Seasonal ecology of ring-tailed lemurs: a comparison of spiny and gallery forest habitats

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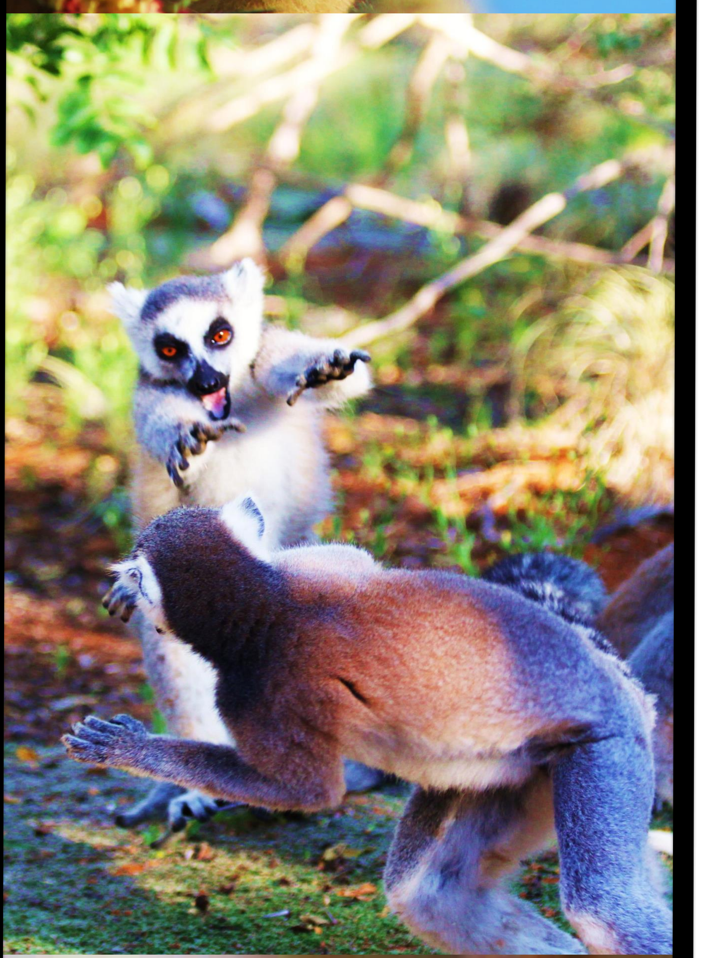


Introduction

Ring-tailed lemurs are a remarkably flexible edge or weed species (Sussman, 1977; Gould et al., 1999; Sauther et al., 1999) that persist in a variety of habitats in southwestern Madagascar including: spiny and xerophytic forests, gallery and deciduous forests, anthropogenically induced savanna, scrub and brush land, and the mesic high altitude forests of the Andringitra mountain range (see Goodman et al., 2006). Each of these habitat types likely present unique challenges in terms of finding food, water and shelter, yet to date, we know little about how these proximate variables affect ring-tailed lemur behavior, nutrition, and ultimately fitness (see Gould, 2006). In two different forest types (spiny and gallery), we examined feeding behavior of ring-tailed lemurs and the nutritional content of their plant foods in order to examine differences between: plant food species and plant part consumed, and intake of macronutrients (crude protein, soluble carbohydrates) and fiber (acid-detergent).

