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Beyond the Gallery Forest: Contrasting Habitat and Diet in *Lemur catta* Troops at Bezà Mahafaly Special Reserve

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Key Words
Ring-tailed lemurs · *Tamarindus indica* · Dry forest · *Propithecus verreauxi* · Sifaka

Abstract
Ring-tailed lemurs have been studied intensively in the Parcel 1 gallery forest of Bezà Mahafaly Special Reserve. Here, we report on lemur groups in a mixture of deciduous dry forest and spiny forest just 5 km to the west. Compared to Parcel 1, Parcel 2 (P2) has a lower density of *Tamarindus indica*, a major dietary plant species for gallery forest lemurs. Recent studies in drier habitats have called into question the association of lemur density and tamarind presence. In order to address this question, we measured forest structure and composition of plant plots between parcels and conducted lemur feeding observations. The trees and shrubs within the parcels did not differ in height or diameter at breast height, but the frequencies of plant species that were common between parcels were significantly different. Numbers of feeding observations on foods common to both parcels did not differ, but their relative rankings within parcels did. Frequencies of food plants corresponded to earlier reports of lemur population densities. However, we found that the ring-tailed lemur diet is a mixture of plants that are eaten in abundance regardless of frequency and those that are locally available. In terms of their reliance on *Tamarindus*, P2 animals appear intermediate between those in gallery forests and nontamarind sites.

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Introduction

The behavioral ecology of wild ring-tailed lemurs has been intensively studied in the gallery forests of Bezà Mahafaly Special Reserve (BMSR) and Berenty Private Reserve that are dominated by *Tamarindus indica* [Jolly, 1966; Sauther et al., 1999; Gould et al., 2003; Blumenfeld-Jones et al., 2006]. The tamarind fruits in these forests constitute the major food item annually for the lemurs, yet *Tamarindus* may be an exotic species to Madagascar, and reliance on its fruit may be of recent origin [Sauther and Cuozzo, 2009]. More recent surveys and field studies of populations from high altitudes to spiny desert scrub have broadened our understanding of what constitutes 'normal' conditions for ring-tailed lemurs [Goodman and Langrand, 1996; Gould et al., 2011; Kelley, 2013; LaFleur et al., 2014]. These sites typically have little to no tamarind trees, yet support sizable ring-tailed lemur populations. In this study, we contribute to studies on non-gallery-forest sites by comparing 2 adjacent ring-tailed lemur habitats at BMSR. Parcel 1 (P1) is the 80 ha deciduous tropical dry forest [Sussman and Rakotozafy, 1994] where the majority of research on lemurs at BMSR has taken place. Parcel 2 (P2) is a 520 ha plot located 5 km to the west of P1 and is composed of a patchwork of dry, deciduous forest and spiny forest [Axel and Maurer, 2010] (fig. 1).

In 2010, we began a comparative study of ring-tailed lemur diets in P1 and P2. While *Tamarindus* was an important lemur food plant in both BMSR parcels, the P1 animals ate the fruit year-round, while consumption in P2 occurred primarily in the dry season [Yamashita et al., 2012]. Because the P2 animals do not inhabit gallery forest and are not as dependent on *Tamarindus* fruit as the P1 lemurs, we wanted to (1) further investigate forest structure and composition between the two parcels, and (2) relate these findings to lemur diets and distribution. Specifically, we ask how diet is influenced by the structure and plant species composition of the local BMSR habitats. We are ultimately interested in exploring how determinants of diet contribute to habitat suitability for these lemurs.

Materials and Methods

Study Sites

The gallery forest on the eastern boundary of P1 lies along the seasonal Sakamena River, with the forest becoming progressively drier to the west [Sussman and Rakotozafy, 1994]. While P1 is surrounded by a fence, the area outside has been degraded by grazing livestock and human subsistence [Sussman et al., 2003; Youssouf Jacky, 2010].

