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Diets of Two Lemur Species in Different Microhabitats in Beza Mahafaly Special Reserve, Madagascar

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Studies of primate diets usually focus on differences that distinguish species or populations. However, variation in diet can occur at a more local level of groups within a population, especially in a non-homogeneous habitat. I compared dietary variation in food composition and toughness across groups of 2 lemur species in Beza Mahafaly special reserve, Madagascar. Beza Mahafaly contains an 80-ha reserve (Parcel 1) that, while small, hosts a dense population of Lemur catta *(ring-tailed lemurs) and* Propithecus verreauxi verreauxi *(sifakas). Microhabitats in the eastern vs. western sides of the parcel are structurally and floristically distinct. Sifakas in this parcel have small, discrete home ranges and are morphological folivores. For these reasons, I expected that the 6 groups studied would eat a different menu of food plants but with similar toughness values. Ring-tailed lemurs have comparatively large, overlapping home ranges, and I expected that the 5 study groups would eat similar foods. Despite living in different microhabitats across the parcel, sifakas exhibit high dietary uniformity both in dietary plant species composition and the toughness of the foods. Food selection in sifakas operates on two distinct levels. Sifaka groups share many key food species that appear independent of local abundances, but the ranking of the foods within each group appears related to availability. Ring-tailed lemur groups are more heterogeneous in the composition of their diets relative to sifakas, though the time spent feeding on individual foods reveals a marked preference for the fruits of* Tamarindus indica *by all groups. Food toughness is consistent across the parcel with the exception of the most western group. Ring-tailed lemurs are highly specific*

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feeders, but indiscriminate nibblers. Sifakas are targeted, balanced feeders. There does not appear to be a consistent microhabitat effect operating across species. Differences within sifaka and ring-tailed lemur populations in food composition and toughness, however, correspond to an east-west microhabitat gradient. Measures of dietary flexibility must take into account not only the plant species consumed and the different parts eaten but also their associated food properties and proportion of time spent feeding on them.

KEY WORDS: lemurs; diet; mechanical properties; food toughness; microhabitats.

INTRODUCTION

Most studies of primate diets have been concerned with differences that discriminate species or populations from one another (Hemingway, 1998; Overdorff and Strait, 1998; Powzyk, 1996; Tan, 1999; Ungar, 1995; Yamashita, 1996, 2000). However, groups within populations can exhibit differences in diet that reveal local conditions and demonstrate degrees of variation within a species. Information on such a fine scale can further provide some measure of dietary flexibility within a species that enables them to cope with environmental perturbations.

Parcel 1 at Beza Mahafaly Special Reserve, Madagascar, presents a unique opportunity to investigate groups of lemur species due to a convergence of several factors: a confined area, high population densities of two lemur species, and presence of distinct microhabitats throughout their range (Sauther *et al.*, 1999).

The reserve is located in southwestern Madagascar and consists of two parcels of land that are set aside as protected areas. The forest is a tropical, deciduous dry forest (Sussman and Rakotozafy, 1994). Parcel 1 is the main research site. Although only 80 ha, it contains dense populations of ring-tailed lemurs (*Lemur catta*) and sifakas (*Propithecus v. verreauxi*) and a diversity of microhabitats ranging in an east-west gradient from a riverine gallery forest to a grassy xeric habitat (Sussman and Rakotozafy, 1994). The differences in microhabitat affect food availability. It is a highly seasonal environment characterized by distinct wet and dry seasons. During the course of the study, the wet season, from November to March, had 772 mm of rainfall with an average daily temperature maximum of 38°C and a minimum of 21°C. In contrast the dry season had 94 mm of rainfall and average maximum and minimum temperatures of 34°C and 12°C, respectively.

Earlier work showed that lemur populations as a whole segregate in Parcel 1 in terms of some mechanical properties of their diets (Yamashita, 1996). Mechanical properties are sensitive to differences within food categories, e.g., all mature leaves do not have the same toughness, which may be important to the lemur consumer and affect food choice but not be evident from an examination of dietary categories alone.

I compared groups within populations of two lemur species and asked if their overall diets are distinct from one another and if lemur groups that occupy the same microhabitat exhibit dietary similarities. I compared diets by contrasting both the plant species eaten by the groups and the time spent feeding on specific plants. Sifakas have restricted home ranges (Kubzdela, 1996, 1997; Richard *et al.*, 1991); therefore, microhabitat differences may affect them to a greater degree than more widely ranging species such as ring-tailed lemurs (Sauther *et al.*, 1999). I predicted that the overall plant species composition of sifaka diets would differ across their range, but that they would exhibit similar toughness values as a result of their specialized morphology. I predicted that ring-tailed lemur groups would have similar diets with similar toughness as a result of larger, more overlapping ranges.

MATERIALS AND METHODS

Microhabitats Within Parcel 1

In a paper on structural analysis of Parcel 1, Sussman and Rakotozafy (1994) described microhabitats by enumerating differences in plant species composition and forest structure between the eastern and western areas. In order to quantify structural differences in microhabitat throughout the parcel, I chose 10 of the 20 plots that Sussman and Rakotozafy used in their phenological analysis in 1994. The 2 × 50-m plots are scattered throughout the parcel and often occur within the home ranges of the focal sifaka and ring-tailed lemur groups (Fig. 1(a), Table I). I identified all trees with dbh > 2.5 cm, measured their diameters, and estimated their heights. The trees are in

Table I. Phenology plot locations compared to Sussman and Rakotozafy (1994)

Plot numbers		
This study	S & R	Location
1	3	Orange E/Pink 1
2	4	Yellow E/Blue 3
3	8	Blue E/Blue 2
4	1	Green E/Pink 2
5	10	Blue E/Pink 3
6	11	Black/Blue 2
7	12	Black/Pink 3
8	14	Yellow W/Pink 3
9	19	Blue W/Pink 1
10	17	Green W/Blue 2

