Ecological flexibility of the southern gentle lemur *Hapalemur meridionalis* in south-east Madagascar: Implications for conservation in a fragmented and seasonal landscape

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Introduction

Madagascar is known for its extreme biodiversity and endemism, and often identified as one of the 'hottest' biodiversity hotspots in the world (Myers et al. 2000; Ganzhorn et al. 2001; Mittermeier et al. 2010), 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. Habitat loss due to slash-and-burn agriculture and timber harvest, charcoal production, cattle grazing, as well as bushmeat hunting, continue to jeopardize lemurs' survival (Schwitzer et al. 2014). As habitat destruction persists in isolating the remaining lemurs to forest fragments, it is imperative to understand the responses of native plants and animals to disturbance and to explore potential options for their conservation.

Ecological flexibility is loosely defined as an organism's ability to adjust to changes within its environment, e.g., anthropogenic, gradual, stochastic, etc. (Nowak & Lee 2013). Specifically, *flexibility* encapsulates modifications to the diet, altering activity and vertical strata, and may also comprise behavioural and physiological components. This ability to expand niche breadth is key to withstanding the risks of anthropogenic and/or stochastic habitat modification (Lee 2003). Gentle (aka bamboo) lemurs (*Hapalemur* spp. / *Prolemur simus*), are known for their dietary predilection for bamboo. Due to their low dietary breadth, bamboo lemur species are believed to be inflexible in terms of behavioural and ecological adaptability, and are regarded as a textbook example of primate specialists. On the other hand, habitat flexibility is

equally important as dietary flexibility. 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.

The bamboo lemurs, genera *Hapalemur*/*Prolemur*, family Lemuridae, are often considered the most specialized of the Malagasy primates. They are small-bodied primates, albeit medium-sized lemurid strepsirrhines. 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. This folivorous genus is peculiar as it displays a dietary predilection for bamboo (Overdorff et al. 1997; Tan 1999; Grassi 2006). 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 1999; Grassi 2001, 2006; Eppley et al. 2011).

Among the most ecologically diverse areas of Madagascar is the Anosy region along the southeast coast (Ramanamanjato et al. 2002). Nearly 90% of the original littoral forest of Madagascar has already been lost. This region provides a complex mosaic of heavily fragmented upland and swamp forest habitats, old and new plantations, and mono-dominant invasive species, and thus presents itself as an excellent model with which to explore the ecological flexibilities among the allegedly inflexible bamboo lemurs that inhabit this system.

Project Aims

These provide a broad scope from which I investigated the ecological flexibility of *H. meridionalis*. These are:

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

2: To investigate the role of an invasive species habitat on the behavioural ecology of a small-bodied folivore.

3: To investigate the costs and benefits associated with expansion to a terrestrial dietary niche by a small, arboreal primate.

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

Methods

Study site

The Mandena littoral forest (24°95'S, 46°99'E; Figure 1) is approximately 10 km north of Tolagnaro (Fort-Dauphin). This degraded and fragmented littoral forest/swamp matrix provides an excellent site model for understanding how the supposedly inflexible *Hapalemur* spp. subsist within an environment devoid of bamboo. The area comprises 148 ha of upland littoral forest, including approximately 82 ha of interspersed swamp and *Melaleuca* swamp that segregate the two largest fragments, allowing exploration into the species' ecological flexibility.

