Determinants of terrestrial feeding in an arboreal primate: the case of the southern bamboo lemur (*Hapalemur meridionalis*)

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Objectives

The proximate and ultimate determinants that may have prompted the shift from an arboreal to terrestrial feeding niche, whether due to environmental change, seasonality, and/or predation pressure, are poorly understood. Within a fragmented littoral forest in southeast Madagascar, a strepsirrhine population of the arboreal *Hapalemur meridionalis* spends a large proportion of time on the ground. We aimed to identify which factors influence terrestrial feeding by an arboreal primate.

Methods

From January to December 2013, we conducted 106 full-day focal follows on three social groups of southern bamboo lemurs *H. meridionalis*. We continuously recorded feeding time on all arboreal and terrestrial food items consumed, as well as whether the focal individual was under the canopy or exposed, and the distance to their nearest conspecific neighbor. All observed food items were collected and analyzed for macronutrient content to allow for dietary quality comparisons. Daily climatic variables (temperature, precipitation), resource seasonality, daily path length, along with dietary and predation risk proxies, were used as fixed effects in a linear mixed model, with the daily proportion of terrestrial feeding as the dependent variable.

Results

Our model indicated that daily terrestrial feeding increased in cooler temperatures, with shorter daily path lengths, and when consumed dietary metabolizable energy increased. All other fixed effects were not significant predictors.

Discussion

Our study indicates that the expansion to a terrestrial dietary niche occurs when the nutritional pay-off is greater in the new strata and predation risk is similar (or less) compared to the original arboreal stratum.

Introduction

It has been suggested that ancestral eutherian orders, including placental mammals, are likely characterized by a terrestrial evolutionary history, with subsequent transitions to arboreality occurring 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 Euarchonta, i.e., ancestral mammals from which Primates radiated (Sussman, 1991; Bloch and Boyer, 2002; Szalay, 2007; Kirk et al., 2008). The subsequent evolutionary shift in some primate species from an arboreal to terrestrial niche is shown through various morphological adaptations, e.g., limb, dental, postcranial, etc. (Gebo and Sargis, 1994; Gebo, 1996; Fleagle, 2013; Motsch et al., 2015). The evolutionary pressures that led to a terrestrial niche, however, are poorly understood.

Foraging is often considered to be a predator-sensitive behavior, whereby foraging success may be outweighed by the necessity to minimize the risk of predation (Schoener, 1971; Altmann, 1974b; Miller, 2002a). For example, a desert population of baboons (*Papio ursinus*) was shown to exploit low-risk, low-quality foraging sites rather than chance foraging on high-quality foods where the risk of predation was higher (Cowlishaw, 1997). Similarly, the impact of potential predator risk on primate foraging behavior has been repeatedly shown (Cords, 2002; Miller, 2002b; Overdorff et al., 2002; Sauther, 2002). While some argue that there is a higher risk of predation on the ground (van Schaik, 1983; Wrangham et al., 1993; Janson and Goldsmith, 1995), others have suggested that primates with arboreal or terrestrial lifestyles may be equally susceptible to predators (Cheney and Wrangham, 1987; Isbell,

1994; Janson and Goldsmith, 1995; Hart, 2007), depending upon whether their feeding or resting sites are more exposed (van Schaik and van Noordwijk, 1989; Janson, 1998). It has also been suggested that predation risk should be greater for animals whose nearest conspecific neighbors are farther away (Hamilton, 1971; Phillips, 1995; Treves, 1998), thus if individuals on exposed substrates are at greater risk of predation, then the presence of neighbors may provide some protection (DiFiore, 2002).

In addition to predation pressure, food distribution and dietary quality are also considered to be 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 certain amino acids and/or minerals (Izawa, 1993; Campbell et al., 2005; Link et al., 2011). 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 nutritional gain from ubiquitous (i.e., rather than clumped) terrestrial food items may have been a catalyst in the transition of an arboreal mammal to a terrestrial dietary niche, though other factors are likely to have played a role, e.g., potential predation risk, thermoregulation, and/or energetic costs of locomotion.