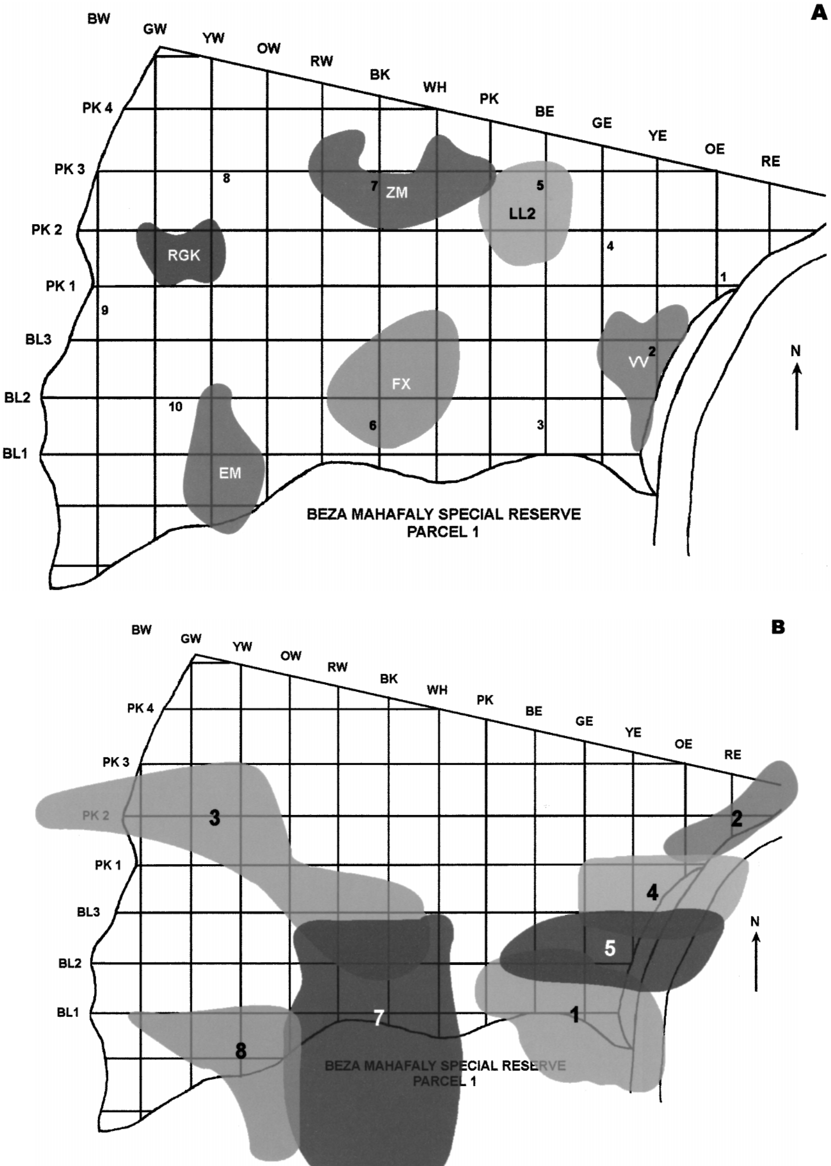


Fig. 1. (a) Home ranges of sifaka groups studied: Rengoroke (RGK), Emelia (EM), Zafmad (ZM), Felix (FX), Lolo 2 (LL2), and Vaovao (VV). Scale: one square approximately equals 1 ha (each side = 100 m). Numbers indicate locations of phenological plots. (b) Home ranges (core areas) of ring-tailed lemur groups. Note: group numbers do not follow those in earlier publications on the groups (Sauther *et al.*, 1999), and there is no Group 6. Map of Parcel 1 modified from Sussman (1991) after Jeff C. Kaufmann.

3 size categories based on dbh and height (Sussman and Rakotozafy, 1994). Small trees have dbh <10 cm and are <5 m tall; medium trees are 10–25 cm dbh and 5–15 m in height; large trees have dbh >25 cm and are >15 m tall.

In addition, I monitored phenophases—new leaf flushes, flowers, fruits, mature leaves—on a 0–4 scale of increasing abundance (from 0 = 0% to 4 = 100%) semi monthly throughout the study period. I contrasted abundance scores and structural characteristics of trees in eastern and western plots to check for differences between the halves of the parcel.

Focal Observations and Plant Collection

I observed 6 sifaka and 5 ring-tailed lemur groups. Sifaka group sizes ranged from 4 to 7 individuals. I marked their locations on a map of Parcel 1. The ranges in Fig. 1(a) are fairly accurate representations of actual home ranges based on observations throughout the year. The study groups were not overlapping; intervening adjacent groups are not shown.

Ring-tailed lemur groups contained from 10 to >14 individuals. In Fig. 1(b) group ranges of *Lemur catta* are approximate and depict the areas where I most often found and followed them. Sightings ad libitum of the groups occurred outside the ranges shown. Groups overlapped extensively (Sauther *et al.*, 1999). I also encountered unidentified groups within Parcel 1, but did not follow them.

Identifying collars and pendants on individual animals facilitated focal observations. I conducted continuous bout observations on focal subjects that were switched every 10 min. I noted time spent on basic behaviors of feeding, movement, resting, and social activities and further detailed feeding behaviors by noting the plant species eaten, the exact part eaten, food preparation techniques employed, and ingestive behaviors.

I tagged foods trees during observations for later collection of specimens. In some cases, lemurs dropped foods, which I collected. I usually collected and tested foods on the same day as observations, or ≤24 h of observation. Many of the foods were either chewed and dropped by the lemurs or had bite marks.

The plant species eaten by intraspecific groups are in Appendix. I checked taxonomic information for floral species in the Appendix and Table II with the TROPICOS database on the Missouri Botanical Gardens website.

Plant Testing

I tested food toughness with a portable tester (Darvell *et al.*, 1996), which can be fitted with interchangeable parts to perform a variety of mechanical

Table II. Distribution of plant species in individual plots

#	Family	Scientific name[a]	Vernacular name	Plot numbers									
				1	2	3	4	5	6	7	8	9	10
1	FABACEAE	*Acacia rovumae*	robontsy		2			1	2				
2	EUPHORBIACEAE	***Acalypha decaryana***	tainajajamena				1						
3	BURSERACEAE	*Commiphora brevicalyx*	taraby			1							
4	CAPPARIDACEAE	*Crateva excelsa*	akaly	1	4	1	5	1					
5	RUBIACEAE	*Enterospermum pruinosum*	mantsake	7	1	1	3		1				
6	TILIACEAE	*Grewia* sp.	malimatse			1							
7	OLEACACEAE	***Noronhia* sp.**	mantsedrano	2				1					
8	APOCYNACEAE	*Roupellina boivinii*	sabonto		2								
9	RUBIACEAE	***Xeromphis* sp.**	lamotimboay	1	5	1		1					
10	FABACEAE	*Acacia bellula*	tratriotse									6	1
11	FABACEAE	*Albizia* sp.	halimboron'ala						9				
12	MELIACEAE	*Cedrelopsis grevei*	katrafay					1		3	1		2
13	BURSERACEAE	*Commiphora simplicifolia*	tsingatse							1			
14	FABACEAE	*Dichrostachys humbertii*	avoha							1			
15	EBENACEAE	***Diospyros sakalavarum***	kibaintsihotse				1		1				
16	STERCULIACEAE	*Dombeya ambalabeensis*	satro						6				
17	BIGNONIACEAE	***Fernandoa madagascariensis***	tsomontsoy						1	2			
18	TILIACEAE	*Grewia franciscana*	tainkafotse						7		3		4
19	TILIACEAE	*Grewia leucophylla*	tratramborondreo						3		3		3
20	TILIACEAE	*Grewia* sp.	maintyfototse									5	
21	TILIACEAE	*Grewia triflora*	sele						1	1			
22	BIGNONIACEAE	***Rhigozum madagascariensis***	hazontaha						1	8		2	
23	SPHAEROSEPALACEAE	*Rhopalocarpus lucidus*	tsiongake										5
24	OPILIACEAE	*Rhopalopilia perrieri*	karimbola									1	
25	EUPHORBIACEAE	*Suregada chauvetiae*	hazombalala								6		1
26	PORTULACEAE	*Talinella dauphinensis*	dango					1			2		2
27	COMBRETACEAE	*Terminalia fatraea*	fatra									1	
28	COMBRETACEAE	*Terminalia mantaly*	taly					1			1		
29			volivazaha										1

30	SALVADORACEAE	*Azima tetracantha*	filofilo	5	6	1	4		4		4		
31	BURSERACEAE	*Commiphora aprevalii*	daro	2				1		3			1
32	BURSERACEAE	***Commiphora grandifolia***	daromangily			1				1			
33	EUPHORBIACEAE	*Euphorbia tirucalli*	famata			3				4	2	4	
34	TILIACEAE	*Grewia calvata (lavanalensis?)*	tsikidrakitse	1							2		
35	TILIACEAE	*Grewia grevei*	kotipoke	1							1		
36	FLACOURTIACEAE	*Physena sessiliflora*	fandriandambo			2						1	
37	MELIACEAE	*Quivisianthe papinae*	valiandro		2	1			1				3
38	SALVADORACEAE	*Salvadora angustifolia*	sasavy	1		1						2	
39	FABACEAE	*Tamarindus indica*	kily	4	5	2	1	5	2		2		1

Note. Eastern distribution of species 1–9 and western distribution of species 10–29. Species 30–39 are in both areas, though even here, individuals tend to clump (or occur in higher numbers) in either the east or west. Total numbers of species = 8 E, 19 W, 12 both. Total numbers of individual trees = 241 in ten plots.

