



Microhabitat Variation and Its Effects on Dietary Composition and Intragroup Feeding Interactions Between Adult Female *Lemur catta* During the Dry Season at Beza Mahafaly Special Reserve, Southwestern Madagascar

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Received: 13 May 2008 / Accepted: 19 August 2008 /
Published online: 21 November 2008
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Abstract We compared diets and female feeding agonism in 2 groups of ring-tailed lemurs living in markedly diverse microhabitats in and near the Beza Mahafaly Reserve, Madagascar during mid-to-late gestation periods and height of the dry season to test predictions concerning differences in resource availability, preferred foods, female rank, and degree and frequency of feeding agonism in relation to usurpability and monopolization of food resources. Quadrat sampling in disturbed forest habitat revealed a greater number of plant species than in the gallery forest home range area, but females in both groups consumed nearly equal numbers of actual food plant species. Higher-ranking females in disturbed forest consumed human food scraps from the researchers camp significantly more often than low-ranking females did, while there was no rank effect for consumption of any food type between females in the gallery forest group. Higher rates of female feeding agonism in both groups occurred around usurpable fruit and leaves, as well as over monopolizable human food scraps in the disturbed forest group. There is no association between degree of agonism and food type in either group, and rate of feeding agonism is similar for both groups. The most highly contested food items came in large packages and were high in nutrients: beneficial foods for gestating females in the height of dry season in southwestern Madagascar.

Keywords diverse habitats · feeding competition · females · *Lemur catta*

Introduction

Within and between primate groups, the abundance and distribution of food resources affect time spent foraging, feeding competition, and, subsequently, female

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relationships (Isbell and Young 2002; Isbell *et al.* 1999; Pruettz and Isbell 2000; Sterck *et al.* 1997; van Schaik 1989; Wrangham 1980), although Sussman and Garber (2007) caution that in many studies, food-related agonism occurs at a very low level, and may not be as important a variable in shaping intragroup female relationships as researchers often assume.

Foods that are patchy and spatially dispersed are indefensible, whereas clumped food sources are more randomly spaced and take up a small enough area that ≥ 1 individuals can defend the resources that they offer, resulting in scramble and contest competition, respectively (Isbell and Young 2002; Isbell *et al.* 1999; van Schaik 1989). In addition, Isbell *et al.* (1998) suggest that feeding site depletion time can be as important as patch size and food distribution.

The temporal and spatial variability of plant and other food resources strongly impact primate diets (Glander and Teaford 1995; Janson and Chapman 1999). Further, certain foods are considered to be of higher quality than others (Janson 1988; Janson and Chapman 1999), and can be patchily dispersed and are seasonally and temporally variable. Such highly desirable foods can result in an increased level of competition between females for their acquisition (Glander and Teaford 1995; Sauther *et al.* 1999). Foods that are readily available may be of good quality, but they are generally produced in amounts that can accommodate all members of the group, thus lessening the need for a high level of competition (Pruettz and Isbell 2000). Levels of agonistic feeding competition between adult females can therefore vary depending on food type.

We examine and compare the diets and agonistic relationships among adult females during the mid-to-late gestation period in two groups of wild ring-tailed lemurs (*Lemur catta*) in different microhabitats: one, lush gallery forest within the Beza Mahafaly Special Reserve (BMSR), Madagascar, and the other, disturbed dry forest just outside of the reserve, where vegetation is sparse due to human influence. These two microhabitats contain food resources of varying availability, abundance and distribution (Gould 1996; Sauther 1992, 1993).

As with most lemur taxa, ring-tailed lemurs are highly seasonal breeders (Jolly 1984; van Horn and Resko 1977; Wright 1999), and reproductive females are strongly affected by southern Madagascar's marked seasonal resource availability (Jolly 1984; Jolly *et al.* 1993; Rasamimanana and Rafidinarivo 1993; Sauther 1991, 1993, 1994, 1998; Sauther *et al.* 1999). We conducted the study during the mid-to-late gestation period, at the height of the dry season (July–September, 2004), when food resources are far scarcer in southern Madagascar than during wet and transitional seasons (Gould 2006; Jolly 1984; Rasamimanana and Rafidinarivo 1993; Sauther 1992, 1994, 1998; Sauther *et al.* 1999). In the Beza Mahafaly region, young leaves and numerous fruit species are abundant during the wet season, whereas in the dry season fruit is rare, and even mature leaves wither, leading to consumption of dried, brown leaves as the dry season progresses (Sauther 1992, 1998). During gestation and early lactation periods, food resources are limited, and reproductive females feed on rare fruit, mature and occasional young leaves, and flowers that appear at the very end of the season (Sauther 1992, 1994, 1998).

Female ring-tailed lemurs within a group belong to a relatively stable linear dominance hierarchy (Jolly 1966; Nakamichi and Koyama 1997; Sauther 1992; Sauther *et al.* 1999; Taylor 1986; Taylor and Sussman 1985) and are typically

involved in more frequent agonistic behavior over desired resources than males are (Sauther and Sussman 1993). Feeding agonism tends to vary depending on the type of food consumed and the season, as Sauther (1992) found more frequent feeding agonism over access to fruit than to leaves, as well as during the dry season.

All of the aforementioned research on diets and feeding agonism in *Lemur catta* has occurred in relatively densely vegetated gallery forests. Given the seasonal nature of both synchronous reproduction and food availability experienced by ring-tailed lemurs, and the marked differences in microhabitat of the 2 focal groups, we tested the following hypotheses related to food distribution and frequency and degree of intragroup female feeding agonism:

- Hypothesis 1: Females within the reserve with home ranges in the dense vegetative areas will have a diet with more numerous food resources that have a high level of distribution, whereas females outside of the reserve will have a diet composed of fewer types of food resources and a lower level of distribution.
- Hypothesis 2: Studies of some primate species characterized by female linear dominance hierarchies reveal that rank positively correlates with access to food resources, e.g., Japanese macaques (Aureli *et al.* 1992), Hanuman langurs (Borries 1993), olive baboons (Barton and Whiten 1993), vervets (Isbell *et al.* 1999; Whitten 1983). We therefore predict that in both groups, high-ranking females will have increased access to more desirable foods than low-ranking females will, and therefore consume more of them.
- Hypothesis 3: In lush areas, primates presumably travel shorter distances to obtain sufficient nutrients than those in sparsely vegetated areas do. More time devoted to searching for and traveling to scarce food resources may mean that feeding competition is higher than in lush areas. Therefore, we predict that the nonreserve group will have a higher frequency and more marked degree of interfemale feeding agonism than that of the reserve group.
- Hypothesis 4: Because smaller food items are less easily usurped (Isbell 1991; Isbell and Pruetz 1998; Isbell *et al.* 1998, 1999; Pruetz and Isbell 2000), we predict that feeding on food items that come in small, bite-sized pieces will result in less feeding competition between adult females.