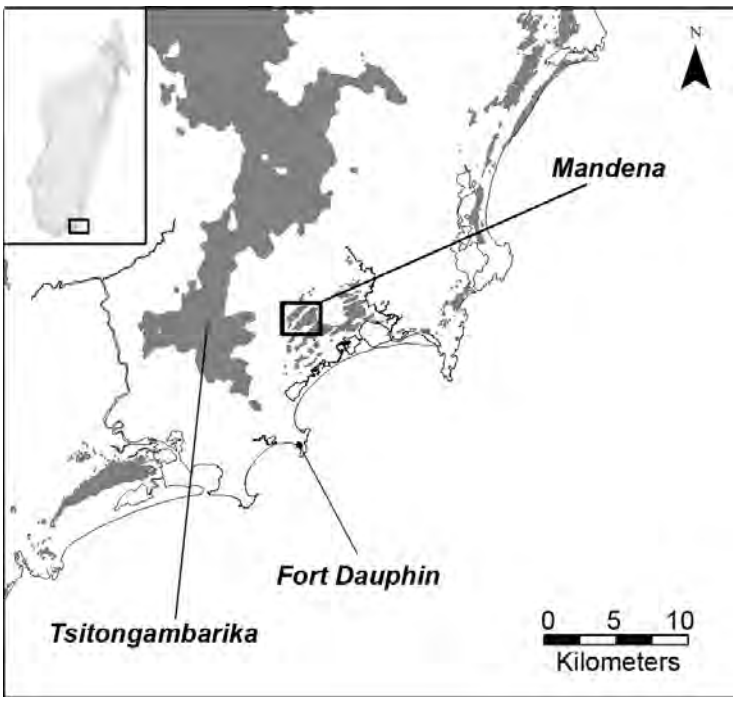

Figure 1. Location of Mandena littoral forest in southeast Madagascar, relative to the larger, continuous forest of Tsitongambarika.

Monthly climatic factors were collected daily within Mandena, including temperature (°C), precipitation (mm), and day length (hrs; Figure 2). In addition, I generated a nocturnal luminosity index (NLI) 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.

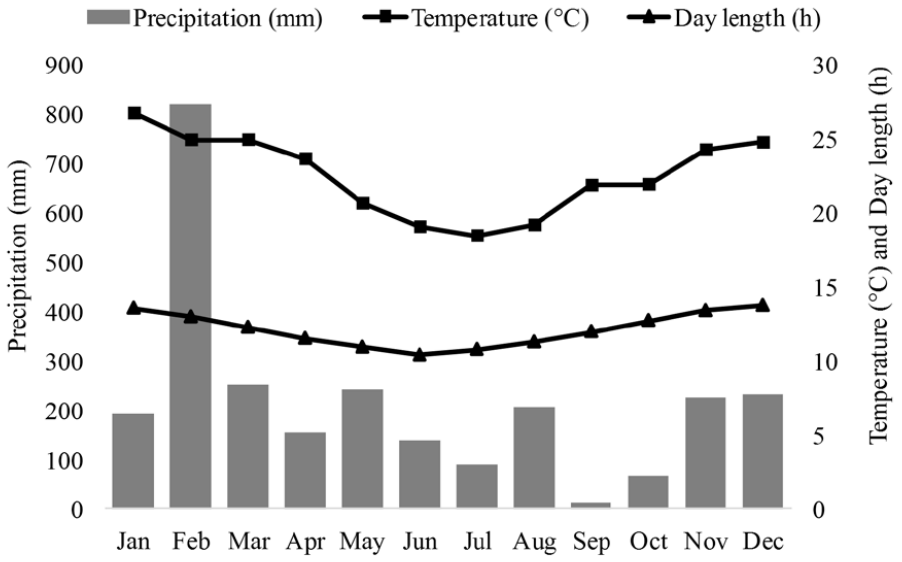

Figure 2. Monthly total precipitation (mm), mean temperature (°C), and mean day length (h) at Mandena in 2013.

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 ± SD; N = 15) (Eppley et al., 2011). 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 ± SD; N = 5).

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 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). 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, I sampled 25 x 100m^2 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 (m^3). I further conducted vertical-line transects within each plot, so as to detail the structure and canopy cover for each these three habitats.

Behavioural and Feeding Sampling

From January to December 2013, I conducted full-day focal follows (sunrise to sunset) with the aim of acquiring 50hrs/month per group for three social groups. Individuals were identified using uniquely coloured pendants. I collected behavioural data via instantaneous focal sampling (Altmann 1974) at 5-min intervals on broad-level activities (resting, feeding, moving, social and other) and noted the habitat (upland, swamp, and *Melaleuca*-swamp) and height (arboreal or terrestrial). In addition, continuous feeding data was recorded each time a focal individual fed, noting 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.

