotomy, we were able to investigate specifically what influenced bamboo lemurs to return

to latrine sites. As groups are cohesive units, both males and females often visit latrines

together, although they do not always display latrine behaviours at each site. Due to this, we

tested each sex separately. Male latrine behaviour was perfectly collinear with preference

sites as males defecated/urinated on each occasion of visiting a preference latrine. As a result,

models to explain variation in preferred latrines were unable to obtain reliable estimates of

the conditional standard error (Hauck & Donner, 1977). To circumvent this issue, we ran two

separate GLMMs, the first with a dataset limited to male-used latrines and the second with

the full dataset where 'males' was not included as a fixed effect. Fixed effects that were

included in various combinations and interactions were location (i.e., non-core area or core

area), season (i.e., non-mating or mating season), type (i.e., non-descript or visually

conspicuous), males (0/1) and females (0/1) that utilised the visited latrine site. Groups were

included as random effect. We then used the anova function to calculate likelihood ratio tests

for model comparison and determined which model had the most explanatory power by

comparing the Akaike's Information Criterion (AIC) for all of the possible models.

While latrine behaviour alone may provide chemical communication between

individuals and/or groups, we wanted to consider the role of scent-marking at latrine sites

separately. To do this, we examined which factors influence the use of scent-marking by

bamboo lemurs during each latrine occurrence. We used the proportion of individuals in a

group (limited to adult individuals) that scent-marked at a latrine as a continuous response in

linear mixed models (LMMs). Similar to the previously described GLMM, we included

location, season, type, male, female, and preference site as fixed effects in various

combinations and biologically relevant interactions. To determine whether scent-marking was

largely driven by males or females, both factors were included separately as fixed effects but

never together in the same model. We also included a full model which contained all of the

fixed effects and a null model that contained only the random effect, which in this case was

the social groups ($N = 3$). The anova function was again used to calculate likelihood ratio

tests and determine which model best fit the data by comparing Akaike's Information

Criterion (AIC) for all possible models. All models were fit using the lmer function of the

lme4 package (Bates et al., 2012) and *P*-values were obtained with a likelihood ratio test

using the afex package (Singmann, 2014), both developed for R statistical software (R

Development Core Team, 2014).

Lastly, we examined the potential factors that may influence an individual to

overmark the scent-mark of a conspecific from their group. All of our observations were

limited to males overmarking female scent-marks, although it is possible that this is not the

rule. Using each latrine occurrence as our unit of analysis, we ran a GLMM to determine

which factors best predicted whether overmarking a conspecific scent-mark (deposited during

the same visit) would occur during a latrine site visit. Our fixed effects included location,

season, preference site, and latrine type. Once again, group was controlled for as a random

effect and we followed the same procedure previously described.

All other statistical analyses were performed using PASW 21.0 (IBM, Inc.) with

significance considered at $P < 0.05$. Data for the *t*-tests were first tested for normality using

the Kolmogorov-Smirnov test and entered the parametric analyses after log transformation as

they were not all normally distributed.

Results

General Latrine Behaviour

Focal observations of *H. meridionalis* totalled 1,762 hours across the three groups, during which time we recorded latrine behavior 429 times across 282 unique latrine sites. Of these, 92.55% were observed to have previous faeces, e.g., piled, hardened, and/or decomposing fibrous material. Females initiated latrine use on 52.45% of occasions, males initiated use on 25.87%, and juvenile individuals initiated use on 21.68% of all occurrences. Bamboo lemurs frequently visited latrine sites as a cohesive group; however, we only included those individuals that defecated/urinated at a specific site as having displayed latrine behaviour. Considering this, 73.43% of all latrine site observations included more than one individual, while 36.36% included greater than or equal to half of group individuals. Furthermore, 29.79% of unique sites were visited more than once, constituting 53.85% of observed defecations during the study. The mean (± SE) height of *H. meridionalis* defecation was 0.41 ± 0.02 m ($N = 429$), with 95.57% of observations occurring between 0 to ≤1 m from the ground. It is interesting to note that 6.10% of the total latrine occurrences involved the lemurs descending directly onto the ground.

Southern bamboo lemurs were highly selective when choosing latrine sites, with both *Uapaca* spp. trees and large terrestrial liana tangles constituting 73.85% of all sites. In a similar manner, dead/fallen trees represent 13.03% of all latrines while the remaining 13.38% constitute twelve various tree species. The lemurs appeared to favour visually conspicuous latrine sites compared to non-descript latrine sites ($\chi^2 = 150.48$, $df = 1$, $P < 0.001$). Furthermore, *Uapaca* tree latrine sites were found to have a significantly larger DBH ($t = 3.783$, $df = 134$, $P < 0.001$), height ($t = 2.241$, $df = 134$, $P = 0.027$), and crown volume ($t = 2.135$, $df = 134$, $P = 0.035$) compared to the *Uapaca* spp. metrics obtained from our botanical

plots. In fact, *Uapaca* spp. presence within the Mandena littoral forest constituted only 1.51% ($N = 22$) of trees in our botanical plots.

Home Range Analyses

As determined by 95% kernel analysis, home range sizes varied: Group 1: 18.39 ha; Group 2: 17.66 ha; Group 3: 6.60 ha; Group 4: 10.43 ha. Of these, there was relatively minimal range overlap, yet all of these overlapping areas did contain latrines, some of which were mutually utilised by groups (Table 2). It is plausible that group 4 shared a few latrines with group 3; however, since we did not conduct true focal follows on group 3 we cannot be certain that they visited these latrine sites that fell within their buffer zone.

Table 2. Percent of territorial overlap between groups, unique latrine sites within, and shared latrine sites utilised by both groups.

Groups	Overlap Area 95% kernel (ha)	Unique latrines Group 1	Group 2	Group 4	Shared latrines N	Times used
1 & 2	0.42	2	2	-	3	12
1 & 4	1.40	14	-	11	5	18
3 & 4	0.30	-	-	4	-	-

Note: There was no area of overlap between groups 1 & 3 and 2 & 4.

Core areas (50% kernel estimate) were analysed for group 1 (7.76 ha), group 2 (3.74 ha), and group 4 (2.09 ha). For each of these areas, multiple latrines were found within the core areas of each group, constituting 29.9% of all latrines in group 1, 35.1% of latrines in group 2, and 36.1% of latrines in group 4. Significantly more unique latrine sites were located in the non-core areas of the lemurs' home ranges as compared to the core areas ($\chi^2 = 30.01$, $df = 1$, $P < 0.001$).

