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Seasonal Feeding Ecology of Ring-Tailed Lemurs: A Comparison of Spiny and Gallery Forest Habitats

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Key Words
Madagascar · Plant foods · Habitat types · Bezà Mahafaly Special Reserve · Tsimanampesotse National Park · Macronutrients · Plant chemistry

Abstract

Although *Lemur catta* persists in many habitat types in southern Madagascar, its ecology has been primarily studied within gallery forests. We compare plant food selection and properties for ring-tailed lemurs in the spiny and gallery forests over the synchronized lactation period (September to March) that includes both the dry and wet seasons. We found no significant habitat-specific differences in the type of plant part consumed per month (i.e. flower, fruit, leaf) or between the intake of soluble carbohydrates. However, the presence and use of *Tamarindus indica* plants appear to elevate protein and fiber intake in the gallery forest lemurs' diets. Protein is especially important for reproductive females who incur the added metabolic costs associated with lactation; however, fiber can disrupt protein digestion. Future work should continue to investigate how variations of protein and fiber affect ring-tailed lemur dietary choice and nutrient acquisition.

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Introduction

Lemur catta (the ring-tailed lemur) is a remarkably flexible edge or weed species [Sussman, 1977; Gould et al., 1999; Sauther et al., 1999] that persists in a variety of habitats in southwestern Madagascar including spiny and xerophytic forests, gallery and deciduous forests, anthropogenically induced savanna, scrub and brush land, rocky outcrop vegetation, and the mesic high-altitude forests of the Andringitra mountain range [Goodman et al., 2006]. Each of these habitat types likely presents

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unique challenges in terms of finding food, water and shelter. Given that a few studies have now focused on ring-tailed lemur's ecology in non-gallery-forest habitats [Gould et al., 2011; Kelley, 2013; Gabriel, 2013], it is now possible to compare across habitats to better understand how proximate variables affect ring-tailed lemur behavior, nutrition and, ultimately, fitness [Gould, 2006].

Ring-tailed lemurs are opportunistic frugivores/folivores, and although they consume varied and diverse plant-based foods throughout the year, their diet at a given time tends to be dominated by a few species [Sauther, 1994, 1998]. Forests in southern Madagascar are extremely seasonal, and animals must cope with a long dry season, wherein food resources are scarce. Female ring-tailed lemurs are in the late gestation and early lactation periods in the dry season, and thus have the added metabolic burden of reproduction when food resources are already low [Jolly, 1984; Sauther, 1994, 1998].

In two different forest types (spiny and gallery), we examined the feeding behavior of ring-tailed lemurs and the nutritional content of their plant foods to understand relationships between habitat type and (1) plant food species and plant part consumed, and (2) plant content of macronutrients (crude protein, soluble carbohydrates) and fiber (acid-detergent fiber, ADF). We predicted that gallery forest lemurs would have access to higher-quality plant foods including young leaves, fruits and flowers, and that both plant parts and the overall nutritional content of their plant foods would be higher in soluble carbohydrates and crude protein, but lower in ADF. We made these predictions knowing that when compared to spiny forests, gallery forests have higher precipitation (and related net primary productivity), and support higher densities of lemurs [see Kelley, 2013, and references therein], which suggests a better-quality resource base.

Methods

Study Sites

The Tsimanampesotse National Park, TNP (24.09° S, 43.83° E; 5 km inland from the Mozambique Channel) and Bezà Mahafaly Special Reserve, BMSR (23.67° S, 44.60° E; 140 km inland from the Mozambique Channel) are both on the Mahafaly Plateau of southwestern Madagascar. Both sites are highly seasonal with the vast majority of rainfall occurring between November and April. In this paper, we compare data collected between September and March.

Tsimanampesotse National Park. Data were collected between 2010 and 2011 in the dry spiny dwarf forests that do not have canopy cover (M.L.). Annual rainfall is usually under 300 mm, and the dry season may be longer than that of the BMSR [Donque, 1975]. The following plant families are most common at TNP: Euphorbiaceae, Didiereaceae, Bombacaceae and Fabaceae. Tamarind trees are present at TNP, but at a low density, and the ring-tailed lemurs do not use tamarind resources to the same extent as they do in gallery forest habitats as the trees are not asynchronous and thus only provide fruits or leaves during discrete periods at TNP [LaFleur, 2012].