Methods

Study Site

Beza Mahafaly Special Reserve (BMSR) is in southwestern Madagascar (23°30'S latitude and 44°E longitude), and was established as a Special Government Reserve in 1986 (Richard *et al.* 1987). Parcel 1 of the reserve, where our study took place, consists of 80 ha of mixed vegetation and includes riverine forest in the eastern part of the reserve, near the Sakamena River, and more xerophytic/scrub forest as one

moves toward the reserve's western boundary (Sussman and Rakotozafy 1994). Immediately outside of the reserve boundaries, degraded deciduous and scrub forest occurs.

Focal Groups

We selected 2 groups of ring-tailed lemurs with differing home ranges and microhabitats: 1 within the reserve boundaries (Green group) and 1 outside of the protected area (Black group). Several researchers have studied Green group extensively since 1987. They inhabit the lush, eastern, gallery forest portion of the reserve (Fig. 1). Green group's home range spans the Sakamena River bank at the eastern boundary of the reserve to *ca.* 400 m west within the reserve, and at times to the opposite side of the river, where the group engages in crop raiding (Sussman 1991; LaFleur 2008). Home range size is *ca.* 17–32 ha depending on seasonal resource availability (Sussman 1991). The area of home range we used was *ca.* 10–12 ha (Sussman 1991). Black group lives outside of the actual reserve and ranges from the western bank of the Sakamena River westward to the research camp: a

Fig. 1 Reserve gallery forest within Green group's home range.



distance of *ca.* 500 m, including the sparse, scrub forest near the camp and deciduous forest near the river (Fig. 2). Black group used *ca.* 12 ha of their home range during the study.

Both Green (reserve group) and Black (nonreserve group) comprised 6 adult females, and had total group memberships of 16 and 17 individuals, respectively, including immatures (Table 1). Before the study, researchers involved in other projects at the site had captured, collared, and tagged individuals in both groups for identification (Cuozzo and Sauter 2006a, b; Gould *et al.* 2005; Gould and Ziegler 2007). We determined female dominance ranks via analysis of agonistic and submissive intragroup interactions (approach/retreats, displacements) between adult females in each group.

Behavioral Data Collection

From July to September 2004, Gemmill and an assistant collected 956 continuous-time focal animal data sessions (Altmann 1974) of 15 min duration (239 h). The number of sessions per focal animal varied from 79 to 81. We collected data on all

Fig. 2 Part of the degraded scrub forest outside of the reserve and part of Black group's home range.



Table 1 Composition of the focal groups

Age/sex class	Green group	Black group	Total
Adult female	6	6	12
Adult male	5	5	10
Subadult	4	3	7
Juvenile	2	2	4
Total	17	16	33

Subjects classed as juveniles were from the October 2003 cohort and were 9–11 mo old during the study period. Subjects classed as subadults were from the 2001 and 2002 birth cohorts.

females in the 2 groups during the morning and afternoon activity periods (0800 to 1130 h and 1400 to 1800 h, respectively) 6 days per week. At the onset of each data collection day, Gemmill and her assistant collected data on 2 females, and at the end of each data collection session, Gemmill and an assistant selected 2 more females, which could not be either of the 2 followed in the prior data collection session. We evenly distributed data collection sessions for each focal animal throughout the day to ensure independence of focal animal sessions and to prevent individuals from being overrepresented in the data set.

We based behavioral categories used in data collection on both previous ethograms constructed for *Lemur catta* (Gould 1994; Jolly 1966; Taylor 1986) and adjustments made to them during preliminary observations in May and June of 2004 to suit this particular study better (Gemmill 2007). We noted all behaviors and their start times during the focal animal session, and during interactions with conspecifics, we recorded the identities of the conspecific(s) involved and the direction of the interaction. If the focal animal engaged in agonistic behavior, as either recipient or initiator, we recorded the severity of agonism (AG) as: AG1 submissive chitter, AG2 displacement, AG3 lunge or charge, or AG4 hit, cuff, slap, push, or chase. We labeled the context of each instance of agonism as one of the following: feeding, social, drinking, resting, intergroup, and unknown. We scored frequency of agonism for the following behavioral categories: feeding, resting, social, drinking, and intergroup encounters. Within the feeding category, we scored agonism in relation to severity and food type. We calculated rates of agonism per hour for each focal female by dividing the number of agonistic interactions in which she was involved, divided by the number of 15-min focal individual sessions collected on her and then multiplied by 4.

We restricted the scoring of feeding behavior to the actual ingestion of food items and excluded search and handling time. When subjects fed on vegetation, we recorded the species and plant part ingested, e.g., leaves, flowers, fruit. Items scored as human food scraps include discarded fruits and vegetables and peelings from human cooking areas in the research camp.

A feeding bout commenced once the focal animal began to feed and terminated when feeding, chewing, and swallowing had not occurred for >10 s (Isbell *et al.* 1998). We recorded a new feeding bout when she moved 2 body lengths between foods or when the ingested food type changed (Isbell *et al.* 1998). We recorded the relative size of the food item consumed as either usurpable or nonusurpable-large or small, respectively (Isbell and Young 2002).

Microhabitat Diversity Data Collection

We collected quadrat samples to determine the prevalence of tree species, and to facilitate comparison between distribution and availability of tree species within the ranges of the study groups. We selected 8 25-m² areas in the home ranges of each study group. We identified and counted tree species within each quadrat, and conducted the following botanical measurements for all trees with a trunk circumference ≥ 4 cm: diameter at breast height, crown diameter, height, crop coverage, and degree of crop ripeness (Janson and Chapman 1999; Koenig *et al.* 1998). We recorded the percentage of these 25-m² areas that were covered by ground vegetation, and the presence and relative amount of any nonplant objects such as human garbage or cattle feces.

