



## Chemical Properties of the Diets of Two Lemur Species in Southwestern Madagascar

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**Abstract** Seasonal dietary variations demonstrate the importance of certain plant parts during the year. A parallel analysis of their nutritional constituents provides further information on underlying patterns of consumption of the plant parts and the relative importance of key nutrients. I studied the diets of *Lemur catta* (ring-tailed lemurs) and *Propithecus verreauxi verreauxi* (sifakas), for 9 mo over a 13-mo period in the highly seasonal tropical dry forest site of Beza Mahafaly in southwestern Madagascar. I tested dietary plant parts for nutrients—protein, free amino acids, and sugars—and for 2 potential deterrents, phenolics and tannins, using plant extracts prepared in the field. I compared consumption of nutrients and secondary compounds throughout the year and between seasons. Nutrients are balanced throughout the year. The 2 lemur species do not appear nutrient-starved in either season, though actual quantities of nutrients and contributing food parts differ for each species. *Lemur catta* consumes high levels of sugar throughout the year, whereas *Propithecus* takes in higher levels of protein. The effects of phenolics and tannins are quantitative, and they appear to deter consumption of plant parts only past a certain threshold. Sifakas consume them in greater quantities than those of ring-tailed lemurs, which appear more sensitive to their effects. Sifakas may have a higher tolerance for secondary plant metabolites, which is consistent with reports for other folivores. The overall stability of nutrients throughout the year indicates no lean period that coincides with the decline in food abundance during the dry season, though actual caloric intake probably decreases.

**Keywords** food availability · nutrients · secondary plant compounds

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## Introduction

Chemical content and nutritional quality of primate diets are well documented (Altmann 1998; Chapman and Chapman 2002; Chapman *et al.* 2003; Conklin-Brittain *et al.* 1998; Curtis 2004; Davies *et al.* 1988; Ganzhorn 2002; Ganzhorn and Wright 1994; Lucas *et al.* 2003; McKey *et al.* 1981; Milton 1979, 2003; Oates *et al.* 1980; Oftedal 1991; Powzyk and Mowry 2003; Remis *et al.* 2001; Rothman *et al.* 2006; Sauther 1995; Wrangham *et al.* 1998). The studies focused on major classes of plant macronutrients—protein, carbohydrates, minerals, and lipids—that provide energy for metabolic processes and are essential to the physiological processes of their consumers.

The choice of which foods to consume involves decisions concerning the costs and benefits of procuring, processing, and digesting potential food items by the consumer. Therefore, the nutritional rewards of each food item are offset by the costs of procuring it, which includes overcoming the mechanical and chemical deterrents manufactured by the plant to discourage herbivory (Freeland and Janzen 1974). Mechanical deterrents take the form of resistant food parts and spines (Kiltie 1982; Kinzey and Norconk 1990; Kursar and Coley 2003; Lucas *et al.* 1991; Lucas and Luke 1984; Lucas *et al.* 2000; Strait 1997; Yamashita 1996), while potential chemical deterrents, such as phenolics and tannins, are classes of secondary compounds produced by plants that appear to have no primary role in their physiology and act as antifeedants (Coley and Kursar 1996; Cork and Foley 1997; Glander 1982; Moore and Foley 2005; Rhoades and Cates 1976; Waterman 1984; Waterman *et al.* 1988).

Secondary plant compounds are not necessarily toxic; their effects depend on the consumer (Glander 1982; Rhoades and Cates 1976). Phenolics are a large class of secondary metabolites that occur in some form in almost all plants (Cork and Foley 1997; Waterman and Mole 1994). They are generally small enough to be absorbed in the digestive tract and can have toxic effects (Waterman and Mole 1994). Common phenolics include gallic acid, flavonoids, and tannins (Waterman and Mole 1994), the latter of which researchers have tested in primate diets (Powzyk and Mowry 2003; Sauther 1995). Tannins are classed as digestibility reducers (Rhoades and Cates 1976) with effects that are quantitative (Cork and Foley 1997). The more widespread and larger condensed tannins have an affinity for binding to proteins and thus disrupting the action of digestive enzymes (Waterman and Mole 1994). Accordingly, symptoms of high tannin consumption can resemble those of malnutrition (Howe and Westley 1988).