[a] Plant species in bold are not food plants for the lemurs.

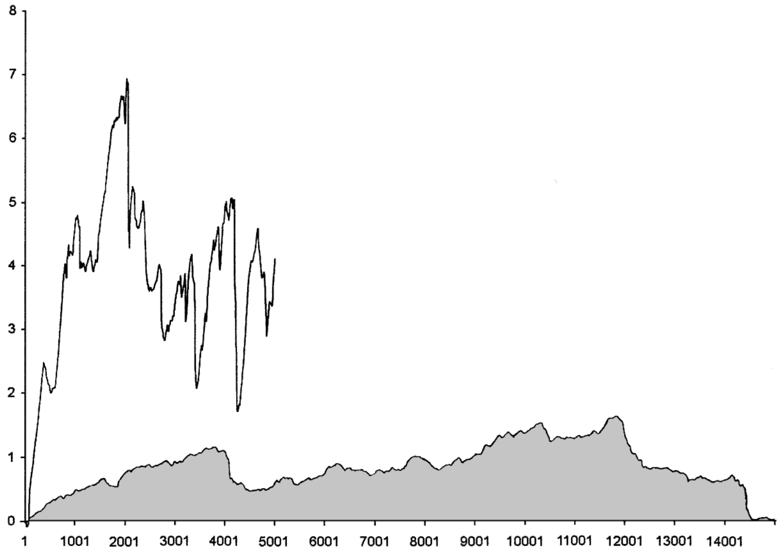


Fig. 2. Toughness comparisons of ripe fruit shell and unripe fruit (shaded portion) of *Tamarindus indica*. Displacement in mm on X-axis; stress in J m^{-2} on Y-axis.

tests. I used a scissors cutting test to measure food toughness. In a scissors test, a food item is placed on open scissor blades that are mounted to the tester. A platform with an attached load cell (either 10 or 100 N) is slowly lowered onto the blades. As they close and cut the food, the force-displacement signal is fed to an electronics box that calculates the integration of the force-displacement curve. After the food is cut to a preset length, a second, empty pass of the scissor blades alone subtracts out the work of friction.

The output on the computer screen is a force-displacement diagram (Fig. 2): force is on the Y-axis and displacement is on the X-axis. The computer program returns toughness values in J m^{-2}, which is the area under the force-displacement curve, or the work of fracture.

I discriminated and tested separately developmental stages of all fruits and leaves eaten by the lemurs and paid careful attention to the exact part of the plant eaten by them. For example, leaf tips of immature leaves are discriminated from leaf bases.

Comparisons of Lemur Groups

I compared dietary similarities of the lemur groups graphically with cluster analyses, using a Euclidean distance metric and nearest-neighbor joining method.

I also quantified dietary overlap in terms of plant species eaten among intraspecific groups by calculating similarity coefficients in SYSTAT for binary, presence/absence data. These coefficients are derived from the numbers of floral species eaten in common by two groups and divided by the total number of floral species. Different coefficients are produced depending on the assumptions made about how tied scores (1-1 or 0-0) are treated. I used the coefficient that excludes 0-0 pairs, so that any two groups compared are not penalized for foods that do not occur in their diets (but occur in others). Furthermore, the method does not assume that all the foods eaten by the species are equally available to all groups. Another approach would be to include all tied scores in the coefficient calculation. This structure assumes that foods that are not eaten by two groups (0-0) are as important as foods that are eaten (1-1). However, the assumption, is that all foods are equally available to all groups, which is not the case.

A qualitative approach like the one above gives information on usage based on the presence of a floral species within a particular microhabitat, but it gives equal weight to foods that may be included infrequently. The correlational index (I_c) takes into account time spent feeding on individual food items (Sussman, 1987). A measure that determines how groups allocate feeding time relates the relative importance of certain plant species to a group. The index is calculated as

$$I_c = \frac{\sum X_i Y_i}{\sqrt{\sum X_i^2 \sum Y_i^2}}$$

in which X and Y are the time spent feeding by the two groups for each i^{th} plant species eaten.

I compared toughness of the plant parts for all groups within species with analysis of variance (ANOVA) and tested contrasts between groups with Bonferroni post hoc tests. Finally, I tested contrasts between species with t-tests using the Bonferroni criterion for multiple tests. Before statistical analyses, I log-transformed all data for normality.

RESULTS

Microhabitat Differences

Sussman and Rakotozafy (1994) separated 20 2×50-m plots into 10 eastern and western plots before their study. Plots further from the river had a higher density of trees, and plots in the eastern half of Parcel 1 had more trees >25 cm dbh. Only *Tamarindus indica* (kily) and *Azima tetracantha* (filofilo) were common in both areas.

My results are very similar to those of Sussman and Rakotozafy (1994) since my plots were a subset of theirs. Plots further from the river had more individual trees (96 in the east, 136 in the west) and higher specific diversity (8 in E, 19 in W, 12 in both). Contrasts of dbh and height are not statistically significant between eastern and western plots, though there are slightly higher numbers of large trees (>25 cm dbh: Fig. 3(a)) and tall trees (height > 15 m: Fig. 3(b)) in the eastern half of Parcel 1.

Table II illustrates the distribution of trees in the 10 plots. Some species were readily assigned as eastern or western, and even those found

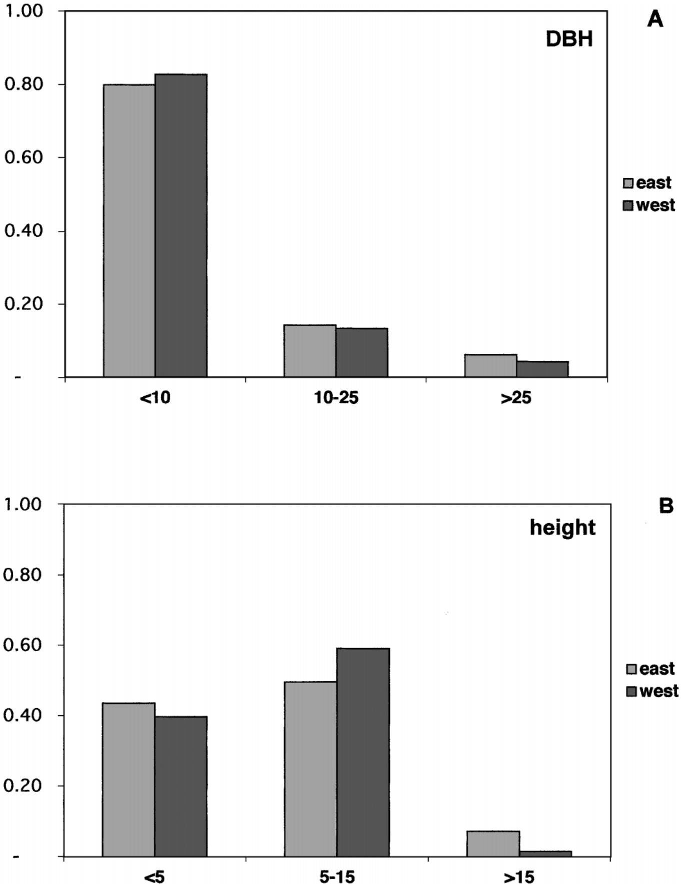


Fig. 3. (a) dbh of trees by percent in eastern vs. western parts of Parcel 1 in 3 size categories. (b) Height of trees by percent in east vs. west in three height categories.