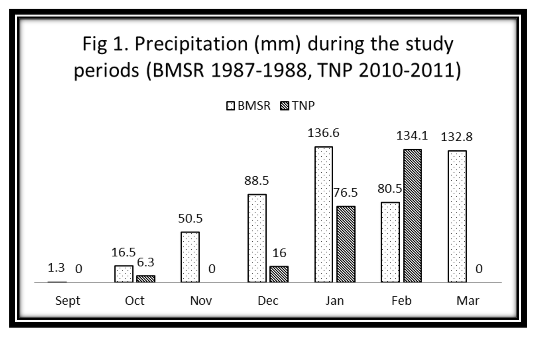
Methods

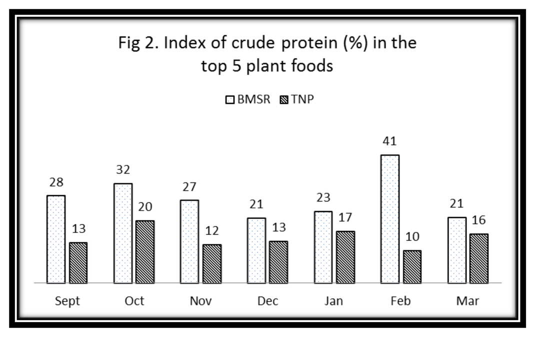
Study sites: TNP and BMSR are both on the Mahafaly Plateau of southwestern Madagascar and are separated by a distance of approximately 135km. Both sites are highly seasonal with the vast majority of rainfall occurring between November and April. **BSMR (23.67°S, 44.60°E).** Data were collected in the riverine forests of parcel one during 1987-1988 (MS). This region has an average annual rainfall of 470mm (Ratsirarson and Richard, 2010). The dry season dramatically reduces food availability, however, this habitat is dominated by *Tamarindus indica* trees (e.g. Sussman and Rakotozafy, 1994), which are a particularly important resource for these ring-tailed lemurs as the trees produce leaves, flowers and fruits year-round and asynchronously (Sauther et al., 1999; Yamashita, 2002, 2008). **TNP (24.09°S, 43.83°E).** Data were collected in the dry spiny dwarf forests during 2010-2011 (ML). Annual rainfall is usually under 300mm and the dry season may be longer than that of BMSR. Tamarind trees are present at TNP, but at a low density, and the ring-tailed lemurs do not appear use tamarind resources to the same extent they do in other gallery forest habitats.

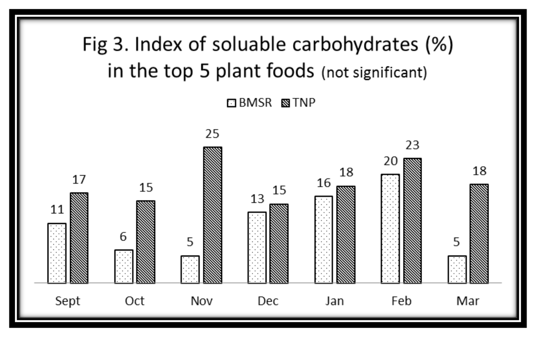
Study species: ***Lemur catta*** are a semi-terrestrial, group-living species with strict female dominance (Jolly, 1966). They have restricted seasonal reproduction with an annual mating period in April or May, depending on locality. Infants are born from late September to early October, and reproductive females lactate during the later portion of the dry season and well into the wet season. Ring-tailed lemurs are opportunistic folivore/frugivores (Sauther, 1994). Behavioral data collection: Scan sampling data (Altmann, 1974) were collected at 5-minute intervals for all visible adult animals in the focal group. When individual lemurs were feeding, the plant species and part were noted. Plant food data: Representative plant foods were collected and dried in the shade, before being transported to the Department of Animal Ecology and Conservation at Hamburg University in Germany. Chemical analyses included: crude protein (nitrogen x 6.25, Kjeldahl method), soluble carbohydrates (equivalent of galactose after acid hydrolization of 50% of the methanol extract), and acid detergent fiber (modified "Ankom fiber analyser"). Abiotic data: Millimeters of rainfall were measured daily at BMSR and TNP. Data analyses: We compared the most frequently consumed plants and plant parts at each study site for each month of both studies. Of the top five most frequently consumed plant foods per month at each site, we created index of each nutritional component measured using the following formula: Protein index = $\sum_{\text{foods 1-5}}$ (% of top five foods consumed * % of protein in food). We then used the Student's T-Test to detect variation within the number of times a plant part (i.e. leaf, flower, fruit) was selected by focal animals, and the monthly index values for nutritional components of the plant foods. ADF content was not obtained for *T. indica* fruits because of methodological problems with the sample. In order to account for the fiber content present in tamarind fruits we carried out calculations using the following substitute values for ADF content: 0% (no ADF present), 7.6% (Gould et al. 2011). The literature value of 7.6% ADF content for tamarind fruit pulp is likely closest to the actual value, while substituting 0% ADF likely under-estimates the fiber content.