Among the strepsirrhine primates of Madagascar (i.e., lemurs), the ring-tailed lemur (*Lemur catta*) is the most terrestrial species, spending approximately 30 to 40% of its time on the ground (Jolly, 1966; Sussman, 1974; Sauther et al., 1999; Cameron and Gould, 2013). Though duration tends to be minimal, the occasional occurrence of terrestrial traveling and/or foraging is exhibited among other lemurs, e.g., collared brown lemurs (*Eulemur collaris*; Lazdane et al., 2014), crowned lemurs (*E. coronatus*; Wilson et al., 1989), red-fronted lemurs (*E. rufifrons*; Sussman, 1974), Verreaux's sifaka (*Propithecus verreauxi*; Richard, 1974),

diademed sifaka (*P. diadema*; Irwin et al., 2007), and indri (*Indri indri*; Pollock, 1975). 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 behavior as an anti-predator strategy (Tan, 2006). Like their name indicates, they are known for their dietary specialization on bamboo, a subfamily of grasses that is widespread throughout the eastern forests of Madagascar (Dransfield, 2000), and at times can make up 85-95% of the bamboo lemur's diet at certain study sites (Wright, 1986; Overdorff et al., 1997; Tan, 1999; Grassi, 2002, 2006). The Alaotran gentle lemur has been an unusual exception within the genus, with its entire population living in the wetlands around Lac Alaotra, a habitat without bamboo. Here, *Hapalemur alaotrensis* have a diet that contains reeds and sedges, yet their dietary breadth remains low (~11spp.) possibly due to the lack of available food options (Mutschler, 1999). Similarly, at the site of Mandena in southeast Madagascar, southern bamboo lemurs (*Hapalemur meridionalis*) inhabit an area that is also devoid of bamboo (Rabenantoandro et al., 2007; Eppley et al., 2015a). Lacking the primary food resource for the genus, *H. meridionalis* focus a portion of their diet on various terrestrial grasses and 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). Their terrestrial grazing often takes place in a sparsely canopied swamp/marsh habitat (Eppley and Donati, 2009; Eppley et al., 2015a), potentially increasing their susceptibility to both aerial and terrestrial predation (Karpanty, 2006; Karpanty and Wright, 2007).

It has been previously suggested that despite the risk of predation, terrestrial foraging in some arboreal species may represent a nutritional fallback strategy when more preferred

food items are seasonally scarce in more degraded and/or naturally patchy habitats (Newton, 1992; Grueter et al., 2009; Barnett et al., 2012). The southern bamboo lemurs of Mandena, a dynamic forest system due to its fragmentation and transitional climatic zone (Ganzhorn et al., 2001), provide an excellent model for exploring the ecological trade-off of costs/benefits and ultimate influences on the transition to a terrestrial niche. Within the littoral forests of southeast Madagascar, dietary resource phenophases peak in the warm austral summer, whereas resources become scarce in the cool austral winter (Bollen and Donati, 2005; Campera et al., 2014). We predicted that:

- Terrestrial feeding would be seasonal, specifically increasing during the cool, dry austral winter when dietary resources (e.g., ripe fruits, flowers, and flushing leaves) become more scarce (Bollen and Donati, 2005; Campera et al., 2014).

- As such, we further predicted that the daily nutritional intake of terrestrial food items would represent a markedly higher dietary quality (i.e., protein/fiber ratio and metabolizable energy) than foods in the arboreal strata at that time, thus representing a benefit for their increased utilization of a potentially risky stratum.

- As daily path length is a response to variation in resource distribution (Koenig et al., 1997; Raño et al., 2016), shorter daily path lengths will predict increased terrestrial feeding due to the ubiquity of terrestrial food items throughout the landscape.

- Furthermore, we predicted that the perceived risk of predation would be greater when bamboo lemurs fed terrestrially (compared to arboreal feeding), and thus individuals should maintain closer proximity to group members when feeding on the ground.

Methods

Study site

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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. This 230 ha area consists of fragmented and degraded littoral forest and interspersed, seasonally-inundated swamp (Eppley et al., 2015a). Among the most threatened habitats in Madagascar (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). The vertical structure of the Mandena littoral forest is relatively low, with an average forest canopy height of approximately 7 m, while the surrounding swamps maintain a slightly lower average canopy height of 6.5 m (Eppley et al., 2015a).