We estimated crown coverage (percentage of leaf, fruit, and flower abundance) for trees and low-level vine coverage used as food species that were suitable for measurement in sample plots in each group's home range (Table II). Suitable trees had a circumference ≥ 4 cm. We determined fruit and leaf abundance via a visual estimation of the tree in question as follows: 0=no coverage, 1=< 10%, 2=10–25%, 3=25–50%, 4=50–75%, 5=75–100%.

We used Morista's Index of Similarity (Morista 1959), an index of comparison for different communities or sample sets, to analyze the ecological count data for the 2 home ranges:

$$C_{\lambda} = \frac{2(\sum X_{i1}X_{i2})}{(\lambda_1 + \lambda_2)N_1 + N_2}$$

wherein:

- X_{i1} number of individuals of species i in sample 1
- X_{i2} number of individuals of species i in sample 2
- N_1 total number of individuals (all species) in sample 1

Table II Estimation of crown coverage (fruit and leaf abundance) for trees and vine coverage used as food species that were suitable for measurement in sample plots in each group's home range

Green (reserve) group	Crown or ground cover estimate
<i>Tamarindus indica</i> (Kily)	Leaves 75%, fruit ca. 25%
Tsingilifilo	Leaves 73%
<i>Crateva excelsa</i> (Akaly)	Leaves 35–50%
<i>Xeromphis</i> sp. (Lamotimboay)	Leaves <35%
<i>Tarennia pruinosa</i> (Mantsaka)	Leaves <35%
Black (nonreserve) group	
<i>Tamarindus indica</i> (Kily)	Leaves ca. 71%, fruit ca. 1%
Tsingilifilo	Leaves ca. 50%
<i>Quisivianthe papionae</i> (Valiandro)	Leaves ca. 48%, flowers 30%
<i>Xeromphis</i> sp. (Lamotimboay)	Leaves <35%
<i>Grewia grevei</i> (Kotipoke)	Leaves <35%
<i>Bakerella</i> sp. (Tamboro)	Vine-ground cover <5%
<i>Pentopetia</i> sp. (Tsompia)	Vine-ground cover <5%

Suitable trees had a circumference ≥ 6 cm.

N_2 total number of individuals (all species) in sample 2
 C_λ measurement of similarity

$$\lambda_1 = \sum (X_{i1} * (X_{i1} - 1)) / N_1(N_1 - 1)$$

and

$$\lambda_2 = \sum (X_{i2} * (X_{i2} - 1)) / N_2(N_2 - 1)$$

The index is scaled from 0.0 to 1/0, with a result of 0.0 signifying no similarity and 1.0 implying complete similarity.

Statistical Analyses

To test for differences in both intra-and intergroup feeding and agonism rates, we used nonparametric analysis of variance tests because focal animal sample sizes ($N=6$ females for each group) were too small to test the assumptions of parametric statistical tests.

Results

Microhabitat Differences

We identified 35 plant species in Green group's home range vs. with 51 in Black group's home range. Ecological count data for the 2 home ranges resulted in an index of similarity value of 0.32 (Morista 1959), indicating a low degree of similarity between the 2 microhabitats (Table III).

Of the plant species we sampled within the reserve, *Tamarindus indica* had the greatest mean height at 18 m; followed by *Crateva excelsa* at a mean height of 9 m. Outside of the reserve, *Quisivianthe papionae* and *Grewia* sp. had the greatest average heights of 12 m followed *Tamarindus indica* at 10 m.

Tamarindus indica had the largest basal area in both microhabitats: 2.6 m² in the reserve and 2.2 m² outside of the reserve. *Tamarindus indica* has the highest relative abundance of all plant species within the reserve microhabitat, but was less than half as abundant outside of the reserve (Table III). *Tamarindus indica* sampled inside the reserve also contained markedly more tamarind fruit than those sampled outside of the reserve (Table II).

Diet and Microhabitat

Green (reserve) group females fed on 24 plant species, vs. 25 by females in Black (non-reserve) group, and 15 food plant species were common to both groups (Table IV). Of the 35 plant species identified in the reserve area sample plots, Green group females fed on 20 (57%) while Black group females used only 16/51(31%) of the identified species in the sample plots in their home range area.

Table III The most prevalent plant species in each microhabitat expressed as a percentage of abundance, determined via quadrat sampling

Reserve group plant species	
Species name	Relative abundance (%) in sampled 25-m ² plots
<i>Tamarindus indica</i> *	24
<i>Grewia</i> sp.*	14
<i>Crateva excelsa</i> *	10
<i>Syregada chauvetiae</i>	10
<i>Grewia triflora</i>	10
Tsingilifilo*	10
<i>Xeromphis</i> sp.*	5
<i>Tarenna pruinosa</i> *	5
<i>Acacia bellula</i>	5
<i>Quisivianthe papionae</i>	5
Vory	5
<i>Argemone mexicana</i> *	98 ^a
Nonreserve group plant species	
Species name	Relative abundance in sampled plots (%)
Tsingilifilo*	16
<i>Strychnos madagascariensis</i>	13
<i>Tamarindus indica</i> *	11
<i>Quisivianthe papionae</i> *	11
<i>Xeromphis</i> sp.*	8
<i>Tarenna pruinosa</i>	8
<i>Grewia</i> sp.	5
<i>Grewia triflora</i>	5
<i>Euphorbia tirucallii</i>	5
<i>Grewia leucophylla</i>	3
<i>Cesalpinia bonduc</i>	3
Tangatanga	3
<i>Abrus precatorius</i>	3
<i>Grewia grevei</i> *	3
<i>Kigelianthe madagascariensis</i>	3
<i>Commiphora aprevalii</i>	3

We identified some species by local names only. Species used as food plants are indicated by an asterisk. ^a*Argemone mexicana* is a thistle occurring only in the riverbed and the abundance value is based on one 25-m² plot.

Figures 3a and b show the 10 most frequently consumed foods for each group. Our focal animals consumed leaves most frequently, followed by fruit and buds/flowers. Females in both groups engaged in geophagy—ingestion of wood/termite leavings—and coprophagy (once in Green group, multiple occasions in Black group), and Black group females ranged into the research camp many times daily, feeding on human food scraps and fecal matter (Table V).