I examined the chemical contents of the diets of 2 lemur species. Lemurs eat a variety of food items annually that fluctuate according to seasonal availability (Sauther 1998; Sauther *et al.* 1999; Yamashita 2002). I investigated patterns of nutrient consumption underlying ingestion of key foods. Specifically, I ask 1) whether nutrients exhibit the same seasonal fluctuations as food availability and 2) if and how the 2 lemur species differ from one another in consumption of certain nutrients and deterrents. I then compare nutrient consumption with plant secondary compounds to assess whether the latter function as effective feeding deterrents.

## Materials and Methods

### Study Site and Species

I conducted observations of *Propithecus verreauxi verreauxi* and *Lemur catta* in the deciduous tropical dry forest of Beza Mahafaly special reserve (25°30'S, 44°40'E) in southwestern Madagascar from February 1999–February 2000. The region is characterized by distinct wet and dry seasons. During the study, the rainy season, from *ca.* November to March, had 772 mm of rainfall, with average daily temperature maxima and minima of 38°C and 21°C. In contrast, the dry season had 94 mm of rainfall and average temperatures of 34°C and 12°C. The primary study site, Parcel 1, is a small (80 ha) area with a diversity of microhabitats ranging from a riverine gallery forest in the east to a xeric habitat to the west (Sussman and Rakotozafy 1994). Parcel 1 contains dense populations of *Propithecus verreauxi verreauxi* and *Lemur catta* (Gould *et al.* 2003; Richard *et al.* 2002; Yamashita 2002).

Ring-tailed lemurs are generalist herbivores (Sauther *et al.* 1999), while sifakas supplement a mostly leafy diet with seeds and fruits (Yamashita 2002). The 2 species are similar in overall body mass [2.2 kg for *Lemur catta* (Gould *et al.* 2003), 2.66–2.88 kg for *Propithecus verreauxi verreauxi* (Richard *et al.* 2000)].

I observed 5 ring-tailed lemur and 6 sifaka groups. Ring-tailed lemur groups contained from 10 to >14 individuals. Sifaka group sizes ranged from 4 to 7 individuals. Identifying collars and pendants on some individuals facilitated focal observations. Sample sizes for behavioral observations were >37 ring-tailed lemurs and 43 sifakas. I conducted continuous bout observations on focal individuals that I switched every 10 min (Altmann, 1974). I recorded time spent on basic behaviors of feeding, movement, resting, and social activities. Average monthly observation times were *ca.* 25 h for each lemur species.

I further detailed feeding behaviors by noting the plant species eaten, the exact part eaten, e.g., young or mature leaves, fruit pulp; food preparation techniques employed; ingestive behaviors; and numbers of plant parts or bites taken of a specific food per minute (feeding rate). I then multiplied the feeding rate by the amount of time spent feeding on each food per month and the mass of individual food parts to obtain an estimate of weighted intake.

### Plant Collection and Abundance Scores

I flagged food trees during observations for later sample collection. In some cases, subjects dropped foods that I collected during observations. I usually collected and tested foods on the day of observations, or at least within 24 h. I took care to collect the exact plant part from the tree or bush on which subjects were feeding. Many of the foods tested were chewed and dropped by the subjects or had adjacent bite marks. Plant species eaten by the lemurs are in the Appendix in Yamashita (2002).

Specific plant parts that were eaten and collected include young and mature leaves, fruit flesh and seeds, flowers, stalks, and shoots (emerging plant material). I identified stalks as the attachment sites of leaf petioles. In addition, the lemurs ingested dirt, water, and bark in small quantities.

I calculated abundance scores from 10 2×50-m phenological plots throughout the parcel. The plots represent a subset of the ones Sussman and Rakotozafy (1994) measured. The selected sites were spaced evenly across the parcel to capture the breadth of the E-W trend of the microhabitats. Because of the density of the lemur populations within Parcel 1, all the plots were within the ranges of one or both of the lemur species. Of the specific lemur groups observed, 7 plots were within the ranges of the ring-tailed lemur groups, and 4 were within the ranges of the sifaka groups. Further, most of the tree species they contained were food species for the 2 species (32 of 39 species=82%) that represented 49% and 72% of the total yearly diets for ring-tailed lemurs and sifakas, respectively (range for groups: *Lemur catta*, 40–66%; *Propithecus verreauxi*, 54–85%; Yamashita, 2002). The lower percentages for the ring-tailed lemurs were related to their greater reliance on lianas and herbaceous vegetation in their diets, which were not quantified in phenology plots. I identified and monitored all trees with diameter-at-breast height (DBH) >2.5 cm monthly for new leaf flushes, flowers, fruits, and mature leaves via a relative scale of 0–4 of increasing abundance (Sussman and Rakotozafy 1994; Yamashita 2002).