The ring-tailed lemurs in P2 primarily inhabited the dry forest, though the troop also ranged to the top of a rocky escarpment to the west (160 m elevation; fig. 1). Their habitat in most directions was bounded by an abrupt transition of dry to spiny forest. The top of the escarpment, which is devoid of *Tamarindus*, represents a drier habitat with stands of *Alluaudia*, a characteristic spiny forest species. The habitat type on the escarpment is not found in P1.

BMSR experiences distinct wet and dry seasons. Generally, a warm, wet season occurs from November to March and a cooler, dry season from April to October. Rainfall amounts are highly variable among years [Lawler et al., 2009].

Plant Plots

In the P2 area, we measured forest composition in eleven 2 × 25 m plots that were approximately evenly spaced throughout the home range of our primary study group (total area = 0.35

Fig. 1. Parcels 1 and 2 in BMSR (terrain map modified from Google maps, map data copyright 2014 Google). The approximate location of P2 plant plots is outlined.

km^2). All trees, shrubs and new growth were identified in the plots, and the heights of all trees with a diameter at breast height (DBH) >2.5 cm were estimated. Phenology plots had previously been established throughout P1 (10 plots), but were 2 × 50 m [Sussman and Rakotozafy, 1994; Yamashita, 2002]. The P1 plots were placed approximately evenly throughout P1 (total area = 1 km^2). The closest plots between parcels were 3 km apart (fig. 1). Height and DBH of trees and shrubs were first averaged within each plot to obtain a single value for each of these variables. We then tested whether the plots within each parcel were independent (not spatially autocorrelated) with a Mantel test. Coordinates of P1 plots were estimated from maps made in 1999. Height and DBH of trees and shrubs in the P1 and P2 plots were compared between parcels with Mann-Whitney *U* tests on the averaged plot values.

We also investigated the distribution of individual plant species among plots. We selected plants that were at least seasonally important to the ring-tailed lemur diet (table 1; *Tamarindus*, *Talinella, Enterospermum*, *Strychnos, Quivisianthe*) or were common plant species in at least 1 parcel *(Euphorbia*, *Dichrostachys*, *Terminalia*, *Acacia*, *Cedrelopsis)*. These latter were also eaten by sympatric populations of *Propithecus verreauxi* (Verreaux's sifaka) in P1 [Yamashita, 2002]. The numbers of plant species between parcels were compared with a G test of independence.

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Table 1. Frequency of selected plant species in plots

Plant species and common name	Parcel 2									Parcel 1								Lc	Pv
	west																east		
Plot No.:	6	10	7/11	3	2	8/9	5	4	1	9	10	8	6/7	3/5	4	2	1		
Tamarindus indica (kily)					3	1					1	2	2	7	1	5	4	x	x
Enterospermum pruinosum (mantsake)			2			1							1	1	3	1	7	x	
Quivisianthe papinae (valiandro)				1							3		1	1	2			x	x
Acacia bellula (tratriotse)								1	2	6	1							x	x
Terminalia mantaly (taly)				2		3		3	2			1		1					x
Cedrelopsis grevei (katrafay)	3	3	1			1					2	1	3	1					x
Euphorbia tirucalli (famata)			3	1	1	16			2	4		2	4	3					x
Talinella grevei (dango)	2		9			4					2	2		1				x	x
Dichrostachys humbertii (avoha)	9		6	1		1	1						1						x
Strychnos madagascariensis (bakoa)		4						2										x	
Total large trees	23	20	24/34	10	9	34/25	3	11	10	22	33	27	38/24	16/13	15	27	25		
Total small trees	57	19	49/214	44	95	71/86	89	89	41	32	48	38	67/23	81/60	74	132	80		
Total lianas	6	1	5/8	9	18	11/6	1	5	20	15	13	12	4/20	69/15	13	85	7		
Total growth	86	40	78/256	63	122	116/117	93	105	71	69	94	77	109/67	166/88	102	244	112		

Plots are aligned along a longitudinal gradient. The closest distance between P1 and P2 plots is 3 km. Plots in P1 are 2 × 50 m and in P2 2 × 25 m. Plots 6 and 10 in the west lie on top of the escarpment. Plots with 2 transect numbers indicate plots at similar longitudes. Lemur consumers are *Lemur catta* (Lc) or *Propithecus verreauxi* (Pv). Total large trees = all trees in each plot with DBH >2.5 cm; total small trees = all trees in each plot with DBH <2.5 cm.