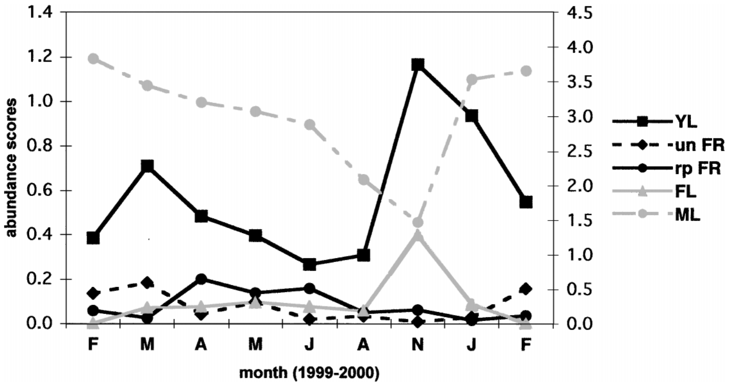


Fig. 4. Abundance scores of major food categories throughout the year averaged from 10 phenological plots. Note: no data for July, September, October, December. Young leaves (YL), unripe and ripe fruit (FR), and flowers (FL) on left Y-axis; mature leaves (ML) on right Y-axis.

throughout the parcel tended to cluster on one side or the other. As noted by Sussman and Rakotozafy (1994), *Azima tetracantha* (#30) and *Tamarindus indica* (#39) occurred in relatively high densities in both areas, though they were less frequent further west. Most of the tree species in the plots are food species for the lemurs, especially for sifakas.

Fruit, immature and mature leaf, and flower availability are indicated in Fig. 4. Phenology of the plots demonstrated only subtle differences between the two sides of the parcel, so I will not discuss results for individual plots. The abundances (Fig. 4) are averages for all plots. The scores generally agree with those of Sauther (1998). New leaf flushes peaked in November during the height of the rainy season, and there was another, smaller peak in March at the end of the rains. Flowering also peaked during the height of the rainy season. Unripe fruits were most abundant in March, preceding a peak for ripe fruits in April. Ripe fruits were available from April to June at the transition between the rainy and dry seasons. Mature leaves were available year-round, though their numbers decreased in the deciduous forest in November, coinciding with the sharp rise in new leaf flushes.

Microhabitats on different sides of the parcel are structurally and floristically distinct.

Group Comparisons of Plant Species

I compared all plant species in the lemur diets across groups. Similarity coefficients for intergroup comparisons are in Tables III and IV. Sifaka

Table III. Dietary overlap among sifaka groups

	RGK	EM	ZM	FX	LL2
EM	.550				
ZM	.391	.412			
FX	.571	.500	.477		
LL2	.314	.350	.244	.382	
VV	.304	.308	.321	.386	.333

groups had a higher degree of dietary overlap ($n = 70, \overline{X} = .390$) than that of ring-tailed lemur groups ($n = 54, \overline{X} = .310$). Adjacent groups were not necessarily the most similar in plant species exploited for either lemur species. Groups of *Lemur catta* groups were not sampled equally. Most of the observations are confined to groups 1, 3, 4, 5, and 7 so I omitted groups 2 and 8 from the analyses.

The dendrogram for sifakas (Fig. 5(a)) shows that Rengoroke and Felix form a tight initial nest; they are then joined by Emelia, Lolo 2, then Zafmad, and finally by Vaovao. Vaovao is the eastmost group near the river; the other groups live in drier habitats further west. Among ring-tailed lemurs (Fig. 5(b)), Groups 1 and 5 form a tight initial nest, joined by 7, then 4 and 3 outside it. Groups 1, 4, and 5 are the eastmost groups; Groups 3 and 7 range further west. The clustering pattern does not reflect an east-west divide.

I also conducted a cluster analysis for a combined species data set with all groups included. The individual specific groups clustered together, which indicates that despite differences in microhabitat and some differences among individual groups, the plant species in lemur diets are species-specific.

The intraspecific correlation indices, which take into account the time spent feeding on each plant species, are an interesting counterpoint to the similarity coefficients (Tables V and VI). Accordingly, sifaka groups had a

Table IV. Dietary overlap among ring-tailed lemur groups

	1	3	4	5
3	.321			
4	.345	.273		
5	.520	.242	.265	
7	.346	.310	.176	.300

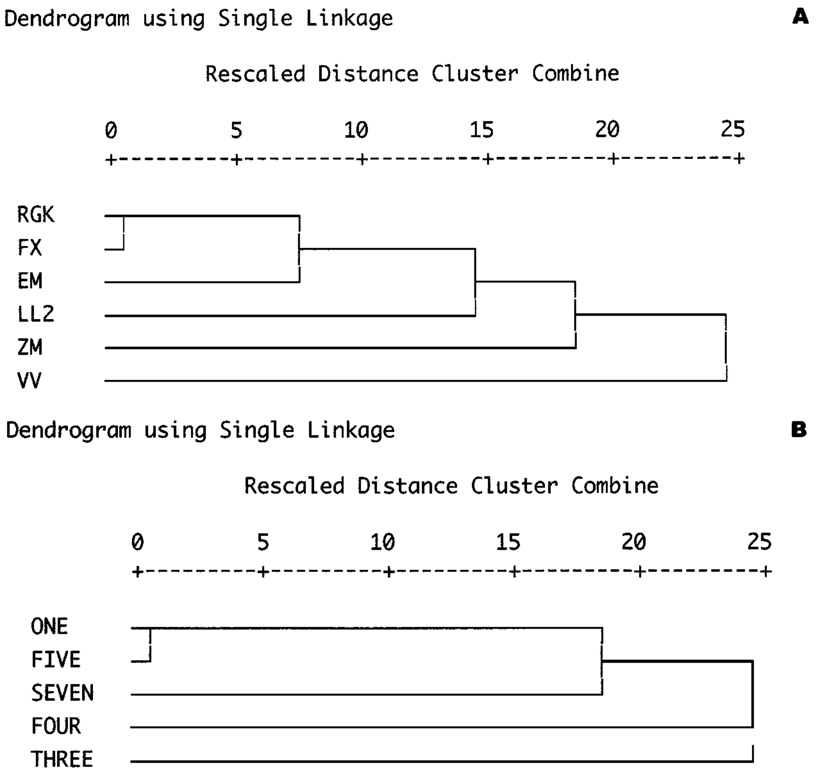


Fig. 5. (a) Dendrogram of sifaka groups based on florisitic diversity of diet. Clustering is Euclidean distance metric, single linkage method. (b) Dendrogram of ring-tailed lemur groups based on florisitic diversity of diet. Clustering is Euclidean distance metric, single linkage method.

lower degree of overlap ($\overline{X} = .593$) than those of ring-tailed lemur groups ($\overline{X} = .670$). With data on how much time lemur groups spend on individual plant species, adjacent groups were generally more similar for both lemur species.