Inter-group Agonism

From January-December 2013, only 13 inter-group agonistic conflicts were recorded, resulting in an overall monthly average (± SE) of 0.008 ± 0.002 inter-group agonistic events/hr. Monthly averages (± SE) of inter-group agonism were very low across all three groups (Group 1: 0.01 ± 0.004/hr; Group 2: 0.007 ± 0.003/hr; Group 4: 0.007 ± 0.004/hr).

Preference Site

The best-fit model to explain the repeated use of a latrine site was the full model (AIC = 509.65, χ^2 = 12.05, df = 1, $P < 0.001$). The male-visited preference sites were significantly more likely to occur in the core area of the group home range, while males also appeared to select more often for the non-descript latrine type (Table 3).

Table 3. Generalized linear mixed model with the best explanatory predictors for returning to a latrine site multiple times relative to males.

Variable	β	SE	Z	P
Fixed effects*				
Intercept	0.6336	0.3758	1.686	0.0918
Location	**0.7763**	**0.2268**	**3.424**	**0.0006**
Season	0.3342	0.2545	1.313	0.1891
Type	**-0.7162**	**0.3499**	**-2.047**	**0.0407**
Random effects				
Group	Variance	0.3496		

*Data set limited to male-visited latrine sites as the fixed effect 'Male' was perfectly collinear with preference site latrines.
Bold indicates factors significant at $P < 0.05$
SE standard error

Considering the entire dataset for preference latrine sites and using the same fixed effects (now including females but removing males), the full model was again the best fit (AIC = 544.97, χ^2 = 10.14, df = 1, $P = 0.001$). Similar to males and thus not driven by one sex, females were shown to significantly return to preference latrine sites, and overall these sites were characterised by occurring within the core areas of group territories (Figure 1).

Unlike the male-used latrines, the latrine type had no significant influence on whether a site

would be more likely to be used multiple times (Table 4). Season had no effect on whether

lemurs would utilise a preference site.

Table 4. Generalized linear mixed model for latrine preference sites.

Variable	β	SE	Z	P
Fixed effects				
Intercept	-1.0902	0.4892	-2.229	0.026
Location	**0.6947**	**0.2200**	**3.158**	**0.002**
Season	0.1715	0.2402	0.714	0.475
Type	-0.5610	0.3322	-1.689	0.091
Female	**1.6710**	**0.3549**	**4.708**	**<0.001**
Random effects				
Group	Variance	0.3895		

Bold indicates factors significant at $P < 0.05$

SE standard error
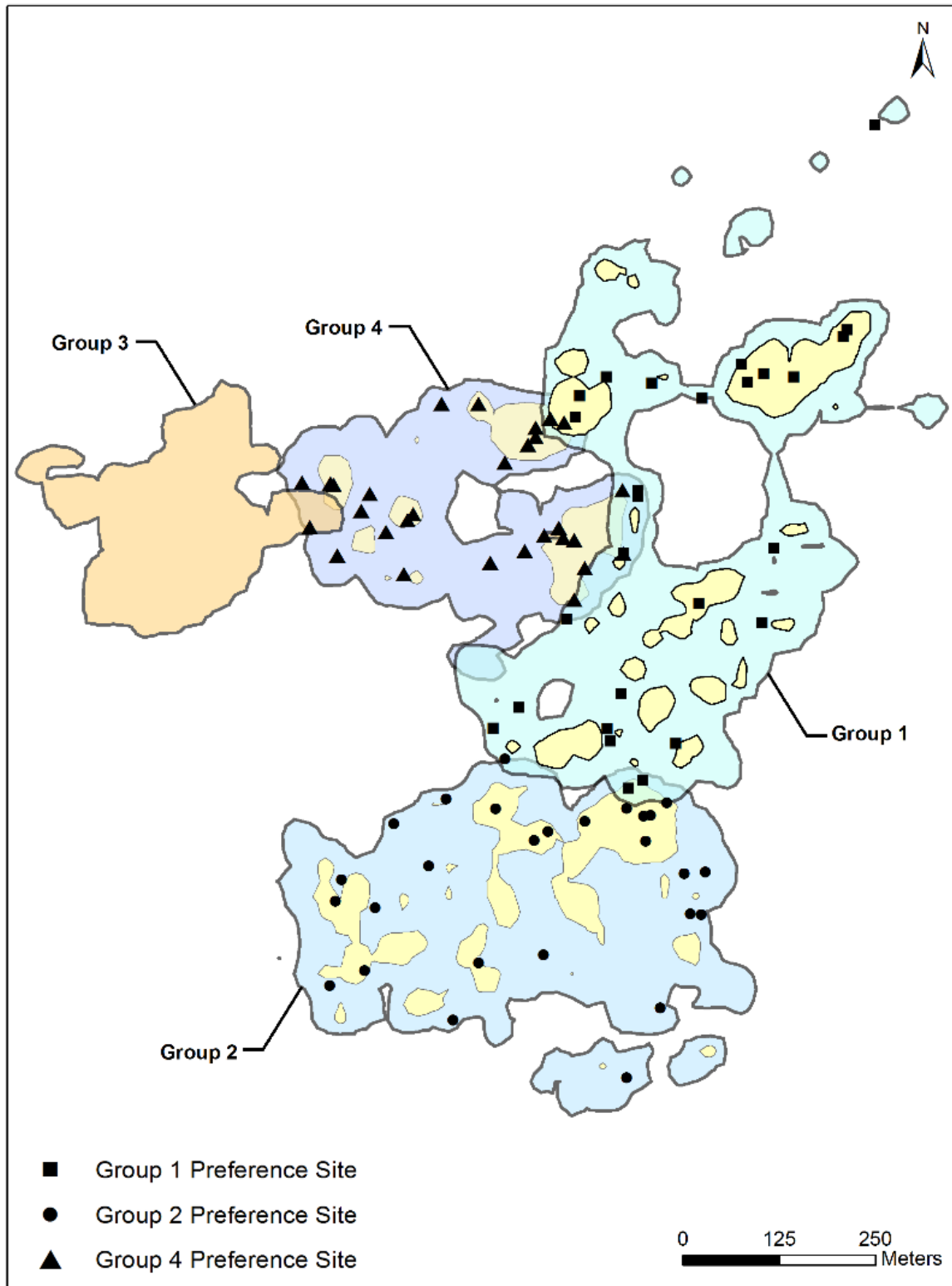
Figure 1. Home ranges (95% kernel) and core areas (50% kernel) of *Hapalemur meridionalis* focal groups at Mandena between January and December 2013. Various points indicate latrine preference sites for each group. Group 3 is included here to display the degree of home range overlap.