Intergroup Feeding Comparison

Females in both groups fed significantly more frequently than they foraged ($\chi^2=11.19$, $df=2$, $p<0.05$), and Black group females foraged more often than females in Green group did (Table VI).

Green group females ingested leaves and fruit at significantly higher rates than Black group females did (leaves: Mann-Whitney *U*-test, $U=1.5$, $p=0.008$; fruit: $U=$

Table IV Plant species and plant parts consumed by females in each group, and species used by both groups in far right column

Plant species Latin names (where possible) and vernacular names	Leaves	Buds	Flowers	Fruit	Wood	Consumed by both groups
Green (reserve) group						
<i>Panicum maximum</i> (Ahibe)	*					*
<i>Crateva excelssa</i> (Akaly)	*					
<i>Tridax procumbens</i> (Angamay)	*					*
(Angarafke)	*					*
(Atapiso)	*					
<i>Marsdenia</i> sp. (Bokabe)	*					*
<i>Argemone mexicana</i> (Fatinboay)	*					
(Fitarasoamboa)	*					
<i>Ipomaea</i> sp.	*	*	*			
<i>Metaporana parvifolia</i> (Kilililo)	*					*
<i>Tamarindus indica</i> (Kily)	*			*	*	*
<i>Grewia grevei</i> (Kotipoke)	*			*		*
<i>Xeromphis</i> sp. (Lamotimboay)	*			*		*
<i>Cryptostegia madagascariensis</i> (Lombiry)	*					*
<i>Tarenna pruinosa</i> (Mantsaka)	*					
<i>Salvadora angustifolia</i> (Sasavy)	*	*				*
<i>Maerua filiformis</i> (Somangy)	*	*				*
<i>Bakerella</i> sp. (Tamboro)	*					*
<i>Combretum</i> sp. (Tamenaka)	*					
(Tarasoamboa)	*	*				
<i>Cynanchum mahafalense</i> (Try)	*	*	*			*
(Tsingilifilo)	*					*
<i>Pentopetia</i> sp. (Tsompia)	*					*
(Velae) Fam. Convolvulaceae			*			
Black (nonreserve) group						
<i>Panicum maximum</i> (Ahibe)	*					
<i>Aloe divaricata</i> (Aloe)	*					
<i>Tridax procumbens</i> (Angamay)	*					
(Angarafke)	*					
(Bea)	*					
<i>Marsdenia</i> sp. (Bokabe)	*				*	
(Dalitse)	*					
<i>Gyrocarpus americanus</i> (Kapaipoty)		*				
<i>Metaporana parvifolia</i> (Kililo)	*			*		
<i>Tamarindus indica</i> (Kily)	*	*		*		
<i>Grewia grevei</i> (Kotipoke)	*			*		
<i>Xeromphis</i> sp. (Lamotimboay)			*	*		
<i>Cryptostegia madagascariensis</i> (Lombiry)	*					
<i>Gouania</i> sp. (Masokara)		*				
<i>Opuntia</i> sp. (Raketa)	*					
<i>Salvadora angustifolia</i> (Sasavy)	*	*	*		*	
<i>Maerua filiformis</i> (Somangy)	*	*				
<i>Bakerella</i> sp. (Tamboro)	*					
<i>Acacia bellula</i> (Tratriotse)	*	*				
<i>Cynanchum mahafalense</i> (Try)		*	*			
(Tsingilifilo)	*					
<i>Pentopetia</i> sp. (Tsompia)	*					
(Vadrianoa)	*					
<i>Quisvianthe papionae</i> (Valiandro)	*	*	*			
(Votapose)	*					

It was not possible to identify the Latin names of all species based on the vernacular names.

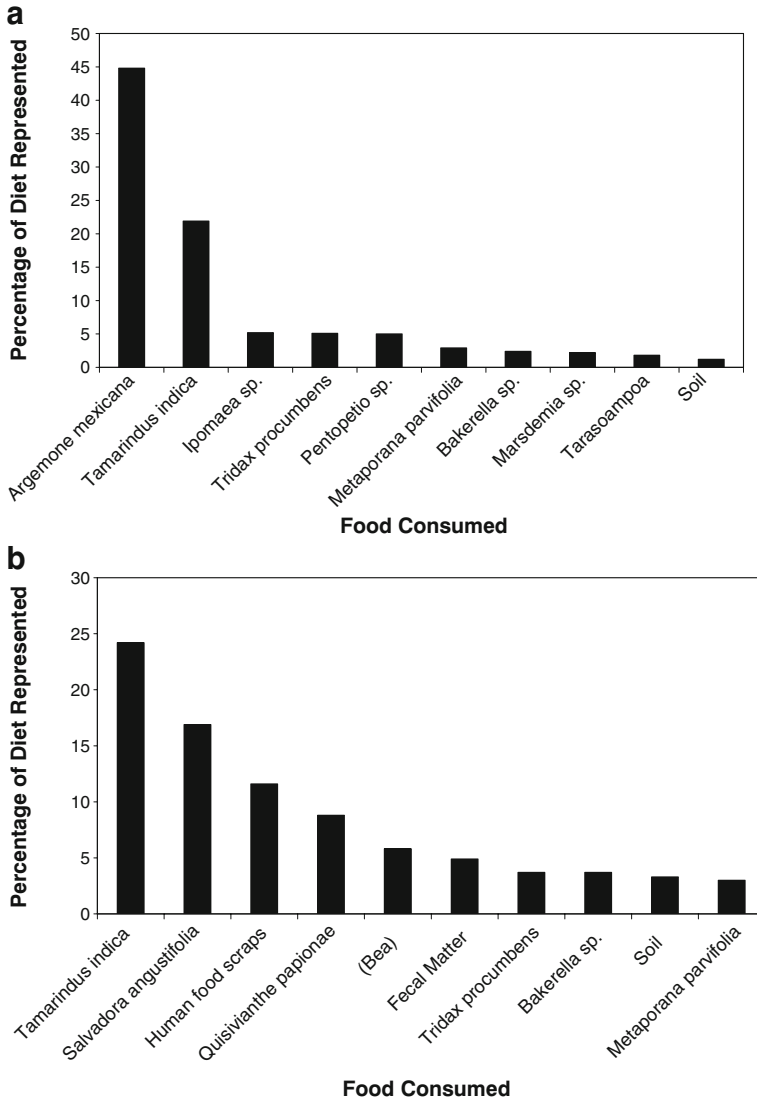


Fig. 3 (a) The top 10 food species consumed by Green group (reserve group) adult females as a percentage of overall diet. (b) The top 10 food species consumed by Black group (nonreserve group) adult females as a percentage of overall diet.