To assess daily climatic factors, which can be highly variable within the littoral zone, temperature (°C) was recorded in 30 min intervals using four Lascar EL-USB-1 data loggers (Lascar Electronics, Inc.; Erie, PA, USA), operated by custom software (EasyLog USB Version 5.45, Lascar Electronics, Inc.). These were located in each of the three Mandena habitats to provide daily averages. Precipitation (mm) was measured daily at 6:00 h 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 (Fausser et al., 2002; Eppley et al., 2015b, c). They live in small social groups, typically one or two adult females and one or two adult males, with an average size of 5.6 ± 1.5 individuals ($N = 5$) (Eppley et al., 2016). Similar to congeners, they are classified as folivores (Eppley et al., 2011).

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In order to expedite 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).

Resource Seasonality Data

To estimate monthly variation in food availability, phenology data were recorded for plant species ($N = 100$) known to produce foods consumed by lemur species within Mandena. Utilizing an established transect that includes both littoral forest and swamp habitats, the first five to six mature (DBH $\geq$ 10 cm) individuals encountered for each plant species were selected to collect phenological data from. Plants ($N = 517$) were observed twice a month for the presence/absence of flowers and fruits (Bollen and Donati, 2005). While we did not collect phenology data on young leaves and grass availability, the former has been previously shown to be highly correlated with fruit availability in the littoral forest habitat (Bollen and Donati, 2005).

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 ($N = 10$) from our three focal groups sampled at least once each month. Continuous sampling (Altmann, 1974a) 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 was recorded as meters above ground for each feeding bout. As individuals occasionally move

between strata while feeding, we time-stamped changes (to the second) in height so as to be exact in how much time they spent feeding on an item in each stratum. A new bout was recorded if there was a 60 second interval with no feeding. Furthermore, to estimate daily path length (DPL), GPS coordinates were recorded in UTM every 15 min.

To estimate exposure to diurnal birds of prey, we collected instantaneous point sampling (Altmann, 1974a) at 5 min intervals of whether the focal subject was located directly under canopy cover, or if the individual was exposed (i.e., no canopy directly above the focal). Two species of hawk are present in Mandena, Madagascar harrier-hawk *Polyboroides radiatus* and Henst's goshawk *Accipiter henstii* (TME, personal observation), both 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 and has been 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 vs terrestrial), we considered our canopy exposure method as an acceptable proxy.

Predation risk of *Hapalemur* spp. is not limited to aerial predators; Eupleridae 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* (Eppley and Ravelomanantsoa, 2015), present potential arboreal and terrestrial predatory threats, respectively. Though bamboo lemurs are known for their cryptic nature, other evolutionary anti-predator strategies may include group

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defense, dilution of risk, or increased vigilance (Hamilton, 1971; Janson, 1992). To test whether *H. meridionalis* employed these strategies, we instantaneously recorded the nearest neighbor to the focal every 5 min, categorized as *close* (≤ 3 m) and *far* (> 3 m). This allowed us to calculate daily proportions for having a close neighbor for both arboreal and terrestrial feeding.

Nutritional Analyses

We collected samples from all known food items we observed the lemurs to consume. These included grass, piths, young and mature liana leaves, young liana stems, flowers, unripe and ripe fruits, fungi, soil, etc., 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 overnight at approximately 40°C in a commercial electric drying oven in an office with stable electricity supply, 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 1 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 analyzed for neutral (NDF) and acid (ADF) detergent fibers, with NDF representing all the insoluble fiber (cellulose, hemicellulose and lignin) and ADF representing the fiber fraction containing cellulose and lignin. Lipid content was determined by extraction using petroleum ether, followed by evaporation of the solvent. Detailed reviews

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of the procedures and their biological relevance are provided by Ortmann et al. (2006),

Donati et al. (2007) and Rothman et al. (2012).

Data Analyses

Our examination of the southern bamboo lemur feeding ecology sought to assess

dietary diversity for annual diets in each of the three social groups via species numbers and

the Simpson's diversity index (Begon et al., 1996).

To evaluate dietary quality of food items consumed daily, we calculated the daily

weighted proportion of dry matter for each nutritional component, 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 daily proportion of feeding records and X_i is the percentage of dry matter of

each chemical parameter for the ith item. Our first measure of dietary quality, protein-to-fiber

ratio, was calculated as crude protein/acid detergent fiber (Milton 1979; 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; Davies et al., 1988;

Ganzhorn 1992; Simmen et al. 2012); 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.