Bezà Mahafaly Special Reserve. Data were collected in the riverine forests of Parcel 1 during 1987–1988 (M.L.S.). This region has an average annual rainfall of 470 mm [Ratsirarson and Richard, 2010]. BMSR habitats contain high, closed canopy forest, which abuts the ephemeral Sakamena River, and are dominated by Fabaceae (particularly *Tamarindus indica*) as well as trees from the families Meliaceae, Salvadoraceae and Rubiaceae. The dry season dramatically reduces food availability [Sauther, 1998; Yamashita, 2002; Whitelaw, 2010]. This habitat is dominated by *T. indica* which is 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; Sauther and Cuozzo, 2009].

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Study Species

Lemur catta is a semiterrestrial, group-living species with strict female dominance [Jolly, 1966]. It exhibits restricted seasonal reproduction with an annual mating period in April or May, depending on locality. Infants are born from late September through early October, and reproductive females lactate during the later portion of the dry season and well into the wet season [Sauther et al., 1999].

Behavioral Data Collection

Diurnal scan sampling data [Altmann, 1974] were collected at 5-min intervals for all visible adult animals in the focal group. At BMSR, all focal animals (n = 16 from 2 groups) had existing nylon collars with unique tags [see Sussman et al., 2012]. At TNP, 6 ring-tailed lemurs from 3 distinct social groups were captured and fitted with radio tracking collars (MOD-080 transmitter configuration, Telonics Inc.) [for protocol, see Sauther and Cuozzo, 2008]. In total, the TNP adult focal animals ranged between 19 and 22 individuals from 2 groups (M.L. was unable to habituate the third group).

Plant Food Data

When individual lemurs were feeding, the plant species and part were noted. Representative plant foods were collected and dried in the shade (TNP) or in a Coleman camp oven (BMSR), before being transported to the Department of Animal Ecology and Conservation at Hamburg University in Germany for chemical analyses. Assays of each plant include analyses of crude protein, soluble carbohydrates and ADF (analytical procedures as per those outlined by Ganzhorn [1988]).

Abiotic Data

We measured the millimeters of rainfall daily at BMSR (September to March 1987–1988) and TNP (September to March 2010–2011).

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 5 most frequently consumed plant foods per month at each site, we created an index of each nutritional component measured using the following formula:

nutritional content index = $\Sigma_{\text{foods 1–5}}$ (percent of top 5 foods consumed · percent of content in food).

We used a 1-way ANOVA to detect significant differences between the two habitats with regard to the proportions of plant parts (i.e. leaf, flower, fruit) selected by focal animals, the nutritional content for plant parts (leaves, flowers, fruits) and the overall nutritional content (crude protein, soluble carbohydrates) or fiber indices of the plant foods. ADF content was not obtained for *T. indica* fruits because of methodological problems with the samples. In order to account for the fiber content present in tamarind fruits, we carried out calculations using the literature value of 7.6% [Gould et al., 2011]. For all tests, significance was set at the $\alpha \leq 0.05$ level using a 2-tailed distribution with values approaching $p = 0.05$ (e.g. $p = 0.051$) being rounded down [Weiss, 2011].

Results

The BMSR received about twice the amount of precipitation of TNP during the study periods (BMSR = 506.7 mm, TNP = 232.9 mm; fig. 1). Moreover, the BMSR received at least some precipitation in 7 of the 8 months studied, while the TNP only received rain in 4 of the 8 months.

We compared approximately 10,000 scan sample scores at each field site between the months of September and March. All plant foods consumed by the ring-tailed lemurs were noted, and the 5 most frequently consumed foods per month are compared here. Comparison of gallery (BMSR) and spiny (TNP) forest ring-tailed lemur plant

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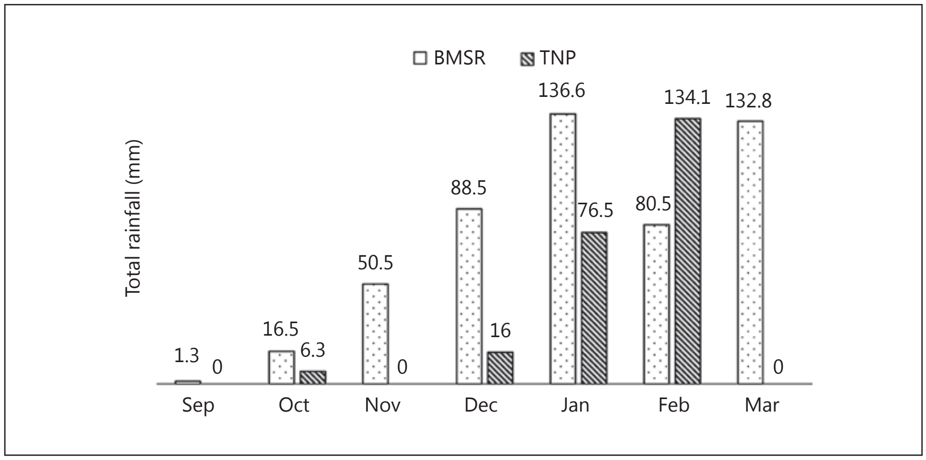

Fig. 1. Precipitation during the study periods (BMSR 1987–1988, TNP 2010–2011).