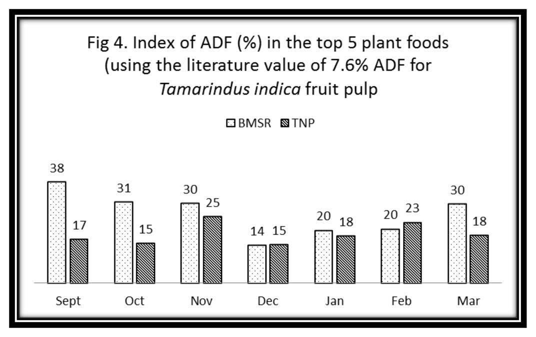
Results

BMSR received about twice the precipitation of TNP during the study periods (BMSR= 506.7mm, TNP= 232.9mm) (Figure 1). Moreover, although BMSR received at least some precipitation in every month of data collection (n=7), TNP did not (n=4). Of the top five foods consumed by ring-tailed lemurs in spiny and gallery forests only *Gyrocarpus americanus* (Kotipoke) was common to both. We found no significant site-specific differences in the type of plant part consumed per month (flower t=1.99, df=12, p=0.069; fruit t=2.013, df=12 p=0.067; leaf t=0.445, df=12, p=0.664). During each month of the study period, the BSMR lemur's plant food protein index was significantly higher than the TNP lemurs (t=4.434, df=12, p=0.001) (Figure 2). Although the BMSR lemurs' plant food index of soluble carbohydrates was lower than the TNP lemurs in each month of the study, these differences were not significant (t=-1.235, df=12, p=0.241) (Figure 3). There was no significant difference found between the BMSR and TNP lemur plant foods ADF content when the fiber content of tamarind fruits were not accounted for (t=1.76, df=12, p=0.110). However, when using the literature value of 7.6% ADF for *T. indica* fruit pulp (Gould et al., 2011) we find that the BMSR lemurs foods contain significantly more fiber when compared to the TNP lemurs foods (t=2.198, df=12, p=0.048) (Figure 4).









Discussion

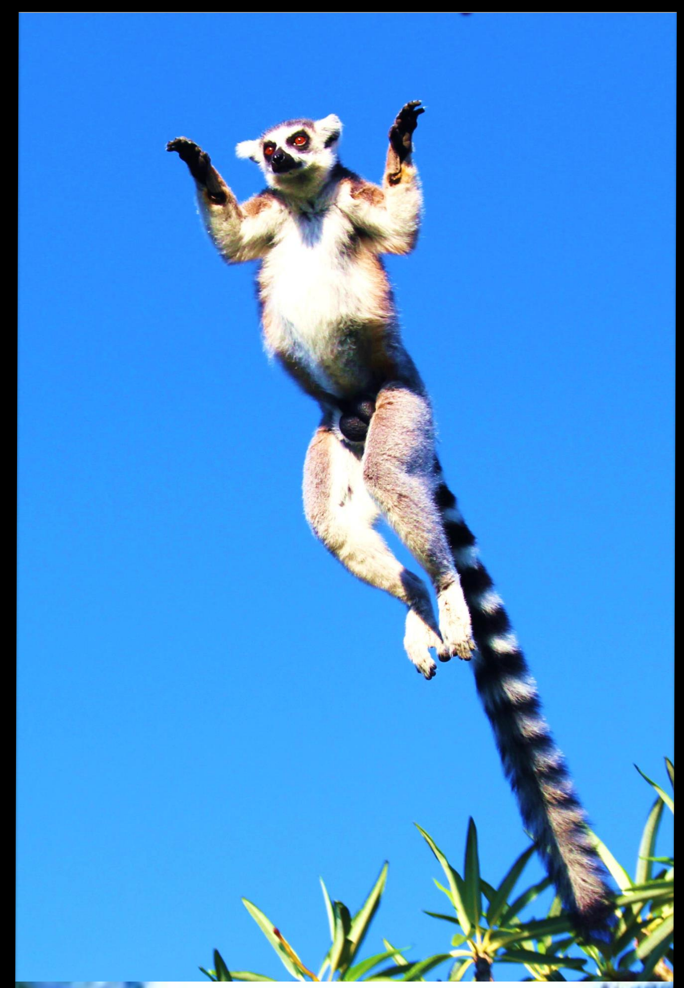
The behavioral ecology of ring-tailed lemurs has been largely typified by data from gallery forest habitats. However, this species persists in a suite of habitat types and is able to adjust to significant environmental perturbations. Comparative data from non-gallery forest habitats are important for understanding the proximate and ultimate causes of plasticity in ring-tailed lemurs.