Latrine Scent-marking

Scent-marking was observed during 71.53% of the 281 latrine behaviour occurrences between June and December 2013. We used a linear mixed model (LMM) to determine which factors best predicted a greater proportion of group individuals to scent-mark at a latrine site. The full model was the best fit (AIC = -66.222, χ^2 = 181.75, df = 1, $P < 0.001$), with a greater proportion of scent-marking occurring in the non-mating season while scent-marking in general was largely driven by males (Table 5).

Table 5. Linear mixed model predicting scent-marking at latrine sites.

Variable	β	SE	95% CI	t	P
Fixed effects					
Intercept	0.076	0.115	-0.16 – 0.31	0.659	0.54
Preference site	0.084	0.069	-0.05 – 0.22	1.218	0.65
Type	0.043	0.066	-0.08 – 0.17	0.659	0.45
Season	**-0.029**	**0.041**	**-0.11 – 0.05**	**-0.699**	**0.003**
Male	**0.507**	**0.037**	**0.44 – 0.58**	**13.75**	**<0.001**
Preference site * type	-0.079	0.074	-0.22 – 0.06	-1.072	0.33
Season * male	-0.158	0.054	-0.26 – -0.05	-2.918	0.70
Random effects					
Group	Variance	0.158			
Residual	Variance	0.206			

Fixed effects that were not part of the best-fit model (location, female) are not included in this table
P-values (significant at $P < 0.05$, indicated in bold) were obtained using likelihood-ratio test
SE standard error, *CI* confidence interval

Overmarking Latrine Scent-marks

Of the observed latrine occurrences between June and December 2013, males overmarked 40.79% of the sites previously scent-marked by females. This involved one or more males immediately counter-marking directly on top of a female scent-mark, whereas we never observed the reciprocal direction. To determine which factor or combination of factors and interactions best predicted this behaviour, we performed a GLMM. The model with the best predictive value (AIC = 311.15, χ^2 = 22.63, df = 1, $P < 0.001$) shows that overmarking is

best fit by non-mating season (Table 6) while the other fixed effects and/or interactions played little to no role.

Table 6. GLMM best fit model for occurrence of male overmarking female scent-marks at latrine sites.

Variable	β	SE	Z	P
Fixed effects				
Intercept	-0.3070	0.4058	-0.757	0.449
Location	-0.4257	0.2953	-1.442	0.149
Season	**-1.3575**	**0.3184**	**-4.263**	**<0.001**
Random effects				
Group	Variance	0.6106		

Fixed effects that were not part of the best-fit model (preference site, type) are not included in this table
Bold indicates factors significant at *P* < 0.05
SE standard error

Discussion

Territorial Defence

Our findings support latrine behaviour among *H. meridionalis* as a means for territorial defence by having latrine sites disproportionately concentrated in the non-core areas of group home ranges. However, our best-fit models support the notion that latrines within the core area of a group home range are more likely to be visited multiple times, i.e., preference sites. This was not influenced by one sex; rather both males and females visited these sites significantly more often. While these data support previous assertions that latrines would be placed in the non-core areas so as to demarcate mammalian territories, their utilisation within both areas of the home range may be better understood when considering other factors, specifically the latrine type.

The vast majority of unique latrine sites were visually conspicuous, and their greater presence throughout the non-core area of each groups' home range may be viewed as a strategy by which they increased the probability of conspecifics locating them (Gosling, 1981). Thus, coupled with minimal home range overlap, their functional role as territorial

defence is wholly justifiable. Interestingly, the data subset of male-used latrines supported non-descript sites as being a better predictor for bamboo lemurs to return to a latrine site in core-areas. It may be speculated that due to the low density rate of *Uapaca* trees, males preferentially returned to non-descript sites so as to increase the deposited faecal matter making the latrine site potentially more conspicuous to non-group conspecifics.

Sexual Advertisement

Although latrine use showed no difference between the mating and non-mating seasons for neither males nor females, scent-marking was shown to increase significantly in the non-mating season. We found no support for the sexual advertising hypothesis as females were found to scent-mark at consistent rates from June – December 2013, a result similar to what has been described in *L. leucopus* (Dröscher & Kappeler, 2014). This is also similar to observations of scent-marking by *Propithecus verreauxi* (Lewis, 2005), *Eulemur fulvus*, *E. macaco* (Fornasieri & Roeder, 1992), *E. rufifrons* (Gould & Overdorff, 2002), and *L. catta* (Mertl-Millhollen, 2006), but in contrast to *L. catta* (Kappeler, 1998; Gould & Overdorff, 2002) and *P. diadema* (Powzyk, 1997) who show an increase in scent-marking during their reproductive season. This also occurs in platyrrhine primates, e.g., *Cebuella pygmaea* (Converse et al., 1995) and *Saguinus mystax* (Heymann, 1998), as well as other mammals, e.g., bushbuck *Tragelaphus scriptus (*Wronski et al., 2006), and meerkat *Suricata suricatta* (Jordan, 2007). It has been well-established in mammals that scent-marking regulates territorial spacing by increasing chances of intercepting conspecific intruders (Gosling, 1981; Barja, 2009), for example, along territorial borders (Kruuk, 1978; Rosell et al., 1998; Brashares & Arcese, 1999), at trail junctions (Barja et al., 2004) or concentrated around key resources (Gorman & Mills, 1984; Mills & Gorman, 1987). While bamboo lemur latrines were significantly concentrated in the non-core areas of each home range, it is equally

intriguing that the majority of these are located at visually conspicuous sites, thus appearing to provide a distinguishable visual signal similar to the latrine site selection of other mammals demarcating their territories.