Nutritional analyses

Food item samples (e.g., young and mature leaves, lianas, flowers, unripe and ripe fruits, fungi, soil etc.) were collected 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. Detailed reviews of the procedures and their biological relevance are provided by Ortman et al. (2006).

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 and further estimated the area (ha) of each habitat type.

Results

Mandena 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).

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

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

I observed *H. meridionalis* for >1,762 hours from January-December, 2013 across 194 focal days. 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). The *Melaleuca* habitat constituted large portions of the home ranges of groups 1 and 4, while it appeared to be minimal for group 2. Despite this, both groups 1 and 4 accessed this invasive habitat often, and group 2 still utilized it on greater than 20% of observation days. Considering focal days, lemurs were observed to access *Melaleuca* habitat on 54.12% of days, although this only constituted 18.55% of our total observation record.

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.

Activity

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. They exhibited a monthly DN ratio (mean ± SE) of 3.98 ± 0.35:1 (*N* = 7) with fluctuations over the course of the study. The activity balance of southern bamboo lemurs was not considerably affected by any climatic factor tested, but was significantly influenced by lunar luminosity. To illustrate this influence of lunar phase on cathemeral activity, an actigram of daily and hourly activity for group 4 from September 2013 is provided in Figure 3. 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).

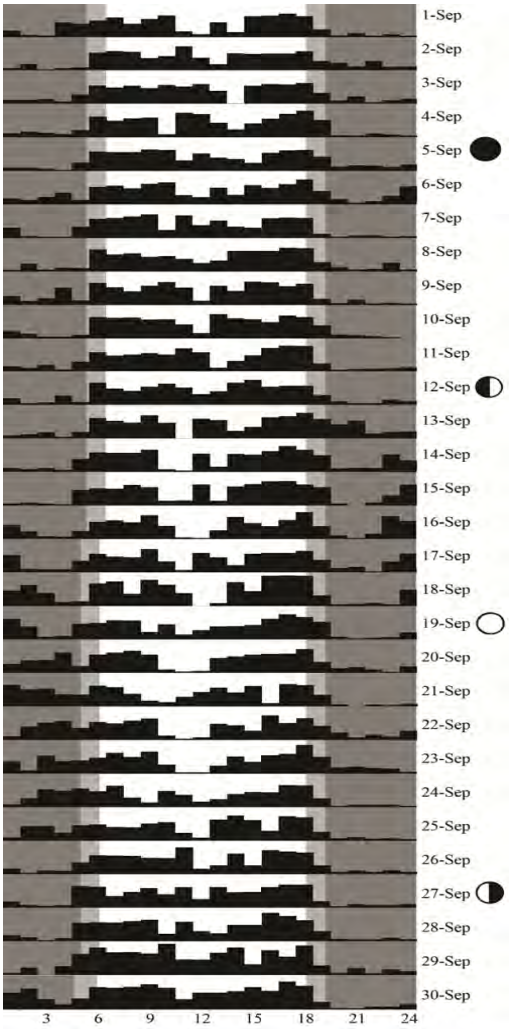

Figure 3. Mean daily 24-h activity recorded in group 4 for the month of September, 2013. Note the increased nocturnal activity occurs mainly around the full moon portion of the month (unfilled circle represents full moon, filled circle represents new moon, and half-filled circles represent intermediate moon phases).

Feeding

I recorded 693.89h of feeding by *H. meridionalis* in Mandena. Overall, they selected for 86 different food items from 72 distinct species in Mandena (Table 3). 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.

Table 3. Number of species eaten and overall percent by each food type selected by *H. meridionalis* groups in Mandena from Jan. – Dec. 2013

	Group 1		Group 2		Group 4		Total	
Food type	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.