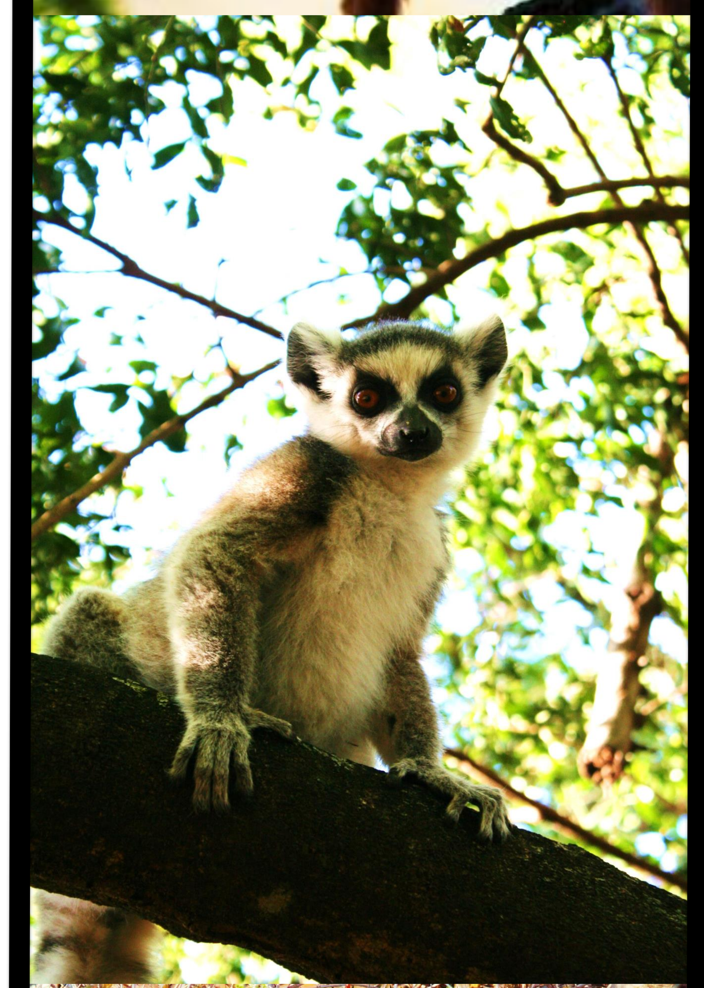
Our results suggest that gallery forest ring-tailed lemurs foods are much higher in crude protein, in part because tamarind trees 1) provide a near steady supply of proteinaceous foods (leaf buds = 64% crude protein, the highest concentration of any measured plant) and because 2) tamarind trees occur in high densities in riverine forests. Conversely, lack of protein-dense foods may be a function of reduced rainfall in spiny forest habitats and comparably low densities of tamarind trees. The most protein dense plants measured from TNP were *Gyrocarpus americanus* (Kotipoke) flowers (crude protein TNP= 28%), which have significantly less protein than most protein dense food from BMSR (64%).