Table V. Correlational indices among sifaka groups

	RGK	EM	ZM	FX	LL2
EM	.691				
ZM	.542	.649			
FX	.694	.587	.715		
LL2	.566	.568	.786	.754	
VV	.329	.504	.559	.510	.448

Table VI. Correlational indices among ring-tailed lemur groups

	1	3	4	5
3	.741			
4	.523	.704		
5	.578	.748	.769	
7	.465	.743	.722	.704

Toughness Among Groups

Food toughness is very similar among sifaka groups (Fig. 6(a)). The ANOVA results indicate that sifakas eat foods of similar toughness (F = 1.614, p = .155). Pairwise tests post hoc of the groups are also not significant for any pair of groups.

In contrast, ring-tailed lemur food toughness is significantly different among groups (F = 3.414, p = .010) [Fig. 6(b)]. Pairwise contrasts of individual groups reveal that foods of Group 3 are tougher than those of Groups 7 (p = .034) and 4 (.022).

Toughness Between Species

Sifakas and ring-tailed lemurs do not differ in the overall toughness of their foods (F = .778, p = .437), though sifakas have slightly tougher diets. However, toughness of ring-tailed lemur diets is probably overestimated. If the problematic food item (ripe fruit of *Tamarindus indica*) is removed, the two species differ in dietary toughness (F = 2.092, p = .037). Interspecific pairwise comparisons of groups are not significant. However, without ripe fruit of *Tamarindus indica*, the Zafmad diet is tougher than those of Groups 4 (p = .000), 5 (.000) and 7 (.001), and Felix foods are tougher than those of Groups 4 (.002) and 5 (.001). In no case is the diet of a ring-tailed lemur group tougher than that of a sifaka group.

DISCUSSION

The hypotheses posed at the beginning of this paper were variably successful in predicting sifaka and ring-tailed lemur dietary behavior. Despite their restricted ranges, sifaka groups eat many of the same plant species counter to prediction, but their overall diets are similar in toughness as expected. Individual groups of *Lemur catta* generally do not have the same menu of plant species as other groups (Table IV), but they concentrate most of their feeding time on the same foods. In terms of food toughness, while one ring-tailed lemur group differs from the rest, the groups are quite similar overall.

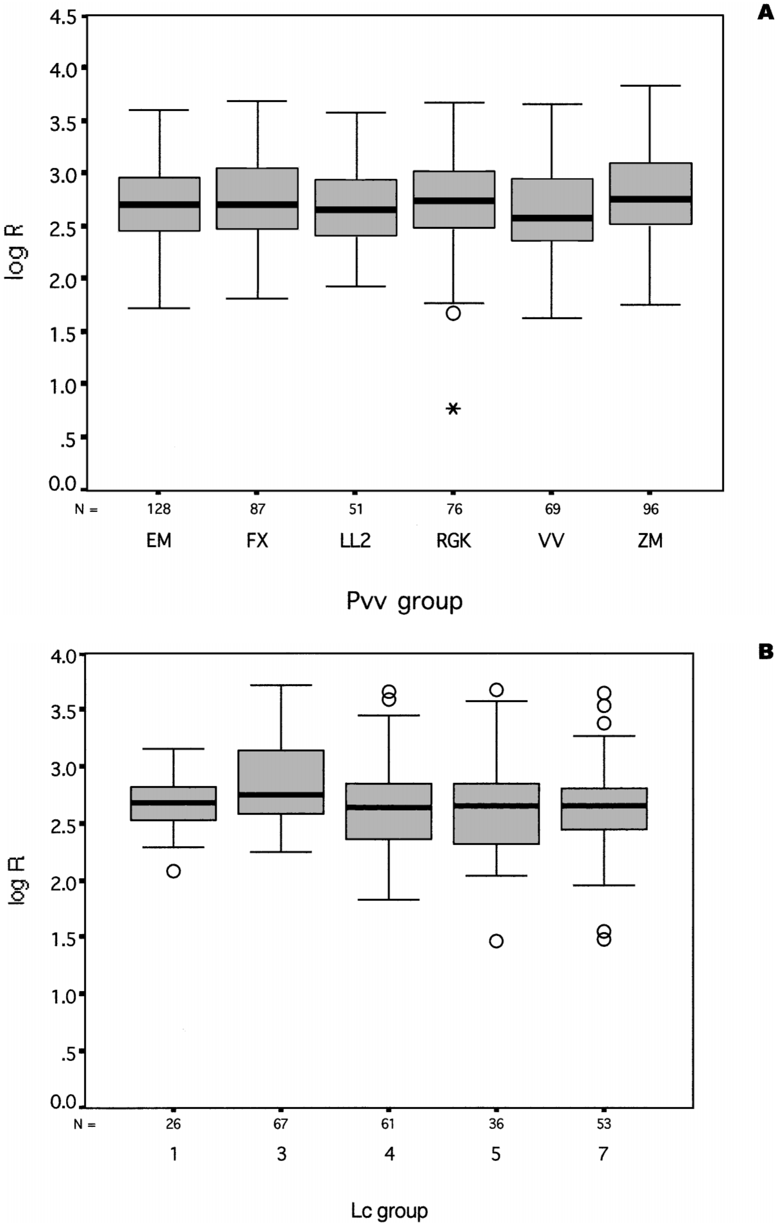


Fig. 6. (a) Dietary toughness across sifaka groups. Boxplot follows conventions: box surrounds 50% of data, median represented by line in box, whiskers connect high and low values, outliers indicated by circles. (b) Dietary toughness across ring-tailed lemur groups. Conventions follow Fig. 6a. Groups 2 and 8 omitted. Upper outliers are ripe fruit of *Tamarindus indica*.

Dietary Composition

The similarity coefficients and correlational indices appear to give contrasting pictures of dietary diversity among the lemur groups. On the basis of floral species consumed, sifakas have higher intergroup overlap than that of ring-tailed lemurs, but when the time spent feeding on the plants is factored in, ring-tailed groups are more similar to one another. The two sets of data relate complementary information. Specifically, they point out the overwhelming importance of the fruit of *Tamarindus indica* in the ring-tailed lemur diet (Table VII; Sauther, 1998; Yamashita, 2000). Kily fruit alone makes up 15–36% of the total yearly diet of ring-tailed lemur groups. The subsidiary diets beyond kily are largely non-overlapping among the groups, as Table IV illustrates.

Sifakas have a more extensive menu of floral species than that of ring-tailed lemurs, but they overlap broadly in the foods that they consume and distribute their feeding time more or less equally on them (Table VII). The rankings of the foods change from group to group.

The diets of the lemurs demonstrate patterns that are not strictly related to microhabitat or general food availability. I define availability simply as presence in phenological plots within or near a lemur group's range; it does not indicate relative abundance scores of phenophases. A lemur group exhibits selectivity when they eat a species that is not present in an overlapping or adjacent phenological plot.

Food selection in sifakas operates on several different levels. First, the actual menu of foods, especially those that overlap among groups, appears to be unrelated to local abundances. Second, the ranking of the foods within each group appears to be related to availability. Selectivity by sifakas is easier to demonstrate because they overlap on a number of floral species. There are several key food species that all the groups eat regardless of general availability, e.g., *Acacia bellula, Euphorbia tirucalli, Gonocrypta grevei* (Table II; Appendix). For example, *Euphorbia tirucalli* is a staple food in the diets of all sifaka groups, yet it is found only in the center and western phenological plots (#s 3, 7, 8, 9). *Acacia bellula* represents an even more extreme example; it is only found in the far western plots (#s 9, 10), yet is in the top 10 foods for all groups except Rengoroke (Table VII), for which it is thirteenth.