### Plant Chemistry

The advantages of performing the extractions and tests (where possible) in the field on fresh material were that some chemicals, such as tannins, change quantitatively in the drying process (Hagerman 1988) and that the method tests foods at the same concentrations the subject experiences. A disadvantage is that the chemical content across plant parts is not standardized for dilution by water content.

I prepared plant extracts from food items collected whenever the lemurs ate a particular plant part throughout the year. As a consequence, I performed multiple tests on the same food at different times of the year (Appendix). The choice of individual parts used in the extractions depended on the size and type of food. For leaf material, shoots, and stalks, I used either parts with bite marks or pieces directly adjacent to them if the individual had eaten the focal part, e.g., leaf tips. For fruits, I used either pieces with bite marks or, if individual fruits or flowers were small, several parts in close proximity to the area where the focal individual was feeding. I made the plant extracts per the protocol of Lucas *et al.* (2003) as follows. I finely cut up the sample with scissors and measured out 0.10 g (wet wt) of plant tissue. I then homogenized the tissue in 50% methanol with a tissue homogenizer and filtered it. I performed all chemical analyses on the resulting plant extracts. I assayed for 3 nutrients: protein, free amino acids (those not bound up in protein), and sugars; and 2 deterrents: total phenolics, which include tannins and condensed tannins. Hagerman (1988) found aqueous acetone to be a better extractor of tannins from leaf material than the methanol that I used for all extractions.

I employed several different tests to assay for plant chemicals. I tested for proteins by adding a reactive dye, Coomassie blue, which attaches to protein molecules, to the extracts as outlined in Bradford (1976), Read and Northcote (1981), and Sapan *et al.* (1999). To test for phenolics, I used a Prussian Blue test developed by Price and

Butler (1977), modified by Hagerman (1998), and reduced to a microassay (Lucas *et al.* 2001). Phenolics oxidize potassium ferricyanide to ferrous ions, which react with ferric chloride to produce a colored product called Prussian blue (Lucas *et al.* 2003). I quantified the strengths of the reactions via spectrophotometry. I then compared the absorbance to a standard reference. For protein, the reference was bovine serum albumin (BSA), expressed in % equivalents. For phenolics, the standard was gallic acid, a simple phenolic acid of small molecular mass that does not precipitate protein (Lucas *et al.* 2001).

I measured tannins—condensed and hydrolyzable—via a modified radial diffusion assay (Hagerman 1987), in which plant extracts are pipetted into wells in an agarose gel embedded with BSA. If tannins were present, they precipitated with the protein. The size of the precipitate rings produced was a measure of the strength of the reaction. Tannin concentrations are expressed in terms of equivalents to quebracho tannin standard curves.

I quantified free amino acids and sugars—glucose, sucrose, and fructose—via high performance liquid chromatography (HPLC), which separates and purifies compounds under high pressure in a column (Waterman and Mole 1994). Li and Wang (Acknowledgments) assayed 17 amino acids, excluding asparagine and glutamine, including 9 essential amino acids: arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, valine; tryptophan was not assayed. The amino acids were assayed without protein hydrolysis; therefore, the quantities reported here are for those not bound up in protein. Free amino acids (FAAs) are more readily absorbed than those bound in protein. I also summed individual FAAs by month and analyzed them separately.

With the exception of HPLC, I conducted all tests at the field site. Methods for the chemical tests performed in the field are discussed in more detail by Lucas *et al.* (2001, 2003).

## Analyses and Statistics

I collected plant parts approximately at the frequency with which they were eaten (Appendix). For all analyses, I calculated intake by multiplying the feeding rate, food mass, and time spent feeding on each food item per month. I then took the weighted intake values and averaged chemicals by plant part within each month to minimize unequal numbers of analyses conducted across months. I compared percentage time spent feeding per month with food availability scores via parametric Pearson correlation coefficients to preserve monthly comparisons of foods eaten and foods available. All other comparisons were nonparametric. I tested each chemical for differences between seasons via Mann-Whitney *U* Z-scores. For the comparison, I grouped the dry season months as April–September and wet season months as November–February. There is no datum for March, September (*Lemur catta*), and October.