When only considering our full-day focal follows (*N* = 106), bamboo lemurs averaged feeding terrestrially for 148.08mins and arboreally for 158.99mins, daily. We used a linear mixed model (LMM) to determine which factors best predicted a greater daily proportion of terrestrial feeding. The best-fit model included significant values for nutritional proxies (metabolizable energy alone and as an interaction with protein-to-fibre ratio), and seasonal climatic influences, i.e., temperature and precipitation.

Discussion

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 luminosity. 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 addition to the flexible activity pattern exhibited by *H. meridionalis* in Mandena, these lemurs, in contrast to congeners, are also able to flexibly adjust to contrasting floristic and structural habitats, exploiting resources that are specific to each environment. All three groups were observed to use all habitat types for all essential and non-essential activities, with slight seasonal differences. Additionally, they exhibited the highest dietary diversity of all *Hapalemur* spp. ever recorded. 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, with confirmed dispersals verifying this function.

Many *Hapalemur* populations remain heavily threatened with extinction; despite this, our body of research provides findings suggestive of the ecological flexibility of this species, which should provide a glimmer of hope. 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.

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. Despite the contrasting differences of the habitats within this anthropogenic landscape, *Hapalemur* persist across all three, utilising the unique guild of available food species/items within each. 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 behavioural 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. Bamboo lemurs' 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*. 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. 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, I 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'

favour. Each of the individual studies within this project implores further investigation of these unique and flexible traits. Together, they demonstrate a level of behavioural 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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Dissemination of Results (on-going)

Peer-reviewed articles

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Submitted and In prep manuscripts

Eppley TM, Donati G, Ramanamanjato J-B, Randriatafika F, Andriamandimbiarisoa LN, Rabehevitra D, Ravelomanantsoa R, Ganzhorn JU (submitted) The use of an invasive species habitat by a small folivorous primate: implications for lemur conservation in Madagascar.

Eppley TM, Ganzhorn JU, Donati G (submitted) Latrine behaviour as a multimodal communicatory signal station in wild lemurs: the case of *Hapalemur meridionalis*

Eppley TM, Donati G, Ravelomanantsoa R, Ganzhorn JU (submitted) Predation of an adult southern bamboo lemur *Hapalemur meridionalis* by a Dumeril's boa *Acrantophis dumerili*.

Eppley TM, Donati G, Ganzhorn JU (submitted) Determinants for terrestrial feeding in an arboreal primate.

Oral presentations

Eppley TM, Ganzhorn JU, Donati G (2014) Influence of abiotic factors on cathemeral activity among southern bamboo lemurs. American Society of Primatologists, Annual meeting, Decatur, Georgia, September 12-15 *Student competition finalist

Eppley TM, Donati G, Ganzhorn JU (2014) Flexible feeding ecology of the southern bamboo lemur (*Hapalemur meridionalis*). International Primatological Society XXV Congress, Hanoi, Vietnam, August 11-16

Donati G, **Eppley TM** (2014) Nocturnal activity and cathemerality in "day-active" lemurs. International Primatological Society XXV Congress, Hanoi, Vietnam, August 11-16

Eppley TM, Donati G, Ganzhorn JU (2014). Cathemeral activity among southern bamboo lemurs (*Hapalemur meridionalis*) in the Mandena littoral forest, southeast Madagascar. Primate Society of Great Britain Spring Meeting, Oxford, United Kingdom, April 8-9

Eppley TM, Donati G, Ganzhorn JU (2013) Swamp corridor utilization by *Hapalemur meridionalis* in a human-altered landscape. International Prosimian Congress, Center Valbio, Ranomafana, Madagascar, August 5-9

Poster presentations

Eppley TM, Donati G, Ganzhorn JU (2013) Forest grazers: the southern bamboo lemur of the Mandena littoral forest. Gesellschaft für Primatologie, Annual meeting, Hamburg, Germany, February 6-8

Eppley TM, Hall K, Donati G, Ganzhorn JU (2013) Observations of affiliative polyspecific association between *Lemur catta* and *Hapalemur meridionalis*. Gesellschaft für Primatologie, Annual meeting, Hamburg, Germany, February 6-8