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Our second dietary quality measure was the weighted metabolizable energy, whereby the energy content of food items was obtained by standard conversion factors: 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 kcal g^{-1}) of diet; L is the proportion of lipids; SP the proportion of soluble proteins; SC the proportion of soluble carbohydrates and [NDF × 0.709] the fraction of NDF which are digested by bamboo lemurs (Campbell et al., 2004).

For the sake of this study, we are treating feeding height as a simple dichotomy, i.e., arboreal (> 0 m) or terrestrial (0 m). To determine the differences in nutritional gain between the arboreal and terrestrial niche, we calculated the two aforementioned nutritional quality measures based on food item intake time within each strata. Furthermore, we calculated a daily proportion of canopy exposure for both strata.

DPL (m) was calculated as the sum of accumulated straight-line distances between successive GPS coordinates from daily full-day focal follows (Suarez, 2006).

For resource seasonality, we calculated a monthly proportion of flower/fruit presence, allowing us to generate a dichotomous variable (abundant/lean) for each month. Similar to previous studies (Bollen and Donati, 2005; Campera et al., 2014), Mandena resource

abundance corresponded to October – March, whereas resource scarcity corresponded to April – September.

To determine which factors influenced terrestrial 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 dependent 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. In order to reduce the necessity for running multiple LMMs and increase statistical power, we calculated the daily differences from terrestrial and arboreal proportional values for the following fixed effects: weighted average of protein-to-fiber ratio and weighted average of metabolizable energy (both as proxies for dietary quality), canopy exposure (as a proxy of exposure to birds of prey), as well as distance to nearest neighbor (proxy for perceived predation risk). This provided one overall comparative value per day rather than one per strata. In addition, we included DPL of the focal individual, resource seasonality, as well as climatic 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) with significance considered at $P < 0.05$. Residuals from the analysis were normally distributed according to the Kolmogorov-Smirnov test.

Results

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Dietary diversity

We observed *H. meridionalis* for 1,762 h, resulting in 694 h of feeding recorded. Overall, southern bamboo lemurs consumed 86 different food items from 72 distinct species in Mandena, with the top ten species contributing 75.95% 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 (Table 1). Graminoids (i.e., species of the families Poaceae and Cyperaceae) are almost exclusively eaten from a terrestrial position, and occur throughout the Mandena littoral forest and marsh/swamp. Terrestrial feeding was not limited to just graminoid species (and soil and water), but rather comprised 29 different items that included forbs, fungi, young liana stems, and fallen fruit. The largest median proportion of time spent feeding terrestrial was in June (0.85), with the greatest number of food items consumed terrestrially occurring in August ($N = 25$). While both of these large values occurred during the austral winter, terrestrial feeding by bamboo lemurs exhibited substantial variation across the entire study period (Fig. 1). This perhaps shown best in the month of February, which was also the month with the highest precipitation, as it exhibited the both lowest median proportion of terrestrial feeding (0.01), as well as the least number of food items consumed while on the ground ($N = 5$).

Concerning dietary diversity, groups 1 and 4 consumed 56 distinct species while group 2 had a slightly lower diversity with 47 species consumed during the year (Table 1). Group 1 had both the highest plant species and family diversity of consumed foods. When analyzed for macronutrient compositions, terrestrial food items were shown to have high nitrogen and fiber (NDF) content compared to those items consumed arboreally, while arboreal food items had higher soluble carbohydrates (SC), acid detergent fibers (ADF), and phenols (Table 2). When only considering our full-day focal follows ($N = 103$), terrestrial

feeding time of these lemurs averaged 143.20 ± 106.71 min (±SD) and arboreal feeding time

averaged 158.08 ± 85.69 min (±SD), daily.

These lemurs also exhibited differences between feeding strata in both dietary quality, i.e.,

terrestrial food items represented higher PF ratio and ME (kcal g^{-1}) compared to arboreal

food items, and predation proxies, i.e., focal lemurs were more often exposed with no canopy

above them when feeding terrestrially, yet they maintained closer proximity to their nearest

neighbor in this stratum compared to when they fed arboreally (Table 3).