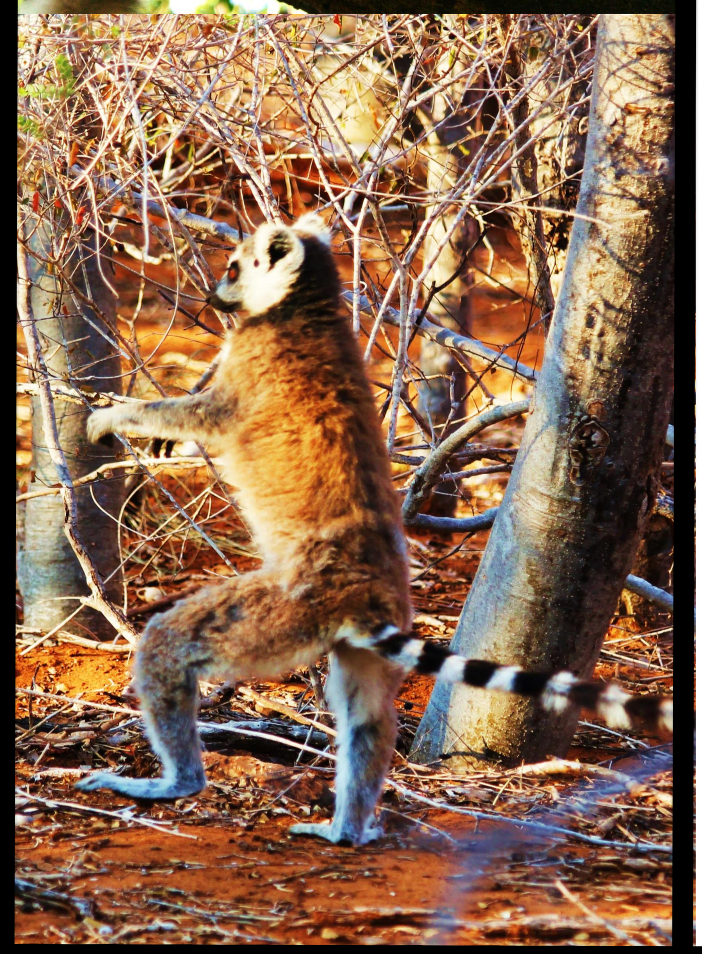
Our results also indicate that gallery forest ring-tailed lemurs foods are higher in ADF. Again, this dietary disparity is likely due to the inclusion of tamarind foods in the BMSR lemurs' foods. Tamarind leaf buds were a top food every month for the BMSR lemurs and these leaves contained the highest measured ADF content (51%). The most ADF dense foods at TNP were the fruits of *Ficus marmorata* (44%), but these compose a relatively small component of the diet (6% October, 6% November). High fiber levels can interfere with nutrient uptake, including protein absorption (Ullrey et al., 2003: Campbell et al., 2000), however, these relationships are not well understood and can vary even between closely related species (see Sponheimer et al., 2003).

Data presented here were collected during the annual time period when female ring-tailed lemurs are lactating, an energetically demanding physiological process. Protein is thought to be a particularly important macronutrient during gestation and lactation, because it provides the nitrogenous building blocks which are essential for DNA replication, body growth and maintenance, and regulation of bodily functions (Ullrey et al., 2003).