Mate-guarding

Overmarking occurs when one individual places its scent mark directly on top of the scent mark of another individual (Johnston et al., 1994), and observations suggest that it is widespread among mammals (Ferkin & Pierce, 2007). Overmarking occurs within breeding pairs and appears to be associated with the acquisition and defence of mates and mating opportunities (Johnston et al., 1997a), with males typically scent-marking on top of the scent-marks of their mates (Jordan, 2007). In contrast, overmarking by females is relatively rare (but see Hurst, 1990; Wolff et al., 2002; Jordan et al., 2011). Among lemurs, males of *P. verreauxi* overmark female scent-marks (Lewis, 2005), a finding similar to ours. One explanation may be that this is an olfactory form of mate-guarding whereby the overmark masks, i.e., reduces the effectiveness of, the original scent (Johnston et al., 1994, 1995; Ferkin, 1999a, b), which may allow the male to disguise the presence of the female (Roper et al., 1986; Jordan, 2007; Wronski et al., 2013). However, it could be argued that the male is simply signalling his presence in addition to the scent-mark of the female, as female pygmy lorises *Nycticebus pygmaeus*, meadow voles *Microtus pennsylvanicus*, and golden hamsters *Mesocricetus auratus* have all been shown to preferentially associate with the male whose scent is directly on top of their scent-mark (Johnston et al., 1997a, b; Fisher et al. 2003; Ferkin et al., 2005). In contrast, female *Eulemur rubriventer* overmark male anogenital scent-marking (Overdorff & Tecot, 2006). Though bamboo lemur overmarking in Mandena occurs mainly during the non-mating season, our mate-guarding hypothesis appears to be supported

as individual dispersal (emigration/immigration) was also found to occur often during this time (TME, pers. observ.).

Latrine observations of the congener *H. griseus* from Analamazaotra Special Reserve described a sequential order of defecation, with adults preceding juvenile individuals (Irwin et al., 2004), and Eppley & Donati (2010) made a similar observation with *H. meridionalis* in Mandena. While females did initiate more than half of latrine utilisations, a behavioural characteristic that was presumed due to females often initiating travel in female-dominated congeners (Waeber & Hemelrijk, 2003; Tan, 2006), our dataset suggests, however, that this is not the rule as juvenile individuals were observed to initiate just slightly less often than males. This shows that these sites are not solely the result of female preference, but rather that latrine sites are easily recognized (either via olfaction or vision) by all age/sex classes.

Thus, the use of certain latrines by more than one group (i.e., the eight latrines within overlapping territorial zones) shows that these may not be solely for territorial demarcation, but also for conveying chemical information to neighbouring groups about female presence and/or male presence/vitality. This latter strategy is based on the observation of both males and females dispersing from their natal group (Eppley, unpublished data). In early November 2012, the only two adult males from group 1 dispersed, leaving only females within the group. By December, a new male was present in the group. It seems likely that the role of a male covering the females' scent-markings at each latrine site may act as a mate-guarding strategy whereby the male's scent will mask the presence of the female (Roper et al., 1986; Jordan, 2007; Wronski et al., 2013).

Anti-predator

Bamboo lemurs are the target of many potential predators, including fossa *Cryptoprocta ferox* (Goodman & Pidgeon, 1999; Sterling & McFadden, 2000), Madagascar

tree boa *Sanzinia madagascariensis* (Goodman et al., 1993; Rakotondravony et al., 1998), Dumeril's boa *Acrantophis dumerili* (Eppley, unpublished data), and several aerial predators, e.g., *Polyboroides radiatus*, *Accipiter francesii*, and *A. henstii* (Goodman et al., 1993; Wright, 1997; Karpanty & Goodman, 1999). While their cryptic nature (Tan, 2006) and cathemeral activity pattern (Mutschler, 1999; Eppley et al., 2015a) may result in an effective anti-predator strategy, latrines also may be hypothesized to have an anti-predator strategy. In particular, it is possible that the concealment of their faeces under stilt-rooted trees, large liana tangles, and fallen dead trees (i.e., horizontal substrate) may theoretically act as a safeguard against predation by impairing the ability of aerial predators to detect the prey population (Viitala et al., 1995; Boonstra et al., 1996).

Potential Ecological Consequences of Latrine Use

Various mammalian latrines appear to be important for soil fertility and seed dispersal (Clevenger, 1996; Dinerstein, 1991; Pigozzi, 1992; Ben-David et al., 1998; Quiroga-Castro & Roldán, 2001), a finding that has been similarly observed in some New World primate species (Feeley, 2005; Pouvelle et al., 2009; González-Zamora et al., 2012) and potentially among lemurs (Wright & Martin, 1995; Ganzhorn & Kappeler, 1996). It has been shown that red howler monkey (*Alouatta seniculus*) latrines not only increase the surrounding soil fertility (Feeley, 2005; Neves et al., 2010), but also increase the viability of defecated seeds (Pouvelle et al., 2009). These examples however include the selection of various fruit species, whereas *H. meridionalis* selected significantly for the stilt-rooted *Uapaca* spp. as latrine sites, potentially suggesting a mutual relationship. While the low density of *Uapaca* trees in the forest and their large stilt-roots make them visibly conspicuous latrine sites, the lemur faeces likely provide fertilizer for the tree, thereby increasing canopy volume and potentially increased fruit production. In turn, *H. meridionalis* select heavily for these fruits during the

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two yearly fruiting periods (July-August and December), ingesting the seeds whole in addition to the pulp (Eppley, unpublished data). Whether *H. meridionalis* swallowing these seeds is an effective method of germination or increasing viability remains unknown; still its occurrence in a folivore is intriguing.

As a large portion of the bamboo lemur annual diet in Mandena is spent grazing on terrestrial graminoids (Eppley et al., 2011; Eppley, unpublished data), it is interesting to discuss the potential benefit of their latrine behaviour. In fact, the utilisation of specified latrines, especially a majority of which confine the faecal matter in a tangled web of stilt-roots and lianas, may assist in avoiding potential contact (Gilbert, 1997). Conversely, defecation in non-specific locations may lead to occasional contact with old feces for (semi-) terrestrial species, potentially influencing parasite transmission/infection (Loudon & Sauther, 2013). Bamboo lemurs were never observed to graze immediately adjacent to latrine sites, thus the chances of ingesting faecal matter, and/or parasitic larvae derived from faeces, would be minimized. Although this may be a secondary benefit of these latrine locations, previous studies have found no support for this hypothesis among non-primate mammals (Page et al., 1999; Logiudice, 2003; Lamoot et al., 2004; Apio et al., 2006).