Lemur Observations and Diet

Most of the individuals in P1 wore identifying collars and pendants [Sauther and Cuozzo, 2009]. The P2 animals were collared in July 2010. Adult and subadult individuals were observed with continuous bout focal observations when possible. Focal animals were switched approximately every 20 min or when the focal animal went out of sight. General feeding observations on the group instead of focal animals were conducted when the animals were at a distance (e.g. feeding in canopy or too unhabituated to allow for close observation) based on the behavior of the majority of animals in view. Data were taken on basic activities (e.g. feeding, movement). During feeding, the precise plant part eaten and ingestive behaviors were documented, and time spent feeding was recorded.

Observations in P1 were conducted in the wet and dry seasons of 2008–2010 for approximately 1 month each (table 2). Ring-tailed lemur troops were followed in P1 in different areas of the parcel to capture known microhabitat differences. The troops ranged from 5 to >15 individuals. Further details are provided in the online supplementary table 1 (for all online suppl. material, see www.karger.com/doi/10.1159/000368896).

Observations in P2 were also conducted for 1 month each in the wet and dry seasons of 2010 and 2012. We primarily followed one semihabituated group ('Group 1') that was composed of 8 adults/subadults and 2 infants in 2010 (online suppl. table 1).

We compared plant species eaten in common between P1 and P2 in 2010 with a G test of independence on count data or the numbers of feeding observations per plant part/species (plant species not confined to the top 5 listed in table 2; plant species and parts entered separately in analysis).

Results

Forest Structure and Composition

The Mantel test indicated that the height and DBH of trees among plots within parcels were not spatially autocorrelated (P1: distance × height: –0.187, $p = 0.95$, $n = 10$; distance × DBH: 0.108, $p = 0.32$, $n = 10$; P2: distance × height: –0.123, $p = 0.81$, $n = 10$; distance × DBH: 0.029, $p = 0.39$, $n = 10$). Using the averaged values for each plot, height and DBH between parcels were not significantly different with Mann-Whitney tests (fig. 2): Mann-Whitney *U*, height: $Z = -1.136$, $p = 0.280$; DBH: $Z = -0.634$, $p = 0.557$.

Frequencies of selected plant species in the phenology plots are shown in table 1. The plots are aligned by longitude, which is a proxy for distance from the river. All the plant species except for *Strychnos* were found in both parcels, and the plant species composition between parcels was significantly different for those plants in table 1 ($G = 66.755$, d.f. = 9, $p < 0.001$).

Seasonal Diet Composition

Several plant species were among the most frequently eaten foods in both parcels. As reported previously, *Tamarindus* fruit was eaten year-round in P1 and largely confined to the dry season in P2 (table 2). In addition, *Talinella* fruit and leaves were eaten frequently in both areas, as were herbaceous *Metaporana* leaves.

Numbers of feeding observations on common plant species between parcels did not differ significantly (wet season, $G = 7.279$, d.f. = 6, $p = 0.296$; dry season, $G = 12.015$, d.f. = 6, $p = 0.062$).