I compared nutrients and secondary compounds averaged by plant part within each month with Spearman's tests of correlation ( $r_s$ ). I explored potential correlations to determine whether subjects ingested chemical compounds in diets in tandem, and especially to establish whether plant secondary compounds actually functioned as deterrents.

## Results

### Consumption of Specific Plant Parts

Different plant parts contributed to lemur diets (Fig. 1). Profiles of plant parts eaten indicated that ring-tailed lemurs consumed fruits and leaf material throughout the year, though their relative importance was seasonal. When fruit consumption declined, the lemurs ate leaf material and flowers more frequently. Sifakas consumed mostly leaf material. Both species ate mature and immature leaves at alternate times of the year, probably driven by new leaf flushes. New leaf consumption and availability correlate positively for both species (*Lemur catta*,  $r=0.816$ ,  $p=0.007$  and *Propithecus verreauxi*,  $r=0.792$ ,  $p=0.011$ ,  $n=9$  for both species; Table 1). Sifakas ate stalks continuously in small amounts throughout the year, and seeds and shoots in discrete periods. Despite their low levels of consumption, these dietary items provided important nutrients at different times of the year.

Food availability was seasonal and declined in the dry season months (Fig. 2). Fruit availability had an interesting time lag with respect to the seasons. Fruit production peaked at the beginning of the dry season (April), then declined throughout the season and slowly increased with the rains. However, time spent feeding on foods was unrelated to food availability in most cases (Table 1). Consumption and availability of young leaves correlate significantly positively for both lemur species, and fruit consumption and ripe fruit availability also correlate significantly in ring-tailed lemurs ( $r=0.792$ ,  $p=0.023$ ,  $n=9$ ).