Even given that some of the phenological plots will miss common foods in a particular microhabitat, it is unlikely that all the plots in a particular segment of the forest would overlook a common tree. The distributions of floral species in Table II also indicate a fair representation of species as related to abundance in the phenological plots, but the trees in the plots are only approximate indicators of floral distribution within the parcel. The breadth of foods in sifaka diets do not appear related to their relative distribution in Parcel 1, though time spent feeding on them may be. For

Table VII. Time spent feeding on top 5 foods (cumulative for year)

Plant sp	Part eaten	%
Propithecus verreauxi verreauxi		
RGK		
Terminalia mantali	ML, FR	0.138
maintyfototse	all leaves	0.107
Tamarindus indica	FL, FR, ML, SD	0.106
Dichrostachys humbertii	all leaves	0.081
Grewia leucophylla	FR	0.073
EM		
Metaporana parvifolia	all leaves	0.116
Quivisianthe papinae	FL	0.086
Terminalia mantali	ML, FR	0.079
Tamarindus indica	FL, FR, ML, SD	0.071
Cedrelopsis grevei	FL & lf buds, all lvs	0.063
ZM		
Tamarindus indica	FL, FR, ML, SD	0.123
Dichrostachys humbertii	all leaves	0.120
Quivisianthe papinae	FL	0.104
sarivagnemba	ML, FL	0.095
Euphorbia tirucalli	yng stalks, FR	0.075
FX		
Dichrostachys humbertii	all leaves	0.146
Tamarindus indica	FL, FR, ML, SD	0.128
Grewia leucophylla	FR	0.115
Acacia rovumae	all leaves, buds	0.096
Acacia bellula	all leaves, FL	0.084
LL2		
Dichrostachys humbertii	all leaves	0.222
Quivisianthe papinae	FL	0.083
Acacia bellula	all leaves, FL	0.078
Tamarindus indica	FL, FR, ML, SD	0.076
Grewia triflora	ML	0.073
VV		
Tamarindus indica	FL, FR, ML, SD	0.141
Acacia rovumae	all leaves, buds	0.138
saritoboara	FR	0.108
roimaintyfototse	ML	0.083
Marsdenia cordifolia	all leaves	0.077
Lemur catta		
Group 1		
Quivisianthe papinae	FL	0.198
Tamarindus indica	FR	0.154
big bokobe	YL	0.097
bark/dead wood (lick)		0.082
river vine	FR	0.073
Group 3		
Tamarindus indica	FR	0.307
Quivisianthe papinae	FL	0.163
Grewia leucophylla	FR	0.124
Metaporana parvifolia	all leaves	0.061
unknown		0.046

(*Continued*)

Table VII. (*Continued*)

Plant sp	Part eaten	%
Group 4		
Tamarindus indica	FR	0.334
Marsdenia cordifolia	all lves, stlk	0.188
Gonocrypta grevei	all leaves	0.083
lianas	all leaves	0.056
saritoboara	FR	0.044
Group 5		
Tamarindus indica	FR	0.360
bark/dead wood (lick)		0.177
lianas	all leaves	0.080
velae	FL	0.054
Pentopetia grevei	all leaves	0.050
Group 7		
Tamarindus indica	FR	0.305
Metaporana parvifolia	all leaves	0.173
Combretum albiflorum	FL	0.104
Azima tetracantha	FR	0.100
Marsdenia cordifolia	all lves, stlk	0.056

example, *Terminalia mantaly* is eaten by all the groups except Vaovao, but the far western groups spend more time eating it, which coincides with its location in phenological plots (Table II). Beyond the species that are eaten in common among the groups, there are plants that are idiosyncratic to one or a few groups that are probably the result of availability.

The dendrograms in Fig. 5 do not support a strong microhabitat effect on food selection. The order of joining the dendrogram is not by adjacent groups, which perhaps reflects the overall similarities of the sifaka diets in Parcel 1 (Fig. 5(a)). In a study on groups of *Propithecus diadema edwardsi*, Hemingway (1998) found a similar pattern of high intergroup overlap in the foods eaten ($\overline{X} = 60\%$) that was not related to availability. For foods in common for all or most of the groups, it appears that sifakas are selective. The far eastern group, Vaovao (VV), is the exception. Its home range includes gallery forest bordering the river. The area is more lush than the west, with unique vegetation. Plants that occur in the drier soils of the west and form a major part of the sifaka diets, e.g., *Dichrostachys humbertii*, *Rhopalocarpus lucidus*, *Anacolosa pervilleana*, *Terminalia mantaly*, and *Terminalia fatraea*, are absent along the river, and are therefore not available to VV.

Similarities in sifaka diets across Parcel 1 follow a general east-west trend for foods that are eaten most frequently (Tables V and VI).

Selectivity in the dietary choices of ring-tailed lemur groups is more difficult to assess because, unlike sifakas, only fruit of *Tamarindus indica* are eaten universally and it is present throughout the parcel. The overlap of numbers of plant species by group is also lower than that for sifakas (Tables III and IV), and I did not count many of the foods eaten by ring-tailed lemurs, especially vines, in phenological plots. However, results of the correlational indices demonstrate that ring-tailed lemurs are more uniform in the foods that they spend the most time eating. The secondary foods in their diets appear to be related largely to local availability and opportunism. For example, fruit of the river vine was eaten by Groups 1 and 5 and appeared to be restricted to their territories on the southern bank of the river in Parcel 1. Similarly, the presence of malimatse in plot #3 falls exactly within the range of Group 1, and tratriotse in plots #9 and 10 is eaten only by Group 3 in the west. Nevertheless, ring-tailed lemur groups exercise some selectivity in their secondary diets. All groups except Group 4 eat the fruit of *Grewia leucophylla*, which occurs only in western phenological plots (Table II, Appendix), and *Cedrelopsis grevei*, which occurs in central and western plots, is eaten by all the groups except Group 1.

The dendrogram for groups of *Lemur catta* demonstrates that, with the exception of Groups 1 and 5, adjacent groups are not the most similar in total food composition (Fig. 5(b)). Because of their wide ranges and the fluidity of their boundaries, however, neighboring groups are not as clearly defined for *Lemur catta*. The cluster demonstrated that Group 3, which has the widest range within the parcel, is the outlier among the groups. Group 7 is more similar to Groups 1 and 5 than another eastern group, Group 4, is. The explanation may lie in the second most frequently eaten food for Group 4, *Marsdenia cordifolia* (bokabe), which was not eaten as frequently by the other eastern groups (Table VII). Bokabe is a vine, and a particularly luxuriant growth of it occurred in the middle of Group 4's territory, where they had primary access to it. Adjacent groups 1 and 5 were often within each other's territories; they form a tight initial nest in the dendrogram. The order of clustering among the eastern groups is somewhat surprising given that fruits are more abundant near the river and form a larger component of the diets of the ring-tailed lemurs that live there (8 fruit species vs. 4 in the west: Appendix). The time spent feeding on individual fruit species other than kily, however, was minimal (Table VII). Nevertheless, comparison between the two data sets demonstrates that while the entire menu of adjacent groups is individually diverse and idiosyncratic, neighboring groups of ring-tailed lemurs concentrate on similar plant species (Table VI).