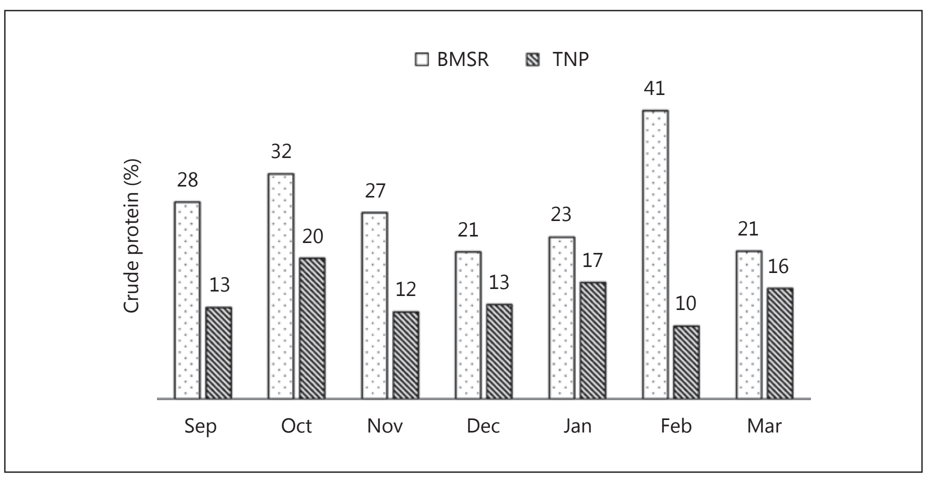

Fig. 2. Index of crude protein in the top 5 plant foods (see Methods for nutritional index formula).

food species, plant part, percentage of top 5 foods, plant nutritional properties (crude protein, carbohydrates and ADF) and the total percentage of the diet that the top 5 foods constitute for that month are presented in table 1. We found no significant site-specific differences in the type of plant part consumed per month (flower f = 3.998, $d.f._{total}$ = 13, p = 0.069; fruit f = 4.054, $d.f._{total}$ = 12, p = 0.067; leaf f = 0.198, $d.f._{total}$ = 12, p = 0.664). In addition, we found no site-specific differences in the nutrient value of plant parts used (protein f = 0.654, $d.f._{total}$ = 5, p = 0.659; carbohydrate f = 1.146, $d.f._{total}$ = 5, p = 0.345; ADF f = 0.960, $d.f._{total}$ = 5, p = 0.449). Of the top 5 foods consumed, at the species level only *Gyrocarpus americanus* was found in each habitat, and at the genus level, only *Talinella* was common to both the gallery and spiny forest (table 1).

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Table 1. Comparison of gallery (BMSR) and spiny (TNP) forest ring-tailed lemur plant food species, plant part, percentage of top 5 foods, plant nutritional properties (crude protein, carbohydrates and ADF) and the total percentage of the diet that the top 5 foods constitute for that month