In terms of resource seasonality, *H. meridionalis* averaged 30.91 ± 4.08% (±SE) terrestrial

feeding daily during resource abundant months, compared to 52.74 ± 3.24% (±SE) daily

feeding on the ground during months of resource scarcity. Furthermore, while southern

bamboo lemurs exhibited an average DPL of 903.91 ± 373.05 m, they displayed some

monthly variation, with the longest DPL equaling 2,224.34 m in February and the shortest

DPL equaling 277.15 m in May (Fig. 2).

Proximate and ultimate determinants of terrestrial feeding

To determine which factors best predicted a greater daily proportion of terrestrial

feeding, we used a linear mixed model (LMM). The best-fit model included significant

values for nutritional proxies (metabolizable energy alone and as an interaction with protein-

to-fiber ratio), DPL, and the climatic influence of temperature (AIC = -7.604, χ^2 = 11.435, *df*

= 1, *P* < 0.001; Table 4). In particular, food items consumed on the ground contained more

metabolizable energy (ME), which was positively related to terrestrial feeding time (Fig. 3a).

Furthermore, DPL was shorter on days with increased terrestrial feeding, resulting in longer

DPLs when bamboo lemurs spent more time arboreally feeding (Fig. 3b). Additionally, daily

terrestrial feeding increased on days with low temperatures (Fig. 3c). The only interaction

that was included in the best-fit model, PF * ME, indicated that for every 0.1 kcal g^{-1} that

terrestrial ME is greater than arboreal ME when there was no difference in PF, *H. meridionalis* spent 2.3 - 5.6% more time feeding on the ground that day. Thus, in terms of the significant interaction of PF * ME, for every percent dry matter increase in the difference of PF ratio, the slope of ME increased by 2.04 kcal g^{-1}. Resource seasonality, daily precipitation, along with the focal individual's proximity to nearest neighbor, canopy exposure, and protein-fiber ratio (PF) intake were not significant predictors of daily increases in terrestrial feeding.

Discussion

Our data show that the daily proportion of terrestrial feeding increased when the temperature decreased. Though these colder temperatures were often within the austral winter, the corresponding resource seasonality was shown to not significantly predict increased terrestrial feeding. While fallen fruits were occasionally fed on from a terrestrial position, the majority of the southern bamboo lemur diet in this stratum consisted of non-bamboo grasses and Cyperaceae pith. In fact, southern bamboo lemurs were not observed to feed on any tree species' leaves; rather, they were only seen consuming the leaves of grasses, liana leaves, and other terrestrial ground cover (such as Asiatic pennywort *Centella asiatica*, Apiaceae). Within each group, young liana stems and their leaves (mostly from *Baroniella camptocarpoides* and *Secamone* sp.) constituted a large portion of their diet, yet were only distributed throughout the littoral forest of Mandena. On the other hand, terrestrial grasses such as *Panicum parvifolium* and *Stenotaphrum dimidiatum* were distributed across both the littoral forest and the swamps. The ubiquity of grasses and reeds in Mandena would appear to provide folivorous primates with an excellent opportunity to expand their dietary niche within this fragmented and degraded littoral landscape.

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Gelada baboons (*Theropithecus gelada*) are often regarded as the only graminivorous (i.e., grass-eating) primate and as such, an excellent model for early primates in savannah-type ecosystems (Dunbar, 1983; Dunbar and Bose, 1991; Fashing et al., 2014). As previous studies and our results showed, *H. meridionalis* exploit a similar niche in which they focus their dietary efforts on graminoids (Eppley and Donati, 2009; Eppley et al., 2011, 2015c). Gelada baboons are large-bodied, large social group monkeys that inhabit high-altitude grasslands with practically no forest cover whereas bamboo lemurs are considerably smaller-bodied, family unit-living primates. While no extant predators (other than humans) remain in the environments where geladas live (Gippoliti and Hunter, 2008), various predators exist for bamboo lemurs, therefore the risks imposed on these two species are wholly disparate. Thus, it would appear that the bamboo lemurs in Mandena provide a suitable model with which to examine the benefits of terrestriality in a forest environment, adding complexity to the evolutionary scenarios of primate terrestriality.