In summary, sifaka groups appear less sensitive to microhabitat in terms of the plants included in their diets and the toughness of their foods. The relative importance of the foods by rank for each group, however, appears specific to local availability. Groups of *Lemur catta* are more idiosyncratic in the content of their diets, but kily fruit is such a dominant food for all the groups that all other foods must be considered secondary. For example, ring-tailed lemur populations experienced high mortality rates during a severe drought in 1991–92 (Gould *et al.*, 1999). The sifakas were not affected to the same degree though adult body masses decreased (Richard *et al.*, 2000).

Although supplemental plant species in ring-tailed lemur diets differ among groups, the primary kily fruit diet was unavailable—the fruiting peak occurs at the end of the wet season (Sauther, 1998; Fig. 4)—and the population declined. The majority of the sifaka diet is composed of leaf material. In the dry season, they incorporate mature leaves, a developmental stage that is generally avoided by ring-tailed lemurs but has the advantage of continuous availability for sifakas.

Taking the two data sets together, ring-tailed lemurs can be characterized as highly specific feeders but indiscriminate nibblers. Sifakas are targeted, balanced feeders.

Toughness Comparisons

Are toughness differences among groups within a species related to microhabitat differences? Few differences are present among sifaka groups in food toughness. Group 3 of *Lemur catta* eat tougher foods than other groups of *L. catta*, which may be related to their broader, western range in Parcel 1.

For sifakas, the extreme eastern group is the most divergent in the plants included in their diets, and for ring-tailed lemurs, the far western group (Group 3) eats tougher foods. Perhaps as a result of their dietary preferences, ring-tailed lemurs tend to cluster in the east near the river (Fig. 1(b)) and sifakas are more abundant in the west of Parcel 1. The outliers for the species occur in the less frequented areas. Toughness comparisons of the non-overlapping secondary dietary choices of ring-tailed lemurs point out the overall similarities of their diets, with the exception of Group 3. In other words, ring-tailed lemurs sample a broad range of foods but are limited by their mechanical properties. Sifakas include absolutely more plant species in their diets than ring-tailed lemurs eat (70 species versus 54), and they eat a broader range of tough foods.

Plants included in lemur diets are species-specific, no matter how much dietary variability is present within a species. Contrasts between species do not immediately point to an east-west divide in food toughness, since the sifaka groups that are most dissimilar from ring-tailed lemur groups (Zafmad and Felix) live in the center of the parcel. They also eat foods with similar toughness to those of ring-tailed lemur Groups 1 and 3 that are eastern and western groups, respectively. Their similarities do not appear to be related to similarities in habitat. Therefore, there is no evidence for a microhabitat effect operating across lemur species in the plant composition and toughness of their foods, which must be related to a strong intraspecific (species-specific) effect. Within each species, the distribution of groups is aligned along an east-west gradient related to preferences of the two species for either a wetter or drier habitat.

Toughness of Fruit of *Tamarindus indica*

Toughness results varied with the inclusion or exclusion of ripe fruit of *Tamarindus indica*. Figure 2 illustrates a force-displacement graph produced by a scissors test of a ripe fruit shell and unripe fruit of *Tamarindus indica*. The ripe shell is extremely brittle, producing many peaks as the scissors cut across it. The sharp drops in force occur when side cracks appear. Toughness of unripe kily fruits = 1313 J m^{-2} (mean value of 7 samples) and toughness of ripe kily fruits = 3504 J m^{-2} (mean of 16 samples: Yamashita, 2000). Toughness of ripe kily fruit shell is overestimated because of the cracks that appear on the side of the directed scissor cut as a result of uncontrolled, explosive crack growth. Instead of measuring toughness by the total displacement (set at 5 mm in the example), a better approximation of how ring-tailed lemurs break open the fruit would be to confine the measurement to the first force peak when the shell is breached. Once the lemurs have broken into the shell, it quickly falls apart.

This is not to say that sifakas never eat ripe kily fruit, but it is not a common food item and they eat it in a restricted time period. Sifakas eat unripe seeds of *Tamarindus indica*. *Lemur catta* will occasionally eat the unripe kily fruit, but again, this is relatively rare. Unripe kily fruit takes more work to breach than ripe fruit shells since it has to be continuously scraped and gnawed. In contrast, once the brittle casing of ripe fruit has been cracked, the jelly-like pulp can be licked off. Further, sifakas and ring-tailed lemurs have definite threshold hardness levels that define the species with sifakas tolerating much higher levels (Yamashita, 2000).

Food toughness and floral specific composition of sifaka diets are remarkably uniform across Parcel 1 (Tables III and IV), which begs the question of explaining what properties of particular foods are attractive to sifakas. Conversely, the foods may not pose significant deterrents to predation that others might. Sifakas are obligate folivores, and the similarities of their diets are probably related to the nutritional content and fiber provided by leaves. However, other dietary similarities such as a taste for seeds of *Tamarindus indica* and stalks of *Euphorbia* require further explanation. The breadth of the diets of *Lemur catta* appear to be relatively more diverse, which may be a result of more fine-grained microhabitat differences than those that I addressed. However, time spent feeding on specific foods show heavy reliance on the fruits of *Tamarindus indica* by ring-tailed lemurs. Sifakas and ring-tailed lemurs also have little overlap in their diets despite living sympatrically in a small area. Although ring-tailed lemurs appear to be more limited by mechanical properties of foods than sifakas are, this alone does not sufficiently explain the marked separation of the two species in the compositions of their diets.