Interestingly, we made additional observations of *H. meridionalis* using visually conspicuous *Uapaca* spp. trees as latrine sites at the lowland rainforest site of Ampasy (24º34'S, 47º09'E, Tsitongambarika) approximately 50 km north of Mandena. This suggests that their selection of conspicuous latrine sites is not limited to Mandena, but may be more widespread throughout the species range. Also, considering the cryptic nature of *Hapalemur* spp., searching these conspicuous sites for latrines (i.e., accumulated faeces) may provide conservationists with a non-traditional sampling method with which to indicate species presence.

Energy Frugality Hypothesis

Drawing from the energy conservation hypothesis (Jolly, 1966, 1984; Richard, 1987, Pereira et al., 1999), the energy frugality hypothesis postulates that the relatively low productivity and resource quality of forests in Madagascar may act as causal factors influencing the evolution of lemur social systems and behavioural adaptations, e.g., female dominance and low rates of agonism (Wright, 1999; but see Curtis, 2004). Irwin and colleagues (2004) later suggested that latrine behaviour (including scent-marking) appear to fit this paradigm whereby they act as a low-energy behavioural response to the ecological challenge of defending resources without increasing agonism and/or vigilance (Mertl, 1975, 1977; Mertl-Millhollen, 1979; Kappeler, 1990). In fact, the significantly larger proportion of latrine sites located in non-core areas support their role as potentially demarcating the territories of bamboo lemur groups. Similar to the large terrestrial liana tangles and dead/fallen trees, *Uapaca* trees are exceptionally conspicuous as they are the only stilt-rooted tree within the Mandena upland littoral forest, with these site types favoured as they provide low horizontal and/or oblique perches from which lemurs can defecate/urinate. In fact, defecating and scent marking at visually conspicuous sites at heights of less than one meter may function to supplement the olfactory signal by creating a visual landmark (Gorman & Mills, 1984; Bowyer et al., 1994; Barja et al., 2004, 2005; Barja, 2009; Nie et al., 2012; Piñeiro & Barja, 2012; Clapham et al., 2013). This strategy stands to increase the likelihood of detection while reducing the potential fitness cost to the signalling group by minimizing both time and energy investment (Gosling, 1981; Gosling & Roberts, 2001; Barja, 2009).

The latrine behaviour of *H. meridionalis* includes composite signals whereby the faeces and scent-marking provide chemical information via olfaction; visual cues are provided via the unique structure of the specified latrine, the scrapes/notches in the substrates where scent-marking occurs, as well as the physical accumulation of faeces. Unlike the

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recently described *Lepilemur leucopus* latrines (Dröscher & Kappeler, 2014), we only observed urine being deposited a few times by a female in conjunction with anogenital scent-marking. While chemical signals are important to both diurnal and nocturnal primates, visual signals would be most beneficial to diurnal species. The southern bamboo lemurs exhibit a cathemeral activity pattern, that is, they can be active during both the light and dark phases of the diel period (Eppley et al., 2015a), and thus the utilisation of multi-sensorial cues would be highly efficient in signalling conspecifics.

In conclusion, our data appear to support the use of latrines and subsequent scent-marking at these sites by *H. meridionalis* for territorial defence, while directional male overmarking of female scent-marks provides plausible support for mate-guarding. The advertisement of sexual cycling at latrine sites by females is not supported by our data. Coupled with the low rates of inter-group agonism and selection of visually conspicuous latrine sites, it appears that bamboo lemur latrine behaviour is in line with the predictions of the energy frugality hypothesis.

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General Discussion

The aim of this concluding chapter is to provide a synopsis of the key findings from the earlier chapters and to discuss them in a broader perspective. I will also discuss some approaches for future studies that may further elucidate the flexible behavioral ecology of these small-bodied primates and how their genus copes within an ever-changing anthropogenic landscape throughout Madagascar.

Through this study I have expounded many of the underlying mechanisms by which the southern bamboo lemurs persist in a habitat devoid of their "preferred" resource. In general, the southern bamboo lemurs of the Mandena littoral forest/swamp matrix fragments exhibited a cathemeral activity pattern, largely influenced by lunar luminance. While these data are the only systematic evidence of cathemerality among *Hapalemur*, anecdotal observations also suggest this (Mutschler, 1999). This is in contrast to what other studies have concluded: that *Hapalemur* do not exhibit any nocturnal activity, such as in the humid forests of Ranomafana National Park (Tan, 1999; Grassi, 2001). Considering the retinal morphology of *Hapalemur*, however, it is likely that all bamboo lemurs are well-equipped for nocturnal activity and possibly exhibit cathemerality, an activity pattern that likely predated the Lemuridae radiation (Donati et al., 2013). It can be argued that the flexibility of a 24-h activity pattern allows the Lemuridae to cope within their environment and maintain niche separation with any potential competitors.

In contrast to congeners, southern bamboo lemurs displayed an ability to adjust across three habitats, and though this was slightly seasonal, they were able to feed and rest for large portions of time in each habitat. Additionally, they exhibited the highest dietary diversity of all *Hapalemur* spp. ever recorded. In addition to the flexible activity pattern exhibited by *H. meridionalis* in Mandena, these lemurs are also able to flexibly adjust to contrasting floristic and structural habitats, exploiting resources that are specific to each environment. Their ability to exploit a mono-dominant invasive species habitat suggested a potentially larger application of our results in maintaining genetic health, whereby corridors could be quickly implemented to provide routes between populations that may have otherwise been isolated. Many studies from various countries have documented that exotic plantation forests can provide habitat for numerous native forest fauna (Gascon et al., 1999; Barbaro et al., 2005, 2008), and primates are not an exception (Michon and de Foresta, 1995; Williams-Guillén et al., 2006; Bonilla-Sánchez et al., 2012). Bamboo lemurs are no different in their use of

alternative and/or degraded habitats, observed appearing relatively adaptable within anthropogenic landscapes (Grassi, 2006; Martinez, 2008). However, these specific instances recorded *Hapalemur* utilizing degraded habitats that were immediately adjacent to larger, less degraded and protected forests. This is in complete contrast to the heavily fragmented forests of Mandena where all three groups were observed to use all habitat types for all essential and non-essential activities. Furthermore, utilization of invasive *Melaleuca* demonstrated its potential role as a riparian corridor to facilitate dispersal, with confirmed dispersals verifying this function.