Table 2. Time spent feeding by ring-tailed lemurs on top 5 foods in each season

Food species	Food part	Habit	Time spent feeding, %
Parcel 1			
Dry season (June) 2008			
Enterospermum pruinosum (mantsake)	Ripe fruit	Shrub	45.1
Tamarindus indica (kily)	Unripe fruit	Tree	23.4
	Ripe fruit	Tree	16.3
Metaporana parvifolia (kililo)	All leaves	Vine	7.8
Salvadora angustifolia (sasavy)	Young leaves	Tree	2.5
Commicarpus commersonii (bea)	Mature leaves	Vine	1.5
Wet season (January) 2010			
Tamarindus indica (kily)	Ripe fruit	Tree	33.0
	Unripe fruit	Tree	2.9
Talinella grevei (dango)	Ripe fruit	Small tree	11.0
Metaporana parvifolia (kililo)	All leaves	Vine	7.0
Misc. ground vines	All leaves	Vine	7.0
Landolphia sp. (piravola)	All leaves	Vine	4.0
Dry season (June–July) 2010			
Tamarindus indica (kily)	Ripe fruit	Tree	34.5
	Unripe fruit	Tree	31.6
Talinella grevei (dango)	All leaves	Small tree	19.1
Metaporana parvifolia (kililo)	All leaves	Vine	4.1
Unknown vine	All leaves	Vine	2.9
Unknown			2.3
Parcel 2			
Wet season (January) 2010			
Talinella grevei (dango)	Ripe fruit	Small tree	17.4
Misc. vines	All leaves	Vine	15.8
Tamarindus indica (kily)	Ripe fruit	Tree	13.6
Strychnos madagascariensis (bakoa)	Ripe fruit	Tree	7.6
Metaporana parvifolia (kililo)	All leaves	Vine	7.1
Dry season (June–July) 2010			
Tamarindus indica (kily)	Ripe fruit	Tree	47.0
	Unripe fruit	Tree	19.9
Talinella grevei (dango)	All leaves	Small tree	15.6
Misc. vines	All leaves	Vine	5.5
Landolphia sp. (piravola)	All leaves	Vine	3.9
Aloe divaricata	All leaves	Small tree	1.6
Wet season (January–February) 2012			
Talinella grevei (dango)	Ripe fruit	Small tree	69.5
Tsyvoanisoa	Ripe fruit	Vine	4.1
Turrae sp. (malainarete)	Ripe fruit	Small tree	3.6
Secamone pachystigma (angalora)	All leaves	Vine	3.0
Taboarandolo	All leaves	Vine	2.9

Percentage time spent feeding was calculated for each season, not annually.

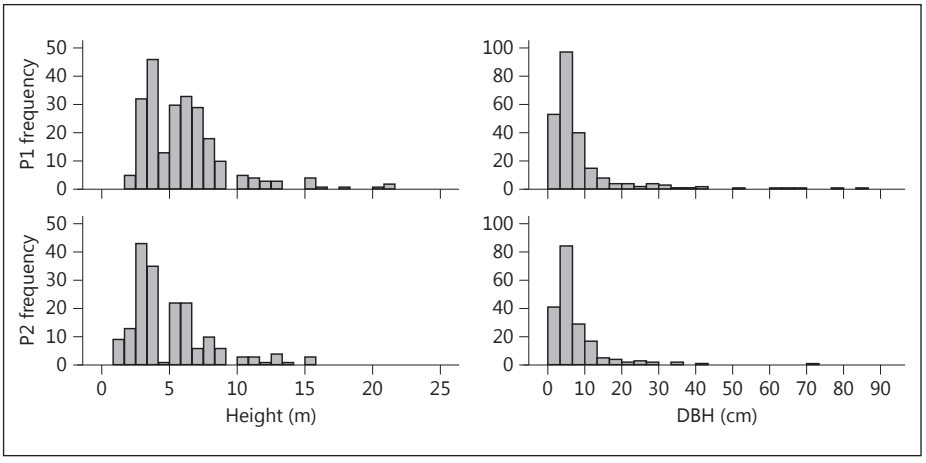

Fig. 2. Height and DBH counts of individual trees/shrubs in P1 and P2 plant plots. All individual plants are >2.5 cm DBH; not scaled for plot size. Parcels are not significantly different with a Mann-Whitney U test. P1: mean height = 5.956 m, SD = 0.865, n = 10; mean DBH = 9.284 cm, SD = 2.338, n = 10; P2: mean height = 5.500 m, SD = 1.417, n = 10; mean DBH = 8.601 cm, SD = 2.980, n = 11. There is no height value for Plot 2 in P1.