4.5, $p=0.030$), whereas Black group females consumed flowers/flower buds significantly more often ($U=0.0$, $p=0.004$) than Green group females did (Fig. 4).

Female Rank and Food Consumption

In Green group, there was no significant difference between the 3 higher-and 3 lower-ranking females in hourly rates of consumption of leaves (Mann-Whitney, $U=4.0$, $p=0.827$), flowers/buds ($U=4.0$, $p=0.827$), or fruit ($U=2.0$, $p=0.275$; Fig. 5a).

Table V Nonplant foods and human food scraps from the research camp consumed by females from Black (nonreserve) group

Soil
Wood
Termite leavings
Feces
Sweet potato (vegetable and peel)
Banana (fruit and peel)
Sugar cane (fresh and Chewed/disgarded by humans)
Unidentified food scraps

Because Black group foraged both in the research camp and in the forest, we analyzed human food scraps and fecal matter in addition to plant food types. There is no rank effect for ingestion rates of flowers and flower buds ($U=4.0$, $\rho=0.724$), fruit ($U=3.0$, $\rho=0.376$), or feces ($U=3.0$, $\rho=0.376$). However, lower-ranking Black group females consumed leaves significantly more often than higher-ranking females did ($U=0.0$, $\rho=0.050$), and females of higher rank consumed human food scraps at a higher rate than subordinate females did ($U=0.0$, $\rho=0.050$; Fig. 5b).

Agonism and General Food Type

Both study groups exhibited significantly more agonism in feeding and social contexts (Green group $\chi^2=19.23$, $df=4$, $p<0.001$; Black group $\chi^2=20.05$, $df=4$, $p<0.001$), and most frequently while feeding (Fig. 6). There was no intergroup difference in rates of feeding agonism (Mann-Whitney U , $U=15.0$, $\rho=0.63$).

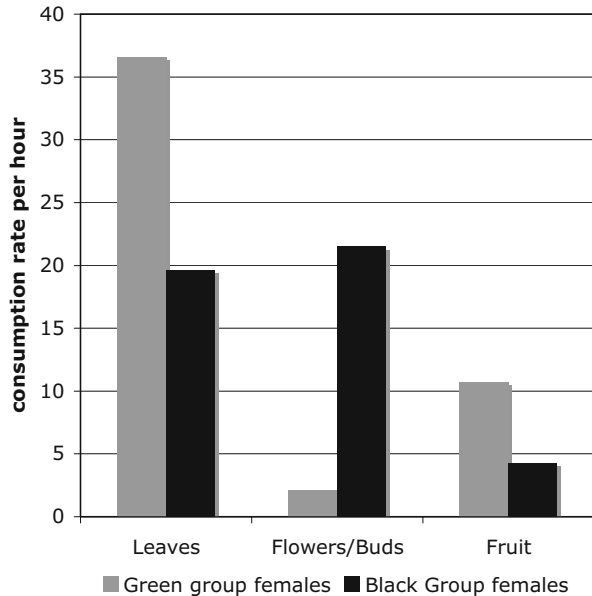
In Green group, a higher proportion of female feeding agonism occurred around leaves and fruit (Fig. 7a), while a large proportion of feeding agonism between Black group females was associated with human food scraps and fecal matter (Fig. 7b).

In neither group was there a significant association among the 4 categories of agonism (Table VII) and food type (Green group females: Kruskal-Wallis, $\chi^2=7.56$, $p=0.11$, $df=4$; Black group females: $\chi^2=13.01$, $p=0.16$, $df=8$), though type 2 agonism (displacement) was more common over leaves between Green group females and occurred slightly more often for fruit, leaves, and human food scraps between Black group females.

Table VI Rate per hour of foraging and feeding instances by females in each focal group and percentage (in parentheses) of foraging or feeding in relation to total number of foraging and feeding records for each group

	Green group ($n=1141$ instances of both foraging and feeding in 120 h total observation time)	Black group ($n=2085$ instances of both foraging and feeding in 199.2 h total observation time)
Foraging instances	1.15/h (13% of foraging and feeding instances)	4.6/h (27% of foraging and feeding instances)
Feeding bouts	8.4/h (87% of foraging and feeding instances)	12.8/h (73% of foraging and feeding instances)

Fig. 4 Comparison of rates of consumption by plant part species by group.



Rate and Degree of Feeding Agonism between Groups

Hourly rate of feeding agonism was similar for both groups (Green group=8.75 instances per hour, Black group=10.3 per hour), and there was no intergroup difference in degree of feeding agonism (Mann-Whitney U -test, $U=5$, $p=0.48$; Table VII).

Agonism and Specific Food Items

We examined percentage of overall feeding agonism between females in relation to the most frequently consumed food types (Table VIII). In Green group, significantly more agonism occurred over leaves of *Argemone mexicana* (Mexican thistle) and fruit and leaves of *Tamarindus indica* (tamarind) ($\chi^2=142.3$, $p<0.001$, $df=4$). In Black group, the percentage of interfemale agonism over tamarind fruit/leaves and human food scraps was higher than for the other 4 food types ($\chi^2=37.6$, $p<0.05$, $df=5$). The 3 food types that resulted in the lowest percentages of feeding agonism were nonusurpable, whereas those that accounted for higher proportions of agonism were usurpable (Table VIII).