Location/month	Plant species	Plant part	Percent top 5 foods	Protein, %	Carbo-hydrates, %	ADF, %
BMSR						
September	*Quisiavanthe papionae*	flowers	67	18.6	13.7	38.4
	Tamarindus indica	leaf buds	21	64.1	4.1	50.5
	Tamarindus indica	fruit	5	12.9	19.3	50.2
	Gyrocarpus americanus	flowers	4	46.9	7.1	17.0
(proportion of total diet = 90%)	*Salvadora angustifolia*	young leaves	3	5.1	4.2	26.9
October	*Salvadora angustifolia*	fruit	55	12.9	15.5	16.1
	Tamarindus indica	leaf buds	27	22.1	12.7	5.6
	Tamarindus indica	fruit	12	6.4	1.3	44.2
	Hildebrandtia sp.	young leaves	3	7.1	9.4	40.2
(proportion of total diet = 84%)	*Acalypha* sp.	young leaves	3	20.3	4.2	26.9
November	*Salvadora angustifolia*	fruit	78	64.1	4.1	50.2
	Tamarindus indica	leaf buds	9	12.9	19.3	50.5
	Hildebrandtia sp.	leaves	6	56.7	4.7	14.3
	Talinella dolphinensis	young leaves	4	17.0	4.9	31.7
(proportion of total diet = 89%)	*Tamarindus indica*	fruit	4	28.4	5.7	13.2
December	*Tamarindus indica*	fruit	51	8.8	12.3	6.8
	Hildebrandtia sp.	leaves	28	11.1	15.9	15.8
	Corralocarpus greveii	young leaves	8	6.4	1.3	44.2
	Gloriosa superba	leaves, stems	7	15.8	3.5	37.4
(proportion of total diet = 75%)	*Marsdenia* sp.	leaf buds	6	20.3	4.2	26.9
January	*Talinella dolphinensis*	fruit	51	64.1	4.1	50.2
	Antidesma petiolare	fruit	17	56.7	4.7	18.6
	Hildebrandtia sp.	young leaves	13	24.3	8.8	35.9
	Tamarindus indica	fruit	10	12.9	19.3	50.2
(proportion of total diet = 78%)	*Grewia clavata*	fruit	8	15.4	41.2	8.8
February	*Talinella dolphinensis*	fruit	41	6.4	1.3	44.2
	Grewia clavata	fruit	36	15.8	3.5	37.4
	Tamarindus indica	fruit	12	5.4	17.5	25.4
	Hildebrandtia sp.	leaves	6	15.8	3.5	37.4
(proportion of total diet = 81%)	*Marsdenia* sp.	young leaves	6	12.9	19.3	50.5
March	*Grewia leucophylla*	fruit	42	27.4	4.7	18.6
	Tamarindus indica	fruit	35	9.6	3.5	21.0
	Rhynchosia sp.	leaves	8	54.4	10.1	31.9
(proportion	*Hildebrandtia* sp.	young leaves	8	35.0	10.7	20.6
of total diet = 70%)	*Corralocarpus greveii*	young leaves	7	15.4	41.2	8.8

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Table 1 (continued)

Location/month	Plant species	Plant part	Percent top 5 foods	Protein, %	Carbo-hydrates, %	ADF, %
TNP						
September	*Neobeguea mahafaliensis*	flowers	94	5.4	17.5	25.4
	Neobeguea mahafaliensis	young leaves	3	17.3	0.0	6.0
	Ficus marmorata	fruit	2	15.8	3.5	37.4
(proportion of total diet = 100%)	*Diospyros manapetsae*	fruit	1	14.6	12.0	11.8
October	*Gyrocarpus americanus*	flowers	57	12.3	14.3	18.2
	Olax androyensis	fruit	15	37.8	22.2	31.7
	Neobeguea mahafaliensis	flowers	20	56.7	4.7	14.3
	Ficus marmorata	fruit	6	12.9	19.3	50.5
(proportion of total diet = 100%)	*Gyrocarpus americanus*	fruit aril	2	25.3	31.5	33.1
November	*Gyrocarpus americanus*	fruit aril	46	18.3	9.5	17.3
	Alluaudia comosa	flowers	26	10.8	8.2	33.4
	Ficus megapoda	fruit	13	26.9	21.1	9.5
	Ficus marmorata	fruit	8	8.1	14.0	15.9
(proportion of total diet = 90%)	*Gyrocarpus americanus*	young leaves	7	16.6	6.8	4.6
December	*Alluaudia comosa*	flowers	45	65.4	14.3	18.2
	Ficus megapoda	fruit	22	25.3	31.5	33.1
	rantsandaka[1]	flowers	18	12.9	19.3	50.5
	Gyrocarpus americanus	young leaves	9	27.4	4.7	18.6
(proportion (of total diet = 96%)	anago[1]	flowers	5	35.0	10.7	20.6
January	liana[2]	young leaves	30	5.4	17.5	25.4
	rantsandaka[1]	flowers	23	18.3	9.5	17.3
	Xerophita dasyliroides	flowers	21	24.8	4.2	17.8
	manolosasavy[1]	fruit	16	9.1	23.7	17.3
(proportion of total diet = 70%)	*Ximenia perrieri*	fruit	10	10.8	8.2	33.4
February	*Ficus megapoda*	fruit	59	20.8	8.8	51.3
	liana[2]	young leaves	14	12.9	19.3	50.5
	Poupartia minor	young leaves	13	39.9	8.9	37.4
	Adonsonia rubrostipa	flowers	9	56.7	4.7	14.3
(proportion of total diet = 95%)	rantsandaka[1]	flowers	5	9.6	4.3	22.7
March	liana[2]	young leaves	39	18.3	9.5	17.3
	Tallinella grevei	fruit	26	16.6	8.3	20.8
	Neobeguea mahafaliensis	mature leaves	14	12.1	9.6	21.5
	Euphorbia stenoclada	stem	12	10.4	5.1	16.2
(proportion of total diet = 90%)	anago[1]	flowers	9	14.6	12.0	11.8