While instances of successful dispersal provide a glimmer of hope, the further fragmentation of remaining forests is of great concern if forest species of Madagascar are to persist (Ganzhorn et al., 2014). Although the fate of all lemur species should be considered precarious due to increasing habitat destruction, the knowledge that some lemurs are able to cope with this degradation (to a certain degree) should be seen as positive. Recent studies have begun to alter our view of *Hapalemur* as dietary specialists, demonstrating dietary flexibility and ability to subsist on items other than bamboo in some populations (Mutschler, 1999; Grassi, 2006; Eppley et al., 2011). Some primate species adapted to narrow ecological specializations may be sensitive to natural or anthropogenic habitat perturbations (Harcourt et al., 2005; Kamilar and Paciulli, 2008), whereas others have been shown to adjust to changing environments (Anderson et al., 2007; Nowak and Lee, 2013).

Competition between species typically occurs in relation to limited resources (Wrangham, 1980; van Schaik 1983; Oates, 1987). This can occur in a habitat that has not met its carrying capacity, or possibly under high predation and/or parasitism costs. Thus, if populations of several different species do not reach the habitat capacity, coexistence may be possible. The same effect can be achieved when high predation pressure or parasitism keeps populations below carrying capacity (Struhsaker, 1981; Terborgh and Janson 1986; van Schaik and Kappeler, 1993). Given the large dietary breadth and increased fruit consumption of *Hapalemur* in Mandena, it would appear that the small group size and low density of sympatric *Eulemur collaris* (Donati et al. 2011) may not be imposing heavy competition (e.g., scramble or contest) over these seasonally and spatially limited resources. In fact, I only observed the collared brown lemurs engage in agonistic interactions directed at the bamboo lemurs on a few occasions. By comparison, other *Hapalemur* spp. live in forests where they are sympatric with more species and larger populations, thus the amount of competition / pressure may be entirely different from Mandena where it is minimal and/or near absent.

Although the inclusion of latrine use by southern bamboo lemurs may seem entirely disparate from the first studies exploring activity, habitat and feeding flexibilities, I believe that their use of latrine sites provides an excellent example of how various flexibilities are manifested. Specifically, in that they are able to use consistently similar structures, i.e. oblique branches near the ground, in widely varying habitats. Identifying their utilization of these sites as territorial demarcation and maintaining communication with neighboring and/or intruding conspecifics, it is remarkable that all three groups preferentially selected latrines that were visually conspicuous, despite each habitat that occurred within their ranges providing contrasting vegetation structures. More so than any other variable we explored, this ability of the southern bamboo lemur to identify a visually conspicuous site/structure for latrine purposes exhibits their true ecological flexibility.

Additional observations from Mandena have further elucidated the flexible behavioral ecology of this small-bodied folivore. Primate-bird associations are occasionally observed in diurnal primates from mainland Africa, Asia, and the Neotropics, yet are reported as absent from Madagascar (Heymann and Hsia, 2014). On two separate occasions, a giant coua (*Coua gigas*) was observed to follow the bamboo lemurs as they foraged on grasses on the forest floor (Eppley et al., 2014). As the diet of *C. gigas* largely consists of arthropods (Goodman and Wilmé, 2003), it is probable that the lemurs flushed arthropod prey from the leaf litter for the coua to exploit (Fontaine, 1980; Boinski and Scott, 1988). An additional explanation for the association could be increased anti-predator vigilance as both species are at risk of aerial and terrestrial predation (Goodman and Wilmé, 2003; Karpanty and Wright, 2007), so the association may be perceived as mutually beneficial (Heymann and Hsia, 2014). While it has been theorized that the absence of primate-non-primate associations in Madagascar is likely related to the scarcity of terrestrial, diurnal and herbivorous mammals (Heymann and Hsia, 2014), our data confirm that *H. meridionalis* fulfill these needs (chapter 1, chapter 3).

Perhaps the most comprehensive exploration of their behavioral flexibility occurred in group 4 in Mandena. It was this group that provided a unique affiliative association between a female ring-tailed lemur (*Lemur catta*) and a group (Eppley et al., 2015). Over the full duration of my field work, and extending from my initial observations of this polyspecific association in 2008, both species appeared to have a mutual understanding of vocalizations, behavioral synchronization, dietary overlap, and possible service exchange, e.g., grooming. We also observed the *L. catta* occasionally attending to the bamboo lemur infant. This included grooming, baby-sitting, and even transporting the infant (Figure 1). The behavioral