Discussion

Microhabitat Differences

There was higher plant specific diversity in the nonreserve microhabitat than in the reserve microhabitat, and there was a low level of phenological similarity between

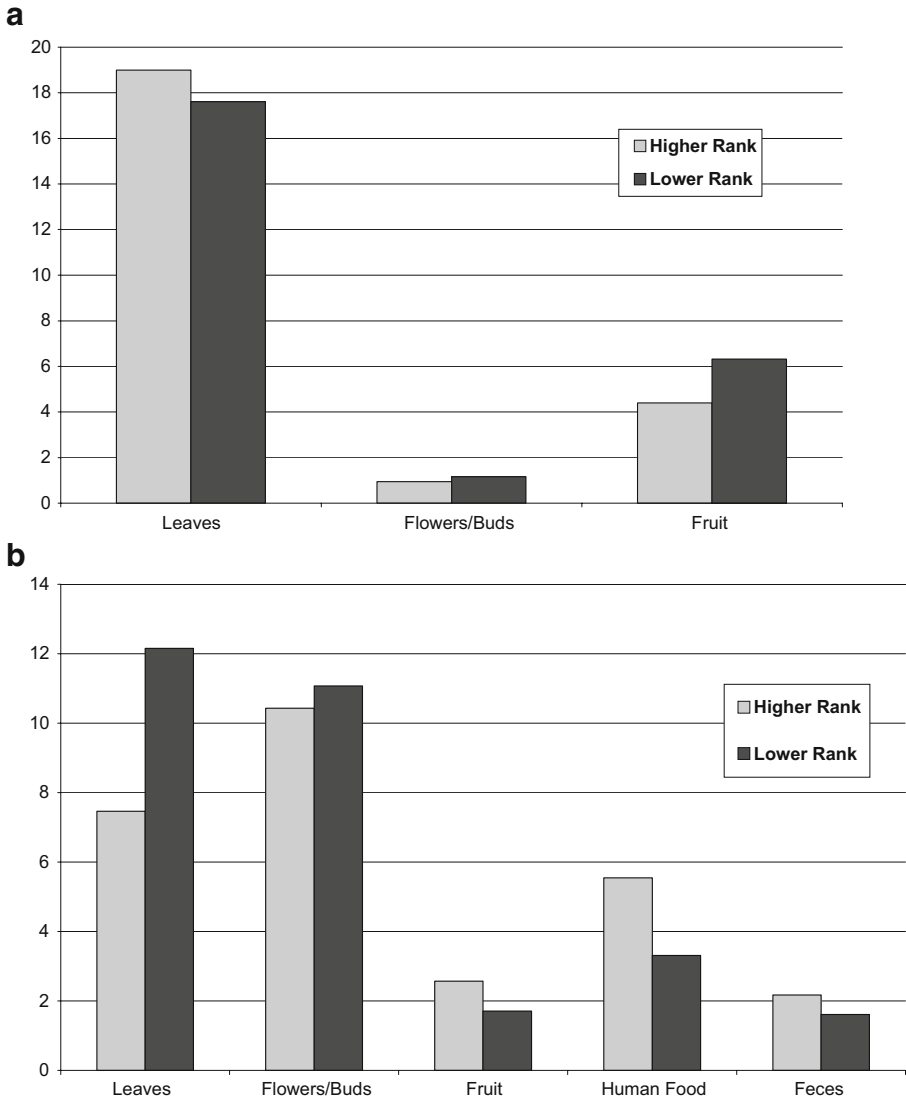
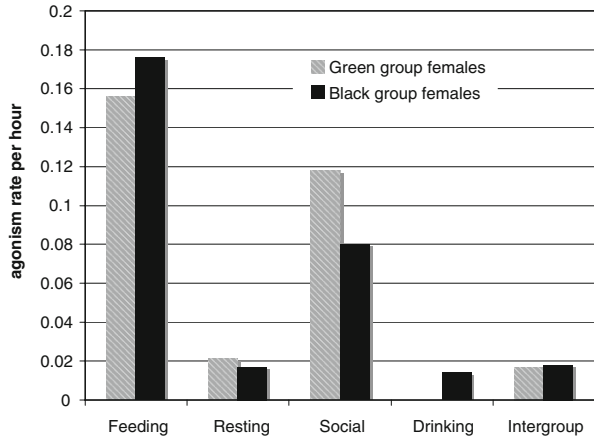


Fig. 5 (a) Comparison of rate of feeding by food type between high-and low-ranking females in Green group. (b) Comparison of rate of feeding by food type between high-and low-ranking females in Black group.

them. However, in terms of actual plant species used as food, both groups used 15 species in common, and 10 (Green group) and 9 (Black group) species uniquely.

Markedly more canopy coverage occurred within the Green group's gallery forest range, where the soil is darker and moister. Such conditions might be necessary for certain trees to reach their growth potential, both in basal area and in height (Hubbell 1979; Kraaj and Ward 2006). However, the dense, gallery forest could also limit deposition and growth of seeds from outside species that could otherwise enter via wind dispersal or human influence (Seidler and Plotkin 2006). The consistent traffic

Fig. 6 Hourly rates of agonism by behavioral context for each group.



of humans and herds of grazing livestock in the nonreserve habitat has likely led to the loss of some plant species still occurring in the protected reserve. However, the germination properties of cattle and goat feces, coupled with sparsely distributed trees, could allow for the propagation of plant species not commonly growing within the gallery forest (Cosyns *et al.* 2006; Olf and Ritchie 1998).

Our hypothesis 1 was not supported because females in both microhabitats consumed nearly identical numbers of plant species. Crown coverage of fruit and leaves of larger food trees was similar in both habitats, with the exception of tamarind trees (*Tamarindus indica*): both tree and fruit abundance was far lower in the nonreserve habitat, which could be an important consideration given the importance of tamarind fruit to gallery and dry forest-dwelling *Lemur catta*. However, nonreserve group females supplemented their diets with human food scraps and nonplant foods in the research camp.

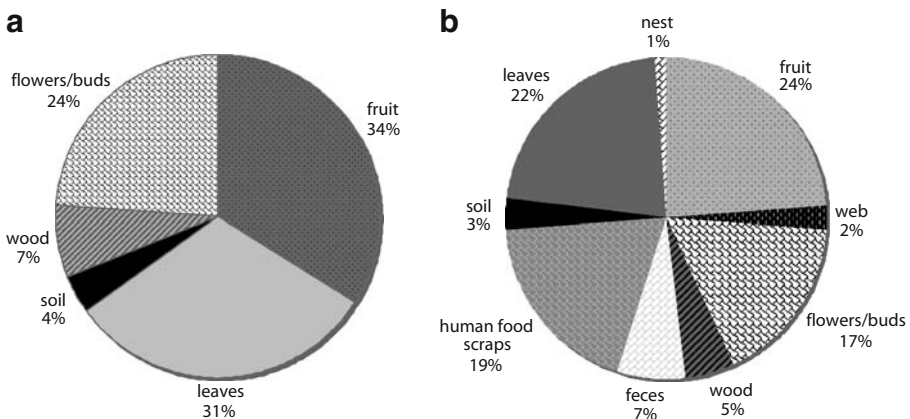


Fig. 7 (a) Proportion of feeding agonism by type of food consumed by adult females residing in the reserve (Green) group. (b) Proportion of feeding agonism by type of food consumed by adult females residing in the nonreserve (Black) group.