[1] Scientific name unknown. [2] Several similar species analyzed together.

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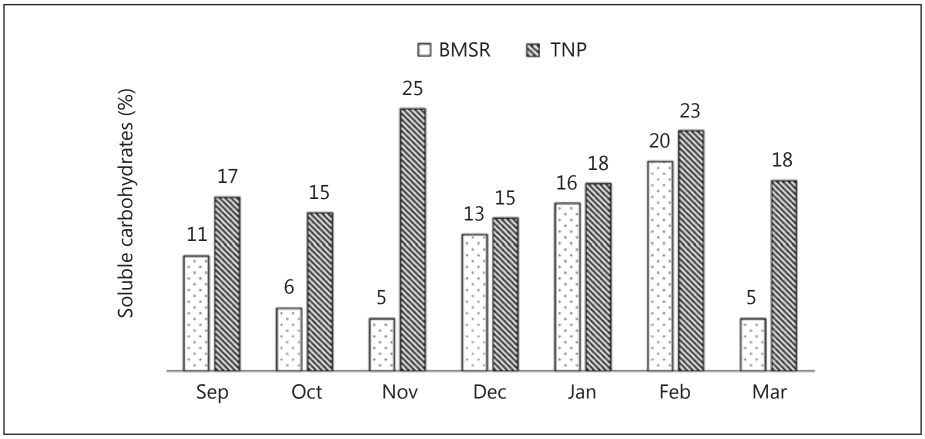

Fig. 3. Index of soluble carbohydrates in the top 5 plant foods (see Methods for nutritional index formula).

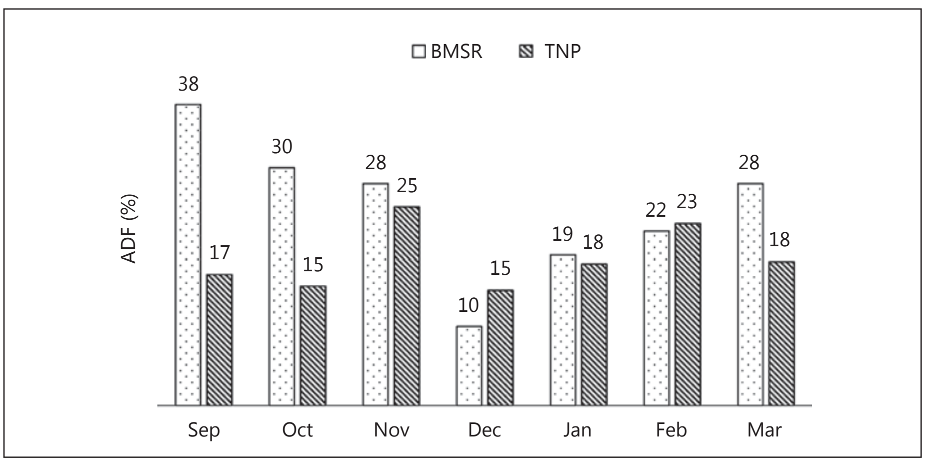

Fig. 4. Index of ADF in the top 5 plant foods (see Methods for nutritional index formula).

Across all months of the study period, the BMSR lemur plant foods' protein index was significantly higher than that of the TNP lemurs ($f = 22.330$, $d.f._{total} = 13$, $p \approx 0.00$; fig. 2). Although the BMSR lemur plant food index of soluble carbohydrates was lower than that of the TNP lemurs in each month of the study, these differences were not significant ($f = 0.409$, $d.f._{total} = 13$, $p = 0.534$; fig. 3). When using the literature value of 7.6% ADF for *T. indica* fruit pulp [Gould et al., 2011], we did find that the BMSR lemurs' foods contained significantly more fiber when compared to the TNP plant foods ($f = 4.686$, $d.f._{total} = 13$, $p = 0.051$; fig. 4). Of note, the very high content of fibrous food in the BMSR diets occurred in September and October, and are double (or more) than those of the TNP diet during those months (fig. 4).