Discussion

Comparisons between P1 and P2 showed that lemur groups within a widespread population can have similar diets. Given that forest structure and numbers of feeding observations on common foods were not significantly different between parcels, it appears that tree/shrub size and food species do not limit lemurs to the P1 area. Though the structure of the tree species in our plots did not differ between parcels, we caution that the plots measured between parcels were not the same size. However, detailed comparisons of feeding time on the foods that comprised the majority of the diet (table 2) with the frequencies of plant species within and between parcels (table 1) reveal more complexity in diet composition.

The plant species eaten by the lemurs are well represented in our plots (tables 1, 2). Nine of the 10 plant species in table 1 are found in both parcels, and individual plant species are more prevalent in one location than in the other. The distribution of *Tamarindus* in our plots is more heavily skewed toward the east (22 trees in P1, 4 in P2; table 1) [Sussman and Rakotozafy, 1994]. As others have noted, ring-tailed lemur densities appear to be correlated with *Tamarindus* abundance in gallery forests [Gould et al., 2003; Blumenfeld-Jones et al., 2006], and their density has been found to be higher along the river in P1 [Axel and Maurer, 2010]. Similarly, the majority of the plant species in table 1 eaten by sifakas are found in the western half of P1 and in P2 [Yamashita, 2002], which coincides with their higher densities in those locations [Axel and Maurer, 2010].

Enterospermum and *Quivisianthe* are more common in the P1 area and are important food plants in the dry season in P1 [Sauther, 1998; Sauther and Cuozzo, 2009]. In contrast, ripe *Talinella* fruit and leaves are major contributors to the diets

in both parcels but are more frequent in the western P1 plots (and generally outside the reserve) (tables 1, 2). Even *Tamarindus* is frequently eaten in P2, though consumption is seasonal (table 2). Comparing the top 5 foods in table 2 between parcels, some foods are highly consumed in both locations regardless of relative frequency (e.g. *Tamarindus*, *Talinella*), while others are eaten in one parcel but not the other (e.g. *Enterospermum* and *Quivisianthe* in P1, *Strychnos* and several species in the 2012 wet season in P2). Of this latter group, only *Enterospermum* is found in both parcels in our plots, suggesting that some contributions to the diet are simply due to availability. The ring-tailed lemur diet at BMSR appears to be comprised of a mixture of 'core' plants that are eaten in abundance regardless of frequency and locally available plants.

With respect to describing suitable habitat for ring-tailed lemurs, P2 is similar to yet distinct from P1. The parcels do not differ in tree height and DBH; however, the composition of the habitats differs, notably in *Tamarindus* density. Studies from other non-gallery forest sites report large ring-tailed lemur group sizes without accompanying increases in *Tamarindus* density. Group sizes of >15 individuals (adults and subadults) inhabit the mixed deciduous/spiny bush forest of Tsimanampesotse National Park where *Tamarindus* has a limited distribution [LaFleur et al., 2014], and groups of 11–15 individuals occur in the far south in Cap Sainte-Marie where there is no tamarind [Kelley, 2013]. We also observed other large groups of ring-tailed lemurs on top of the escarpment while following our primary study group. The decoupling of lemur population densities from *Tamarindus* densities suggests that their co-occurrence may not be as common as previously assumed or may even have occurred recently [Goodman et al., 2006]. The P2 ring-tailed lemur group, with its seasonal reliance on *Tamarindus* and inclusion of local foods, is intermediate between groups in gallery forest and non-tamarind sites. Our findings here lay the groundwork for continued monitoring and research in the P2 extension of the well-studied gallery forest population at BMSR.

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