Table VII Hourly rates of feeding agonism by agonism level for each group

Feeding agonism level AG1=low AG4=high	AG1 Submissive vocalization (chitter)	AG2 Displacement	AG3 Lunge or charge	AG4 Hit, cuff, slap, push, or chase
Green group	4.05	4.70	0.25	0.35
Black group	4.15	4.91	0.91	0.56

Diet and Microhabitat

Green group females in the reserve focused mainly on 2 food sources: *Tamarindus indica* (tamarind) and *Argemone mexicana* (Mexican prickly poppy), which composed 70% of their diet, while the nonreserve Black group females used their top plant food species more proportionately.

Green group females ate significantly more leaves and fruit than nonreserve females did. Both the abundance of Mexican prickly poppy leaves and fruiting tamarind trees within Green group's home range and the fact that few tamarind trees were fruiting in Black group's range during the study period contributed to the marked difference. Similarly, Black group females consumed significantly more buds/flowers because large trees of *Salvadora angustifolia* in their home range were flowering during the study period.

Argemone mexicana is suggested to be a critical fallback food for *Lemur catta* in the gallery forest at Beza Mahafaly during the dry season (Simmen *et al.* 2006; LaFleur 2008), and *Tamarindus indica* is considered an important keystone species for gallery forest dwelling *Lemur catta* at both Beza Mahafaly and Berenty field sites (Blumenfeld Jones *et al.* 2006; Gould *et al.* 1999; Koyama *et al.* 2006; Mertl-Millhollen *et al.* 2003; Rasamimanana and Rafidinarivo 1993; Sauther 1992, 1998; Sauther *et al.* 1999; Simmen *et al.* 2006; Yamashita 2002), because tamarind trees produce new leaves and fruit year-round and individual trees within an area are on different reproductive cycles at a given time (Simmen *et al.* 2006). Further, tamarind fruit and leaves are high in protein and calcium (Mertl-Millhollen *et al.* 2003; Rasamimanana and Rafidinarivo 1993; Sauther 1992, 1994), which are important

Table VIII Proportion of feeding agonism related to the top 5 (Green group) and top 6 (Black group) most frequently consumed plant species

Green group females Food species and food type	% of agonism	Black group females Food species and food type	% of agonism
Leaves of <i>Argemone mexicana</i> (U)	66	Fruit (U) and leaves (U) of <i>Tamarindus indica</i>	Fruit=33.2 Leaves=0.8
Fruit (U) and leaves (U) of <i>Tamarindus indica</i>	Fruit=19.3 Leaves=0.7	Human food scraps (U)	27
<i>Tridax procumbens</i> leaves (U)	8	Leaves/ flowers (U) of <i>Salvadora angustifolia</i>	14
Leaves of <i>Ipomaea</i> sp. (N)	5	Fecal matter (U)	9
Leaves of <i>Pentopetia</i> sp. (N)	1	Bea leaves (U)	9
		Leaves and flowers (N) of <i>Quisvianthe papinae</i>	7

U = usurpable food item; N = nonusurpable food item.

nutrients for reproductive females. Few other species in the region produce fruit and flowers during July and August; thus ring-tailed lemurs take advantage of the temporally diverse cycles (Gould *et al.* 1999; Sauther 1992, 1998). In our study, *Tamarindus indica* was important, composing 25% of the total food consumed in both groups, but was used to a lesser degree than documented in other gallery forest studies: 35–60% (Koyama *et al.* 2006; Mertl-Millhollen *et al.* 2003; Rasamimanana and Rafidinarivo 1993; Sauther 1992).

Human foods. Human food scraps were an important part of the diet of Black group females. Living in close proximity to human habitation provides many primate groups with the opportunity to sample novel human foods, e.g., olive baboons (Altmann *et al.* 1993; Strum 1984), long-tailed macaques (Fuentes *et al.* 2002), rhesus macaques (Ghimire 2000), Tibetan macaques (Zhao 1999), red colobus (Siex and Struhsaker 1998), and vervets (Saj *et al.* 1999). Saj *et al.* (1999) suggested that human foods are usually of higher quality than wild food; therefore individuals can meet their nutritional needs more rapidly, leading to improved foraging efficiency and increased resting and social time.

Optimal foraging theory suggests that animals should seek to maximize their net rate of energy intake at high benefit and low cost (Pyke *et al.* 1977). During seasons of food scarcity and physiologically demanding periods such as gestation and lactation, the costs of not finding additional food resources could be great. Human foods are usually higher in calories, and in the case of food scraps produced at the BMSR camp, could be more abundant at times than wild foods are. Nevertheless, it is difficult to determine whether feeding on human foods as practiced by the nonreserve group reflects optimal foraging requirements due to resource scarcity, or is simply an example of individuals developing a preference for human foods (Altmann and Muruthi 1988).

Coprophagy. Fecal matter ranked 6th among the top 10 most frequently consumed foods by Black group. Explanations regarding the function of coprophagy by primates in natural habitats suggest that it could indicate insufficient roughage (Fritz *et al.* 1992) and food scarcity (Goodall 1986), and could contribute to the digestion of cellulose (Collett *et al.* 1984) or aid with the assimilation of vitamins and aid nutrient uptake, and provide energy (Fish *et al.* 2007; Graczyk and Cranfield 2003; Hladik 1978; Krief *et al.* 2004; Oxnard 1966). Although they are certainly plausible benefits for the ingestion of fecal matter by Black group females, there are potential costs. Sauther *et al.* (2006) suggested that the relatively recent arrival of humans and domestic livestock on Madagascar has meant that new parasites and diseases have likely been introduced into wild lemur populations living near human habitats, and that coprophagy in such situations exposes lemurs to potentially higher parasitic loads.