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Discussion

The feeding ecology of the ring-tailed lemur has been largely typified by data from gallery forest habitats. However, this species persists in a suite of habitat types [Goodman et al., 2006] and is able to adjust to significant environmental perturbations [Gould et al., 1999; LaFleur and Gould, 2009]. Comparative feeding ecology data from non-gallery-forest habitats that are now emerging [Gould et al., 2011; LaFleur, 2012; Cameron and Gould, 2013; Gabriel, 2013; Kelley, 2013; LaFleur et al., 2014] are important for understanding the remarkable ecological flexibility of *L. catta*. Furthermore, given the rapid rates of land conversion and forest loss occurring in Madagascar [see Schwitzer et al., 2014], it is important that we understand variables that determine whether ring-tailed lemurs can persist over the long-term in highly disturbed or marginal habitats.

The gallery and spiny forest ring-tailed lemurs varied considerably regarding preferred plant species. Of the top 5 foods consumed at both sites, only one, *G. americanus*, was common to both. Nonetheless, we found no significant differences between the type of plant part selected (leaves, flowers, fruits). This is reminiscent of Sussman's [1987] 'species-specific' dietary pattern concept, where he posits that each primate species has particular dietary preferences due to their morphological and physiological traits, which then affect taste preference, food processing and digestion. As such, while particular plant species may be different, conspecifics will utilize similar numbers and proportions of particular food items. Such dietary flexibility indicates that ring-tailed lemurs may be able to persist in a wide range of habitat types because they are morphological and physiological generalists, and are able to exploit seasonally available resources regardless of the particular plant species present.

Although the plant parts consumed by gallery and spiny forest lemurs were similar, the top 5 foods emphasized by the BMSR gallery forest ring-tailed lemurs were significantly higher in crude protein and ADF (especially during the birth months of September and October; fig. 4), but not different in soluble carbohydrates, when compared to the top 5 food resources for the spiny forest lemurs, a pattern consistent across all months (fig. 2). Tamarind trees occur in high densities in riverine forests, and only rarely in spiny forest (such as where there is accessible underground water) [Sussman and Rakotozafy, 1994; LaFleur, 2012]. Moreover, because tamarind trees produce leaves and fruits asynchronously at BMSR, they provide a reliable fallback resource across normal, noncyclone years [Sauther and Cuozzo, 2009; LaFleur and Gould, 2009]. Indeed during every month of our study at BMSR, tamarind leaf buds or fruits were among the top 5 foods and provided between 5.4 (fruit) and 64.1% (leaf buds) crude protein (table 1). The increased ADF intake at BSMR was also likely primarily driven by the ingestion of tamarind fruits (50% ADF), young leaves (51% ADF) and to some extent flowers (table 1). Lastly, since the leaves and fruits of tamarind trees are not particularly high in carbohydrates (4 and 19%, respectively), the gallery forest lemurs did not have access to a higher sugar content by way of tamarind foods. In sum, during this research, the BMSR lemurs may have a nutritional tradeoff in that they accept high fiber values in order to access high protein levels from tamarind. Conversely, the overall lower protein density at TNP may be a function of low densities of tamarind trees, and/or low rainfall in spiny forest habitats [Donque, 1975]. However, the aforementioned claims need to be explored further, including how both of these factors influence infant survivorship and subsequent reproduction, and whether sex differences in diet are apparent.

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What then is the limit to ecological flexibility in *L. catta*? Ring-tailed lemurs are able to persist in highly degraded and fragmented areas and habitats where plant foods are of poor quality [e.g. Kelley, 2011; Gould and Gabriel, 2014]. They also live in the most arid habitats in Madagascar, where low precipitation limits forest primary productivity, and food resources are low in quantity. Ring-tailed lemurs are able to exploit seasonally available resources regardless of the particular plant species present, which indirectly implies that they are physiological and morphological generalists. They do however need some areas of refuge (e.g. trees, shrubs, caves), in addition to sufficient food resources, although they can cope with variations in macronutrient (crude protein) and fiber (ADF) content within their foods. Long-term viability of ring-tailed lemurs in extremely isolated or altered habitats is not yet known, but populations are likely to be more affected by genetic bottlenecks [Parga et al., 2012] and inability to disperse across discontinuous habitat than by diet, given their ability to exploit similar plant parts, yet persist on differing macronutrient contents.

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