flexibility exhibited by both species has allowed the successful integration of the female ring-tailed lemur. While polyspecific associations are well documented among mammals Stensland et al., 2003), particularly primates (Cords, 1990, 2000; Heymann and Buchanan-Smith, 2000; Heymann, 2011; Cords and Würsig, 2014), they have rarely been observed in strepsirrhines. Phylogenetically we have known these two species are closely related but otherwise maintain wholly different group organization and feeding preferences, but this observed long-term association displays a shared repertoire whereby these two species are able to communicate, subsist, and survive.
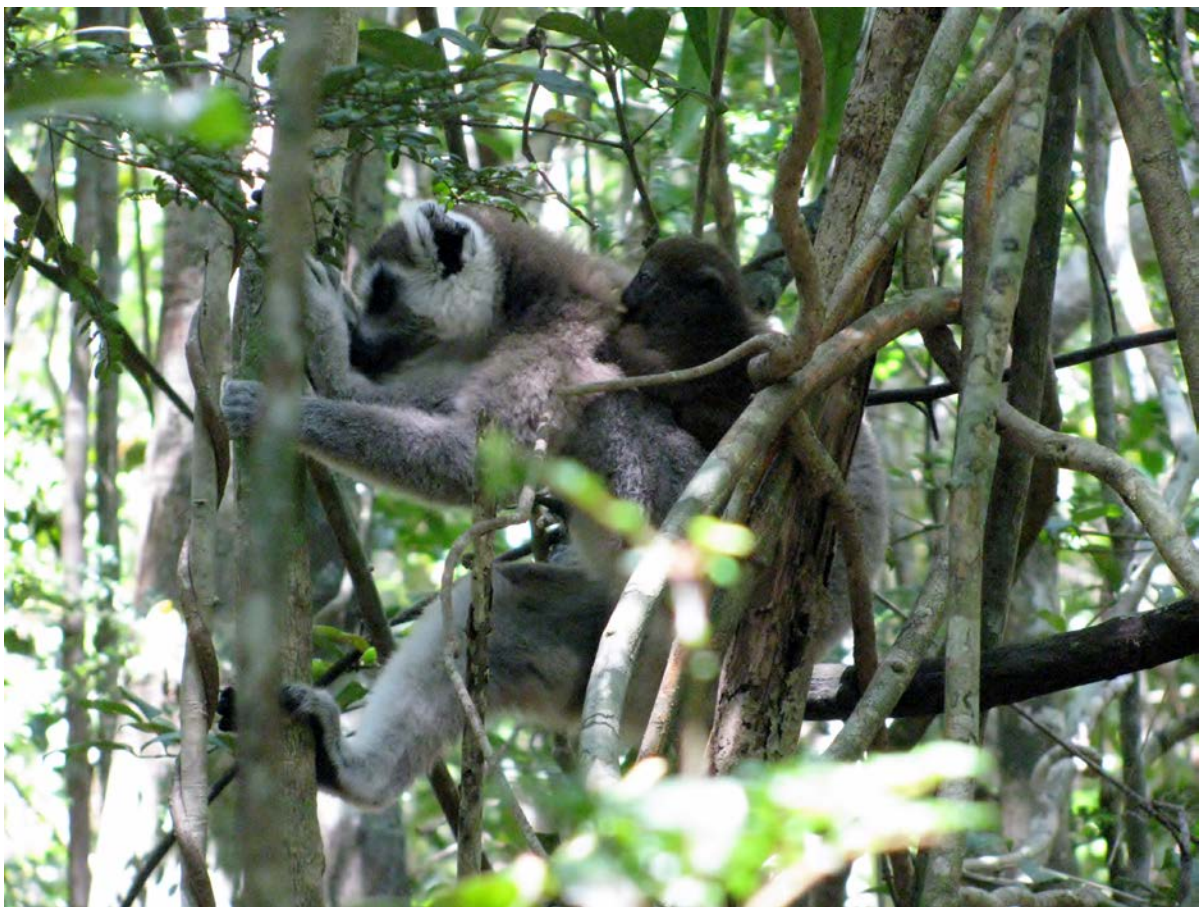
Figure 1. Female *L. catta* grooms her foot while the infant *H. meridionalis* climbs on her back and grooms. These 'babysitting' situations appeared to provide the mother southern bamboo lemur (Female 2) relief from the infant by allowing her to forage without the extra cost of carrying and protecting the infant (Eppley et al., 2015).

Anthropogenic habitat disturbance may benefit *Hapalemur* in several ways. It can increase the heterogeneity of a forest and therefore increase the amount or density of food resources (Oates, 1996). Disturbance can increase the relative abundance of certain plant species that may be preferred food sources, such as pioneer and light-gap species, and

terrestrial herbaceous vegetation (Oates, 1996). Light gaps created by tree falls and/or selective felling may help to maintain floristic diversity by harboring a higher density of tree stems (Brokaw and Busing, 2000) and or terrestrial graminoids. These gaps can also increase the number of early successional specialists, which tend to have leaves with increased protein, less fiber, and lower phenolic content, as well as increasing the quantity of young leaves and improving the quality of mature leaves (Ganzhorn, 1992; Ganzhorn, 1995; Oates, 1996). Our finding that *H. meridionalis* exhibit a flexible behavioral and feeding ecology is not all that surprising. Congeners exploit bamboo, which is highly prevalent in their habitat and thrives particularly well in slightly disturbed areas (Brown and Zunino, 1990; Peres, 1997). The increased sunlight reaching both the canopy and forest floor further increases the quantity and quality of staple foods (bamboo and leaves) and provides higher quality supplemental foods (light-gap species and introduced species). Ultimately, it may be that human-modified landscapes with habitat matrices may have potential conservation value as vital refuges (Chapman and Lambert, 2000; Riley, 2007).

Close to the visitor camp at Mandena and outside of the forest fragment, lies a patch of woody bamboo that was planted here by ecology monitoring teams in the 1990s. This was a result of having observed Hapalemur in the littoral forest, and immediately questioning how these animals were surviving without their "preferred" resource. This woody bamboo is not native to the littoral forests of southeast Madagascar, and does not occur anywhere within the forest fragments, except for in the initial location it was planted, with little spread. Interestingly, one group of *Hapalemur* do occasionally visit this bamboo stand, similar to what would be expected of congeners. As is the case with numerous flexible ecology studies conducted on primates in highly seasonal environments, it is not entirely out of the question to consider that these species did not evolve in tandem with woody bamboos, but rather have evolved an ability to exploit abrasive fibrous materials, whether they be woody bamboos, herbaceous grasses, sedges, or reeds. Numerous species display this ability, some for very large proportions of their monthly and annual diets, yet no one has yet questioned how these other primates cope with potential cyanogenic toxins within their diet. Is it possible that all hindgut fermenters could possibly denature cyanide through some as of yet unknown process?

Though this body of research provides findings suggestive of the ecological flexibility of this species, they are not immune to extinction. Many of their, and congeneric, populations remain heavily threatened with complete extirpation. Despite this, these findings should

provide a glimmer of hope with elucidating the potential flexibilities that they display. With many sites completely fragmented and no potential dispersal routes remaining for many lemur species, we must take action to facilitate their ability to naturally disperse to new groups, and thus maintain genetic diversity. Similar to the conclusion of Grassi (2001) every aspect of the behavioral ecology of *Hapalemur* is adapted to suit the home range used and the resources available therein. Despite the contrasting differences of the habitats within this anthropogenic landscape, *Hapalemur* persist across all three, utilizing the unique guild of available food species/items within each.