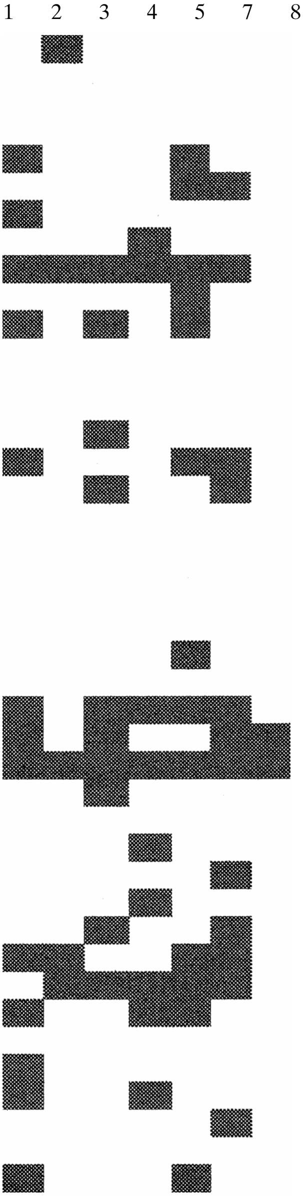
APPENDIX: PLANT SPECIES IN LEMUR DIETS

Plant sp[a]		Propithecus verreauxi					
Vernacular name[b]	*Part eaten*[c]	RGK	EM	ZM	FX	LL2	VV
acacia	YL		▨	▨			
akaly	ML			▨			
andranahaka	stalk						
angalora	YL			▨			▨
armed tree	YL					▨	
avoha	all leaves, FR	▨	▨	▨	▨	▨	
bageda	ML						
bea	ML						
big bokabe	rachis, YL						
big leaf vine	petiole						
bokabe	all leaves (all leaves, stalk)		▨			▨	▨
“clematis” vine	ML						
dango	FL, FR, all leaves (YL, stalk)		▨	▨	▨		
daro	YL, ML			▨			▨
famata	stalks, FR	▨	▨	▨	▨	▨	▨
fandriandambo	all leaves	▨	▨	▨	▨	▨	▨
fatra	ML,YL(FL, FR)	▨	▨				
filofilo	FR	▨	▨	▨			▨
forimbitike	ML						
hafotse ampelambatotse	YL			▨			
halimboron’ala	YL				▨	▨	
hary	all leaves						▨
hazombalala	FR	▨					
heart vine	ML					▨	
herb	all leaves						
karimbola mitsy	YL	▨					▨
katrafay	FL & leaf buds, all leaves, FR (ML, YL, shoots)	▨	▨	▨	▨	▨	
kililo	all leaves	▨	▨	▨	▨		▨
kily	FL, FR, ML, unrp sd (FR, YL, FL)	▨	▨	▨	▨	▨	▨
kisenendolo	all leaves						
kitohitohy	all leaves		▨				
kompitse	all leaves	▨	▨	▨	▨	▨	▨
kotipoke	YL, ML	▨	▨		▨	▨	▨
lamoty	FR						
large kililo	ML	▨					
latex vines	all leaves	▨		▨	▨	▨	▨
lianas	all leaves	▨	▨		▨	▨	▨
lisinamboa	all leaves						
maintyfototse	all leaves	▨	▨		▨		
malimatse	FR			▨			
mantsake	FR						
oxiala	ML						
pira	YL			▨			
river vine	FR						
robontsy	leaf buds, YL, ML	▨	▨	▨	▨	▨	▨
roi	FL, YL		▨			▨	
roimaintyfototse	ML	▨	▨	▨		▨	▨

(*Continued*)

Appendix: (*Continued*)

Lemur catta



Scientific name	*Family*
Acacia sp.	FABACEAE
Crateva excelsa	CAPPARACEAE
Commelina sp.	COMMELINACEAE
Secamone sp.	ASCLEPIADACEAE
Dichrostachys humbertii	FABACEAE
Marsdenia cordifolia	ASCLEPIADACEAE
Talinella dauphinensis	PORTULACACEAE
Commiphora aprevalii	BURSERACEAE
Euphorbia tirucalli	EUPHORBIACEAE
Physena sessiliflora	CAPPARACEAE
Terminalia fatraea	COMBRETACEAE
Azima tetracantha	SALVADORACEAE
	VERBENACEAE
Acacia sp?	FABACEAE
Albizia sp.	FABACEAE
Bridelia pervilleana	EUPHORBIACEAE
Suregada chauvetiae	EUPHORBIACEAE
Dialium madagascariense	FABACEAE
Cedrelopsis grevei	MELIACEAE
Metaporana parvifolia	CONVOLVULACEAE
Tamarindus indica	FABACEAE
Gonocrypta grevei	ASCLEPIADACEAE
Grewia grevei	TILIACEAE
Flacourtia ramontchii	FLACOURTIACEAE
Grewia sp.	TILIACEAE
Grewia sp.	TILIACEAE
Enterospermum pruinosum	RUBIACEAE
Dioscorea sp.	DIOSCOREACEAE
Landolphia sp.	APOCYNACEAE
Acacia rovumae	FABACEAE
Acacia sp.	FABACEAE

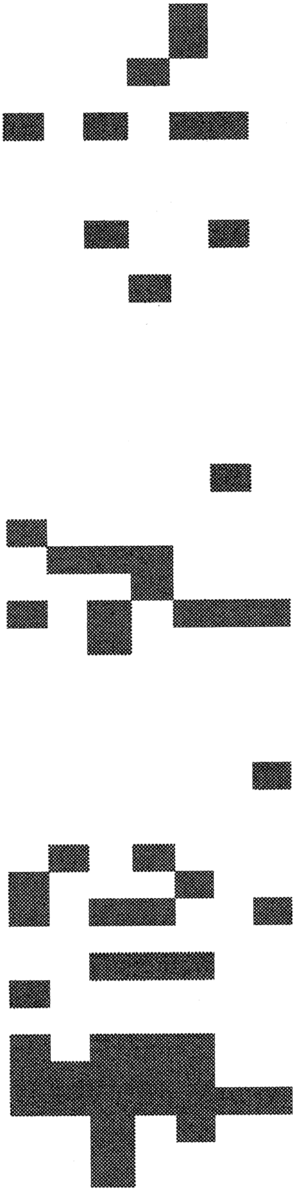
(*Continued*)

Appendix: (*Continued*)

Plant sp[a]		Propithecus verreauxi					
sabonto	all leaves	▨	▨				▨
sagnatry	all leaves						
sarirotsy	FR						
saritoboara	FR						▨
sarivagnemba	ML, FL			▨	▨		
sasavy	needles, bark (FR, all leaves)	▨	▨	▨	▨		
satro?	ML, stalk					▨	
sele bohoke	YL						▨
sele	all leaves		▨	▨	▨	▨	▨
shrubs	all leaves, FL	▨	▨				
small tree	YL	▨					
soamangy	FL						
tagnatagna	ML						▨
tainkafotse	YL, FR	▨		▨			
talivorokoko	YL			▨			
taly	FR, all leaves	▨	▨	▨	▨	▨	
tamboro be	ML				▨		▨
tamenake	stalk			▨			
tanjaka	FR, ML	▨	▨				
taraby	YL		▨				
taritarike	FL						
teloravy	all leaves						
totonga	all leaves						
tratraborondreo	FR, FL	▨	▨		▨	▨	
tratriotse	all leaves, FL	▨	▨	▨	▨	▨	▨
triplet vine	ML						▨
tsianagnampo	ML						▨
tsikembakemba	YL		▨				
tsikidrakitse	all leaves	▨					
tsinaikibo	all leaves		▨				
tsingatse	FR		▨	▨			
tsiongake	all leaves	▨	▨				
tsipoteke	YL, ML						
tsompia	ML, YL			▨		▨	▨
valiandro	FL	▨	▨	▨	▨	▨	▨
varo	FL			▨			
velae	FL, leaves						
voafogna	FR						
voamena	all leaves				▨	▨	▨
bark							
water		▨					
unknown	all leaves (FR, all leaves)	▨	▨	▨	▨	▨	▨
dirt							
insects/water?							
grass/insects?							

(*Continued*)

Appendix: (*Continued*)



Lemur catta	
Roupellina boivinii	APOCYNACEAE
Tragia tiverneana	EUPHORBIACEAE
Salvadora angustifolia	SALVADORACEAE
Dombeya sp.	STERCULIACEAE
Grewia grandidieri	TILIACEAE
Grewia triflora	TILIACEAE
Maerua filiformis	CAPPARACEAE
	EUPHORBIACEAE
Grewia franciscana	TILIACEAE
Terminalia seyrigii	COMBRETACEAE
Terminalia mantaly	COMBRETACEAE
	ASCLEPIADACEAE
Combretum sp.	COMBRETACEAE
Anacolosa pervilleana	OLACACEAE
Commiphora brevicalyx	BURSERACEAE
Combretum albiflorum	COMBRETACEAE
Aristolochia sp.	ARISTOLOCHIACEAE
Grewia leucophylla	TILIACEAE
Acacia bellula	FABACEAE
Commiphora simplicifolia	BURSERACEAE
Rhopalocarpus lucidus	SPHAEROSEPALACEAE
Pentopetia sp.	ASCLEPIADACEAE
Quivisianthe papinae	MELIACEAE
	CONVOLVULACEAE
Antidesma petiolare	EUPHORBIACEAE

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[a] Total numbers of plants are less than reported in text because unknowns are consolidated.
[b] Foods common to both lemur species are in bold.
[c] Additional plant species eaten by *Lemur catta* are in parentheses.

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