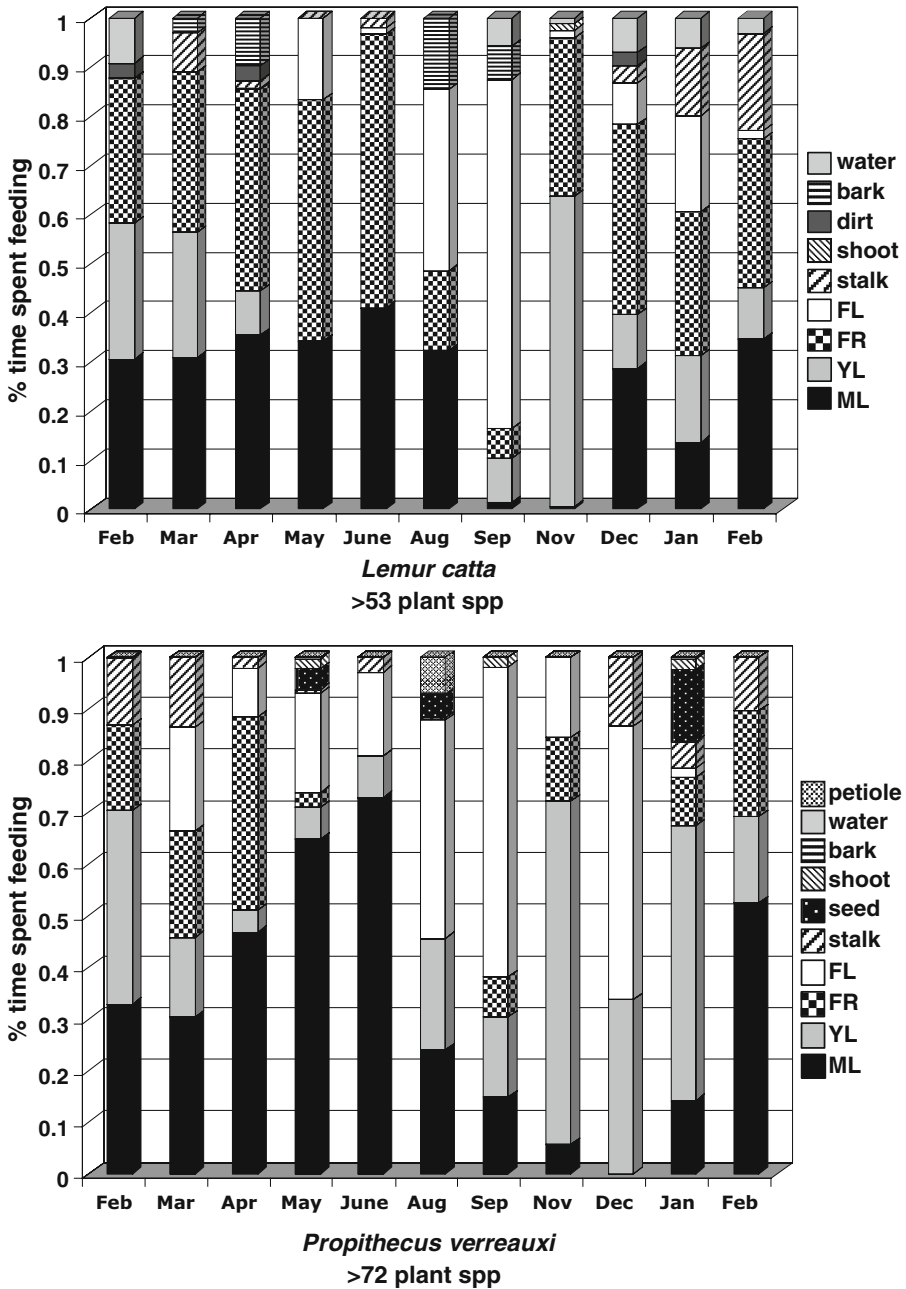
### Nutrient Consumption

None of the interspecific comparisons of dietary chemicals is significantly different except for proteins (Table 2). I did not compare tannins because of their minimal presence (detected in 1 of 135 samples assayed) in the diet of the ring-tailed lemurs.

Of the 3 sugars assayed, glucose and fructose concentrations correlate highly with one another ( $r_s=0.920$ ,  $p<0.0001$ ,  $n=267$ ). Sucrose, a disaccharide, was present in low concentrations in fruit versus the monosaccharides, which agrees with the results of Riba-Hernández *et al.* (2003; this study: sucrose  $\times$  glucose:  $r_s=-0.102$ ,  $p=0.097$ ,  $n=267$ ; fructose  $\times$  sucrose:  $r_s=-0.089$ ,  $p=0.145$ ,  $n=267$ ). Therefore, results presented here are confined to glucose.

Results of intraspecific seasonal differences in nutrient intake are in Table 3 and Figs. 3, 4, 5, 6 and 7. No interseason comparison for either species is significantly different. Only glucose levels in the sifaka diet approach significance (Mann-Whitney  $U$ , glucose:  $Z=-1.693$ ,  $p=0.091$ ,  $n=19$  wet, 21 dry). The large differences in intake of certain chemicals in the lemur diets are in Figs. 3, 4, 5, 6 and 7. *Lemur catta* consumes much higher quantities of FAAs and sugars than those of *Propithecus verreauxi*, which takes in more protein, phenolics, and tannins.

Individual amino acids assayed are in Table 4. I calculated annual totals by first standardizing FAAs by the vol/mass (5 ml/0.10 g) of the samples, then multiplying them by the weighted intake value. Proline was the most abundant FAA consumed and was obtained from a variety of food species (Fig. 4). For *Lemur catta*, the 5



**Fig. 1** Percentage of time spent feeding on food parts by month. See Table 1 for comparisons with food availability.

FAAs present in the highest quantities based on yearly totals were proline, aspartic acid, valine, arginine, and alanine. For *Propithecus verreauxi*, the most common were proline, glutamic acid, and alanine. Of the essential amino acids, *Lemur catta* took in only valine, arginine, lysine, and threonine in any quantity, and consumed

**Table 1** Correlations of food availability and time spent feeding<sup>a</sup>

	YL/ YL <sup>b</sup>	ML/ ML	Whole FR/unripe FR	Whole FR/ripe FR	Seed <sup>c</sup> /unripe FR	Seed/ripe FR	FL/ FL
<i>Lemur catta</i> <sup>d</sup>	0.816**	0.484	-0.128	0.740*			-
<i>Propithecus verreauxi</i>	0.792*	0.361	0.326	0.180	-0.332	-0.347	0.158