Future Directions

Future research focusing on the behavioral ecology of *H. meridionalis* groups living in forests with woody bamboo stands, e.g., Andohahela NP Parcel 1, will help elucidate the full extent of their ecological flexibility and/or intra- and inter-specific variability. Specifically, the areas of most interest are: (1) if there are other *Hapalemur* populations that live in sites devoid of woody bamboo, do they employ similar behavioral, ecological, and physiological strategies as we see among the Mandena bamboo lemurs? (2) Both *H. alaotrensis* and *H. meridionalis* display seasonal constraints on cathemeral activity, yet while the former's diet is strictly folivorous with an exceedingly low dietary breadth, the latter displays a very large dietary breadth and seasonal flexibility that may impose a biotic constraint on their diel activity pattern. Thus, during the cool, austral winter when the phenological productivity of the littoral forest is low, it may be that *H. meridionalis* employ a cathemeral activity pattern to cope with the increased consumption of fiber in their diet, although this hypothesis was initially proposed when only frugivorous *Eulemur* spp. were known to exhibit cathemerality (Engqvist and Richard, 1991). It may be that the ubiquity of bamboo throughout many *Hapalemur* spp. geographic ranges allows these animals to decrease the extent of their energy use. It is possible that the distribution of resources have an effect on their sociobiology. (3) Are the bamboo lemurs living in the degraded forest fragments display larger endoparasite loads compared to conspecifics from less degraded and more continuous habitats? Furthermore, though descending to the terrestrial stratum provides foods with greater metabolizable energy, do they come at the cost of increasing susceptibility to parasites? (4) Additionally, as indicators of stress, do *Hapalemur* within these sites of varying degradation and continuity (i.e., Mandena, Tstitongambarika, and Andohahela) display any variance in glucocorticoid levels?

On a methodological level, the use of visually conspicuous latrine sites may be an excellent, albeit unconventional, measure by which to gauge the presence of this species within other forests. The cryptic nature of this species often does not allow for standard survey methods, and the results are often misleading. While conducting daily reconnaissance surveys throughout the Ampasy valley in northern Tsitongambarika (described in Nguyen et al., 2013) from July –September 2012, I managed to observe bamboo lemurs on a few occasions engaging in latrine behavior at *Uapaca* spp. stilt-roots within one meter of the ground. In fact, searching throughout this lowland humid forest valley, we were able to identify additional latrine sites located under these stilt-rooted trees. The cryptic nature of bamboo lemur species often leads to inaccurate population density estimates and difficulty in monitoring (Guillera-Arroita et al., 2010a, 2010b; Olsen et al., 2012); it may be that searching these visually conspicuous sites for accumulated fecal deposits could provide a measure by which presence/absence could be assessed.

The exhibited group differences in habitat utilization indicate that *H. meridionalis* are highly adaptable, displaying an ecological flexibility that allows them to persist across a mosaic of distinct habitats. More specifically, their use of an invasive species-dominant habitat, one that acts as a riparian corridor, appears to facilitate and maintain movement between the Mandena littoral fragments as well as the larger continuous humid forests. Non-native species have the ability to catastrophically dismantle the ecological integrity of habitats; however, their ability to facilitate dispersal within fragmented landscapes and thus potentially circumvent faunal genetic erosion should be carefully considered in tandem within future conservation management plans and native reforestation efforts. It is possible that this more comprehensive understanding of both the behavioral plasticity and dietary flexibilities of *H. meridionalis* may indicate that this species is a suitable candidate for re/introduction to habitats that are otherwise devoid of bamboo.

Conclusion

Although previous studies have highlighted the dietary specializations of the bamboo lemur clade (*Hapalemur/Prolemur*), my study has shown that these specializations may simply be part of a larger, more complex repertoire. The site of Mandena was the ideal location from which to conduct these studies, given the lack of all bamboo (woody, liana, herbaceous), similar to Lac Alaotra; however, the complexity of the habitat mosaic at Mandena added an intricate layer with which to explore ecological flexibilities. The preceding chapters (articles and manuscripts) have described, in detail, behavioral flexibilities that have allowed southern bamboo lemurs to persist in a degraded forest and swamp within a fragmented habitat. Their employment of a cathemeral activity pattern, proximately controlled by lunar luminosity, allows these cryptic lemurs to expand their activities into the night, similar to other lemurids, specifically, *Eulemur* spp. and *Lemur catta*. Their use of visually conspicuous latrine sites throughout their home range allow for neighboring or intruding conspecifics to quickly gauge the territory and possibly demographics of the group. This appears likely to assist in reduced resource and territorial defense, which may explain the extremely low rates of inter-group agonism. Mandena is a matrix of forest and swamp habitats, but one would assume that the invasion of *Melaleuca quinquenervia* in the more open marsh/swamp area would eliminate the possibilities for lemur species to disperse to the larger continuous forest of nearby Tsitongambarika. However, we quickly realized that the vertical structure of these exotic trees, in addition to their constant harvest for wood by locals, permitted the continued growth of the terrestrial herbaceous vegetation, specifically graminoids, which the *Hapalemur* preferred to eat. Lastly, the large proportion of terrestrial grazing allowed for a unique perspective on the proximate factors that influence an arboreal species to descend to the ground. Accounting for only our complete day follows (>80% day length), southern bamboo lemurs displayed a near even split between arboreal and terrestrial feeding. With terrestrial grazing providing increased metabolizable energy intake while maintaining an even risk of predation, it seems only likely that the benefit is in the lemurs' favor. Despite the nutritional pay-off, the lemurs still show a strong preference towards feeding in closer proximity to group conspecifics, increasing group vigilance and/or dilution effect. Each of these chapters implores further investigation of these unique and flexible traits. Together, these studies demonstrate a level of behavioral and ecological flexibility that

had not been observed before among *Hapalemur*, and may be the underlying mechanism that allows these bamboo lemurs to persist in heavily altered environments.

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Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe nur unter Verwendung der angeführten Literatur angefertigt habe.

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Timothy Michael Eppley

Erklärung zum Promotionsvorhaben Hiermit erkläre ich, dass ich zuvor noch keiner Promotionsprüfung unterzogen wurde, sowie ich mich noch um keine Zulassung an der Universität Hamburg bzw. einer anderen Universität beworben habe. Weiterhin habe ich noch keiner Universität oder ähnlichen Einrichtung eine Dissertation vorgelegt.

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Timothy Michael Eppley