Nutritional pay-off

As we predicted, the nutritional quality of bamboo lemur daily intake increased with terrestrial feeding, an interesting finding considering that 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). Our results showed that metabolizable energy increased while feeding in the terrestrial stratum increased, whereas protein-fiber ratio was not significantly predictive. Furthermore, the positive relationship between ME and terrestrial feeding became stronger when the proportional difference between terrestrial and arboreal feeding became larger. This is the opposite for PF ratio, in that despite the general mean difference of food item values between these strata, its relationship with terrestrial feeding actually becomes weaker as the proportional difference

between daily feeding in the terrestrial and arboreal strata becomes larger. 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 southern bamboo lemurs of Mandena display a dietary breadth beyond what has been previously recorded for any *Hapalemur* spp. (Table 5). Furthermore, their ability to include such a wide variety of fruits (34 spp.) in their dietary niche is exceptional for a folivorous species, which in fact was more than the total number of food species consumed 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 (Eppley, unpublished data). The low frequency of terrestrially consumed food species observed in February (Fig. 1) is potentially due to the increased rainfall during that month, which increased water depth in the swamp areas by approximately two meters and inhibited our ability to follow the animals there (Eppley et al., 2015a), thus biasing our full-day focal observations to days spent in relatively drier areas. Whether or not conspecifics of *H. meridionalis* in larger continuous forests select for a more specialized diet, these data suggest that based on this fragmented population the species should be considered feeding generalists.

The challenge of meeting energy requirements is faced by many primates (for examples and reviews see e.g., Vogel et al., 2012; Irwin et al., 2014), 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). For example, mineral concentrations such as sodium in plants are often associated with primates coming to the ground (Izawa, 1993; Campbell et al., 2005; Link et al., 2011), thus primates likely only consume the

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minimum amount necessary to meet their needs (Rode et al., 2003). The large proportion of time spent feeding on the ground by *Hapalemur* in our study seems unlikely to be in response to reduced mineral concentrations, however, especially since the daily PF ratio and ME from terrestrial food items were of greater value compared to arboreal items. The location of our study, however, is an intricate matrix of upland littoral forest and swamps (Eppley et al., 2015a), 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.

Snub-nosed monkeys (*Rhinopithecus* spp.) exhibit 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). Unlike these other primates, terrestrial feeding by *H. meridionalis* occurred year-round and was not seasonally determined by resource lean periods. Furthermore, they largely grazed in swamp areas of densely distributed grasses and reeds, which would presumably result in closer neighbor proximities. Our results, however, do not support this.

Considering other folivorous primates, black and white colobus monkeys (*Colobus guereza*) from Kibale National Park in Uganda were shown to increase their daily path length as foods became less abundant (Harris et al., 2010). This is similar to the frugivorous white-bellied spider monkeys (*Ateles belzebuth belzebuth*), a species observed to travel greater distances in the wet season (Nunes, 1995), displaying longer daily paths when feeding trees are further apart from one another (Suarez 2006). While our only seasonal and/or climatic factor shown to influence terrestrial feeding was colder temperatures, daily path length

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similarly decreased as terrestrial feeding increased. This is likely due to the clumped, yet ubiquitous, distribution of graminoids throughout the Mandena littoral forest and swamp, allowing the lemurs to graze for longer periods of time in one area rather than spend time traveling between scattered food resources.

Predation risk

Predation pressure by arboreal and terrestrial species likely occurs at a similar rate (Shattuck and Williams, 2010), and 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 pattern (Eppley et al., 2015b), 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). According to our model, canopy exposure did not influence increased terrestrial feeding. Furthermore, these lemurs often traveled between the littoral forest and swamp habitats, which required terrestrial travel to cross the open gaps (Eppley et al., 2015a), potentially increasing their risk from both aerial and terrestrial predators. This does not mean that *H. meridionalis* were without regard to their surroundings, they still maintained vigilance and alarm-called if they noticed a potential aerial or terrestrial threat. Examples include alarming and descending from the canopy when seeing an aerial raptor (e.g., *Accipiter henstii*, *Buteo brachypterus*, and *Polyboroides radiatus*), alarm-barking and ascending trees when encountering snakes (e.g., *Acrantophis dumerili* and *Leioheterodon madagascariensis*), and even alarm-barking and fleeing when encountering Eupleridae carnivores (e.g., *Galidia elegans*). Also during the study period, two feral dogs (*Canis familiaris*) were observed within Mandena and on three occasions we witnessed encounters whereby they chased grazing bamboo lemurs, forcing the group to ascend trees for protection