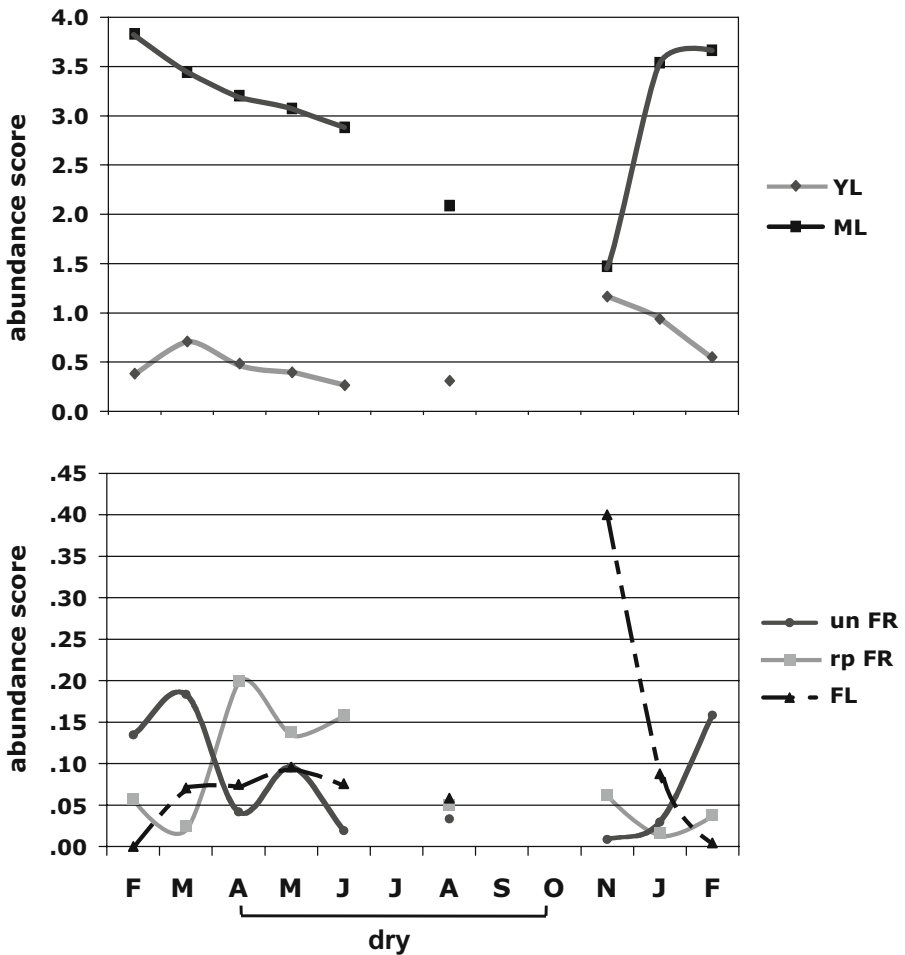
<sup>a</sup> Pearson correlation coefficients (*r*).

<sup>b</sup> Part eaten/food available.

<sup>c</sup> No seed value for *Lemur catta* because seeds were rarely eaten.

<sup>d</sup> *n* = 9 for all comparisons.

\**p* < 0.05, \*\**p* < 0.01.



**Fig. 2** Abundance scores of major food categories throughout the year averaged from 10 phenological plots. Unripe and ripe fruit (FR) and flowers (FL) on bottom graph; young (YL) and mature leaves (ML) on top graph. Note differences in scale of y-axis between graphs.



**Table 2** Interspecific species comparisons<sup>a</sup> of dietary chemicals

	<i>n</i> <sup>b</sup>	Z-score ( $\mu$ , SD)	<i>p</i> -value
Proteins	33, 43	-2.363 (16.260, 39.384)	0.018
FAAs	31, 43	-0.564 (260.883, 753.750)	0.573
Sugar	30, 40	-0.024 (1093.195, 3630.918)	0.981
Phenolics	33, 43	-1.818 (16.085, 33.509)	0.069

<sup>a</sup> Mann-Whitney *U* Z-scores.

<sup>b</sup> *n* values: *Lemur catta*, *Propithecus verreauxi*.

histidine in trace amounts. For *Propithecus verreauxi*, arginine and valine were present in the highest amounts, and isoleucine, lysine, histidine, and leucine the least.