Although the vast majority of our knowledge on ring-tailed lemur ecology comes from gallery forest sites, comparative data from the other habitats where these animals persist are important for understanding their ecological flexibility and the limits of their tolerance. Here, we demonstrate that habitat can affect certain macronutrients and fiber content in the plant foods of ring-tailed lemurs. It is possible that the BMSR ring-tailed lemurs benefit from a fitness advantage given the relatively elevated protein content of consumed plant foods, however this needs to be explored further alongside data the effects of fiber intake, and how these influence infant survivorship and subsequent reproduction.







Literature Cited: **Altmann J**. 1974. Observational study of behavior: Sampling methods. Behaviour 49:227-267. **Campbell JL, Eisemann JH, Williams CV, Glenn KM**. 2000. Description of the gastrointestinal tract of five lemur species: *Propithecus tattersalli*, *Propithecus verreauxi coquereli*, *Varecia variegata*, *Hapalemur griseus*, and *Lemur catta*. American Journal of Primatology 52(3):133-142. **Goodman SM, Rakotoarisoa SV, Wilm L**. 2006. The distribution and biogeography of the Ringtailed Lemur (*Lemur catta*). In: Ring-Tailed Lemur Biology. Jolly A, Koyama N, Rasamimanana H, and Sussman RW, eds. New York: Springer. p. 3–15. **Gould L**. 2006. Lemur catta Ecology: What we know and what we need to know. In: Lemurs: Ecology and Evolution. Gould L, Sauther M, eds. Springer: New York. p 257-276. **Gould L, Sussman R, and Sauther M**. 1999. Natural disasters and primate populations: The effects of a 2-year drought on a naturally occurring population of ring-tailed lemurs (*Lemur catta*) in Southwestern Madagascar. International Journal of Primatology 20:69-84. **Jolly A**. 1966. Lemur behaviour: a Madagascar field study. Chicago: University of Chicago Press. **Sauther ML**. 1994. Wild plant use by pregnant and lactating ring-tailed lemurs, with implications for early hominid foraging. In: Eating on the Wild Side. Etkin NL, ed. Tucson: University of Arizona Press. p 240–256. **Sauther ML, Sussman RW, Gould L**. 1999. The socioecology of the ring-tailed lemur: Thirty-five years of research. Evolutionary Anthropology 8(4):120-132. **Sponheimer M, Robinson T, Ayliffe L, Passey B, Roeder B, Shipley L, Lopez E, Cerling T, Dearing D, Ehleringer J**. 2003. An experimental study of carbon-isotope fractionation between diet, hair, and feces of mammalian herbivores. Canadian Journal of Zoology81(5):871-876. **Sussman RW**. 1977. Distribution of the Malagasy lemurs, part 2: *Lemur catta* and *Lemur fulvus* in southern and western Madagascar. Annals of the New York Academy of Science 293:170-184. **Sussman RW, Rakotozafy A**. 1994. Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. Biotropica 26:241–254. **Ullrey D, Allen M, Ausman L, Conklin-Brittain N, Edwards M, Erwin J, Holick M, Hopkins D, Lewis S, Lonnerdal B, Rudel L. 2003**. Nutritional requirements of non-human primates, second revised edition. National Research Council: Committee on animal nutrition. The National Academic Press, Washington, D.C., USA. **Yamashita N**. 2002. Diets of two sympatric lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar. International Journal of Primatology 23:1025–1051. **Yamashita N**. 2008. Chemical properties of the diets of two lemur species in southwestern Madagascar. International Journal of Primatology 29(2):339-364.

Acknowledgements

Funding: (ML) National Science Foundation Doctoral Dissertation Improvement Grant, Natural Science and Engineering Research Council Post Graduate Scholarship, National Geographic Research and Exploration Grant, American Society of Primatologists Small Research Grant; (MS) National Science Foundation, Fulbright, Leakey, Sigma Xi, Boise Fund, National Geographic Society. We also thank the government of Madagascar, University of Toliara, University of Antananarivo, and the lemurs.

THE BEZA MAHAFALY LEMUR BIOLOGY PROJECT