(TME, personal observations). 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 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). While some arboreal species may experience increased predation pressure when shifting to a terrestrial niche (Newell, 1998, 1999), terrestrial behavior by more ecologically flexible species may better facilitate movement and potential dispersal throughout a landscape, lessening the impacts of genetic erosion and habitat fragmentation (Pahl et al., 1988; Laurance, 1990; Ancrenaz et al., 2014). One confirmed successful act of predation was recorded among our groups of bamboo lemurs, using radio telemetry we discovered a male Dumeril's boa (*Acrantophis dumerili*) had preyed on an adult female *H. meridionalis* from group 1. The large terrestrial boa was located in a vast swamp area where the bamboo lemurs often feed terrestrially, thus it is likely that she was captured while on the ground (Eppley and Ravelomanantsoa, 2015).

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 (Fleagle, 2013), allowing them to extend their niche to the terrestrial stratum. Similarly, 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

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behavior are often associated with disturbed habitats whereby animals traverse open areas

between forest fragments, potentially increasing their exposure to predators (Takemoto,

2004). Unlike southern bamboo lemurs, which readily descended to the ground without

hesitation or prolonged vigilance, spider monkeys appear very nervous when terrestrial,

continually scanning the area and taking long periods of time before fully descending

(Campbell et al., 2005), in addition to maintaining closer nearest neighbor proximities when

exposed (DiFiore, 2002). In fact, a multi-site analysis found that in sites with more intact

predator communities (i.e., greater perceived risk of predation), spider monkeys only

occasionally ($\leq$ 5% of sampling) fed on the ground when nutritional returns were high

(Campbell et al., 2005). In contrast, spider monkey terrestriality occurred more frequently

where predator populations were less intact, and included social behaviors and traversing

gaps in forest cover (Campbell et al., 2005).

Additional costs

The utilization of a terrestrial dietary niche likely imposes additional costs on bamboo

lemurs. The gastrointestinal tract of *Hapalemur* spp. certainly assists in their elevated ability

to digest fiber, 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 to 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; Cuozzo and Yamashita, 2007; Yamashita et al.,

2009; Kaiser et al., 2013), 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). In collared brown lemurs, endo-parasite prevalence has been shown to be higher in the degraded area of Mandena compared to more intact fragments of littoral forest (Lazdane et al. 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., 2016).

Conclusion

Considered in whole, our results suggest that the initial expansion to a terrestrial dietary niche may have occurred when the nutritional pay-off was greater in the new strata and predation risk was similar (or less) compared to the original arboreal stratum. While terrestrial feeding was not due to seasonal resource availability, there was a proximate climatic influence of temperature as well as a decreased daily path length. Furthermore, perceived predation risk (as shown through canopy exposure and nearest neighbor proximity) did not influence terrestrial feeding. Our data present strong evidence for the ability of this species to subsist in anthropogenically-disturbed environments, demonstrating that they may be more flexible than some of their congeners (e.g., *H. alaotrensis*, *H. aureus*). 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 primary 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; Fausser et al., 2002). In the absence of these foods, *H. meridionalis* in Mandena appear to have greatly expanded their dietary diversity while utilizing a terrestrial feeding niche, where food items represented a greater dietary quality.

Acknowledgements

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Figure Legends

Fig. 1. Monthly proportion of terrestrial feeding (box plots indicate medians, inter-quartiles and ranges) and monthly total of food species consumed terrestrially by *H. meridionalis* in Mandena between Jan. – Dec., 2013.

Fig. 2. Box plots of the medians, inter-quartiles, and ranges of daily path length traveled monthly by *H. meridionalis* in Mandena between Jan. – Dec., 2012.

Fig. 3. Scatter plot (with trend line and variance) showing the relationship between the daily proportion of terrestrial feeding by *H. meridionalis* and (a) ME (kcal g^{-1}) intake, (b) daily path length, and (c) mean temperature.