Female Rank and Food Type

The female dominance hierarchy in a ring-tailed lemur group is linear, transitive, and relatively stable (Nakamichi and Koyama 1997; Sauther 1992; Sauther *et al.* 1999; Taylor 1986). During our study, female dominance rank remained stable in both groups.

Hypothesis 2 was supported for Black group wherein lower-ranking females in Black fed more frequently on leaves, and higher-ranking females fed significantly

more often on human foods, which are of higher quality (Saj *et al.* 1999). Female rank did not affect frequency of food consumption in Green group, and higher-ranking females did not feed on higher-quality foods, such as fruit, more often than their lower-ranking conspecifics did. This contrasts with the results of Sauther (1992, 2002), who found that higher-ranking females in BMSR's gallery forest consumed significantly more fruit than those of lower rank did. The lower availability of fruit during our dry season study compared with in the rainy season could be a confounding variable, but high rank would likely entitle the individual to the few fruit available. It is likely that rank as related to food consumption varies from year to year and from one gallery forest group to another.

Hypothesis 3 also was not supported: Black group females exhibited neither higher rates nor more severe feeding agonism in their sparser environment vs. that of Green group's lush gallery forest habitat. Home range use by Black group was not markedly greater than that of Green group, though Black group females foraged more frequently than females in Green group did.

Food Size and Distribution and Feeding Competition

Reserve group The high rate of agonism associated with *Argemone mexicana* could be related to the fact that it grows in the dry riverbed of the Sakamena, but that the riverbed is submerged between October and March (Gould *et al.* 1999; Ratsirarson *et al.* 2001; Sauther 1992); therefore *Argemone mexicana* is a seasonal, temporal food source, and the only one available in the riverbank when it is exposed. *Argemone mexicana* is high in protein and other essential nutrients (LaFleur 2008), and occurs in concentrated clumps. An individual sits at one plant and ingests the relatively large, thorny leaves slowly one at a time probably to avoid injuring its mouth (LaFleur 2008). Thus, individual plants are monopolizable, and leaves are easily usurpable, even though an entire area is not. Isbell (1991) suggested that if clumped monopolizable foods are present, then a hierarchical priority of access should be evident. However, despite the high proportion of agonism associated with this important seasonal food resource, rank effects were not apparent between females, probably because of the wide distribution of *Argemone mexicana* in the riverbed. Lower-ranking individuals can easily move to a different plant if displaced and if the leaves upon which they were feeding were usurped. In an earlier study at the site, Sauther (1992) also noted a high degree of agonism and no rank effect for *Argemone mexicana*.

Tamarindus indica are randomly distributed throughout the reserve, i.e., not growing in clumps, and had large, full crowns. An entire group of ring-tailed lemurs can spread out and feed within a tamarind tree crown without a great deal of interaction between individuals, which reduces the opportunity for one individual to monopolize a particular area. According to female feeding competition theory (Isbell 1991; Isbell and Pruettz 1998; Isbell *et al.* 1999), a species such as *Tamarindus indica*, which produces food year-round and is of substantial height, width, and crown area, should cause marked feeding agonism and competition. Competition should not be intense at a feeding site that is not rapidly depleted and has a fairly even distribution of resources throughout because an entire group can

disperse and feed without needing to contest for resources. In a year-long study at BMSR gallery forest, Sauther (1992) found both low agonism rates and no rank effects in relation to *Tamarindus indica*. However, during our study, the second highest rate of feeding agonism occurred over tamarind fruit and leaves, though higher-ranking females did not consume more of them than females of lower rank did. Again, such agonism is probably related to the size of the items versus other food items consumed in the dry season, i.e., individuals must hold the foods manually and take multiple bites, and as such, the size properties and usurpability of the items contributed to higher rates of agonism.

Nonreserve group The highest feeding agonism over frequently ingested food resources occurred over tamarind leaves and fruit, followed by human food scraps. Human food scraps in the research camp were distributed in discrete patches: food peeling areas and garbage pits behind each camp residence were small enough for only 1 or 2 high-ranking females to monopolize at one time. Thus, monopolizability, but not usurpability, is related to this food resource. One could consider fecal matter a novel food source, but lemurs frequently consumed it (6th of the 10 top foods). The clumped distribution of fecal matter, longer processing time at the food site, and size of the food item resulted in opportunities for usurpability, and the factors in turn related to high rates of agonism when consumed (Isbell 1991; Isbell and Pruetz 1998; Isbell *et al.* 1999). Wood containing termite leavings, spider webs, and bird's nests are also novel food items that lemurs rarely ingested and they were highly contested.

Our hypothesis 4 was supported for both groups: greater instances of agonism occurred over larger, usurpable food items.

Conclusions

The dry season, when female *Lemur catta* are pregnant and lactating, is a time of limited resources, both within and outside of the BMSR (Sauther 1992, 1994, 1998), and interfemale feeding competition is highest (Sauther 1993). During mid-to-late gestation and at the height of the dry season, monopolizability, quality, and size of food resources in both microhabitats dictated the type of competition that we recorded for females of both study groups, i.e., both situations strongly suggested contest competition (van Schaik 1989) and feeding models related to monopolizability and usurpability as proposed by Isbell (1991), Isbell and Pruetz (1998), and Isbell *et al.* (1999). Contest competition was directly influenced by type and quality of food consumed. When reserve group females fed on usurpable leaves of *Argemone mexicana* and fruit and leaves of *Tamarindus indica* which are high in protein, calories, and other nutrients, agonism rates were elevated and rank expressed. When nonreserve group females fed on monopolizable and nutritious human foods at the BMSR camp, a high proportion of agonism occurred, and high-ranking females had priority of access.

Acknowledgments We thank ANGAP and Joel Ratsirarson, ESSA-Forêts, Université d'Antananarivo for research facilitation and for granting us permission to conduct this study at BMSR. A. Gemmill

especially thanks B. Temple and D. Razanadrainy for their excellent research assistance in the field, and Dada for plant identification. This project was funded by a grant to L. Gould from the Natural Sciences and Engineering Research Council of Canada (NSERC). All research described in this manuscript complied with protocols approved by the University of Victoria's Animal Care Committee.

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