### Comparisons of Nutrients and Secondary Compounds

Almost all chemicals assayed correlate highly with one another (Table 5). The exception is protein  $\times$  sugar in ring-tailed lemurs ( $r_s=0.309$ ,  $p=0.097$ ,  $n=30$ ). Both chemical deterrents correlate with one other and with the nutrients assayed.

## Discussion

The nutrient analyses indicate that 1) nutrients are balanced across seasons for both species, though there is variation in individual chemicals; 2) plant secondary compounds do not appear to deter predation, especially by sifakas; and 3) the 2 lemur species take in different quantities of both nutrients and deterrents, probably driven by different anatomical and physiological requirements.

**Table 3** Intraspecific comparisons<sup>a</sup> of chemicals between seasons<sup>b</sup>

Species	Proteins	FAA	Sugar	Phenolics	Tannins
<i>Lemur catta</i>	-0.976 (15; 13.102, 24.94) <sup>c</sup> (18; 3.151, 4.371) <sup>d</sup>	-0.949 (15; 595.058, 1540.22) (16; 155.00, 292.124)	-0.720 (12; 2019.171, 3726.684) (18; 1965.73, 6359.327)	-0.398 (15; 11.053, 23.583) (18; 6.204, 10.937)	
<i>Propithecus verreauxi</i>	-0.576 (21; 36.028, 67.564) (22; 10.269, 13.384)	-1.239 (21; 265.771, 436.552) (22; 105.377, 193.182)	-1.693 (19; 638.996, 998.028) (21; 227.121, 624.809)	-0.340 (21; 26.459, 50.973) (22; 17.434, 29.27)	-0.131 (4; 30.363, 25.845) (11; 146.945, 223.52)

<sup>a</sup> Mann-Whitney *U* Z-scores.

<sup>b</sup> Dry season months: April–September; wet season: November–February.

<sup>c</sup> *n*,  $\mu$ , SD for dry season.

<sup>d</sup> *n*,  $\mu$ , SD for wet season.

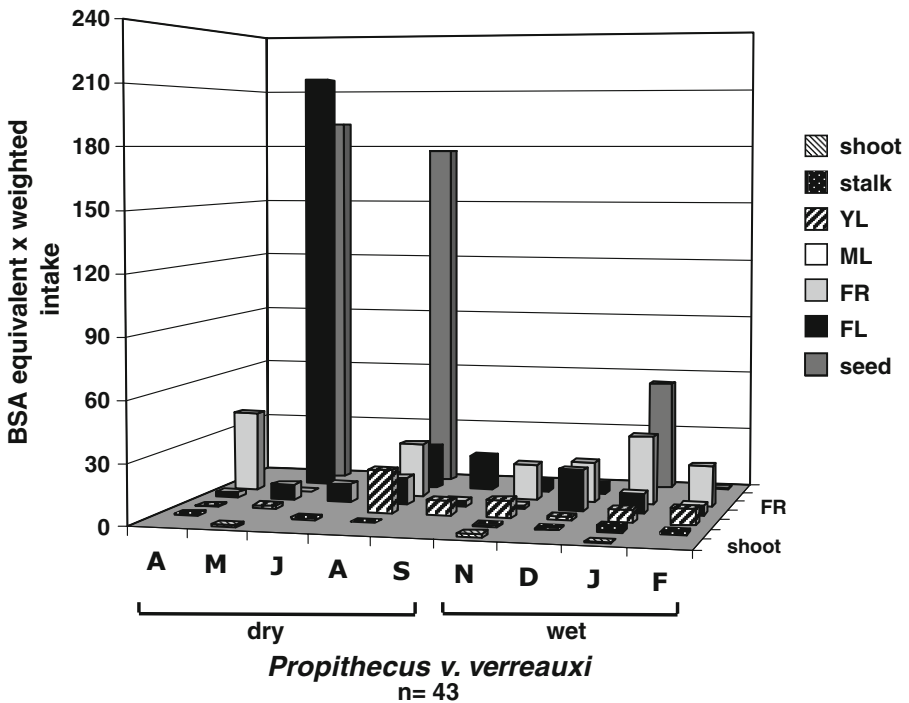
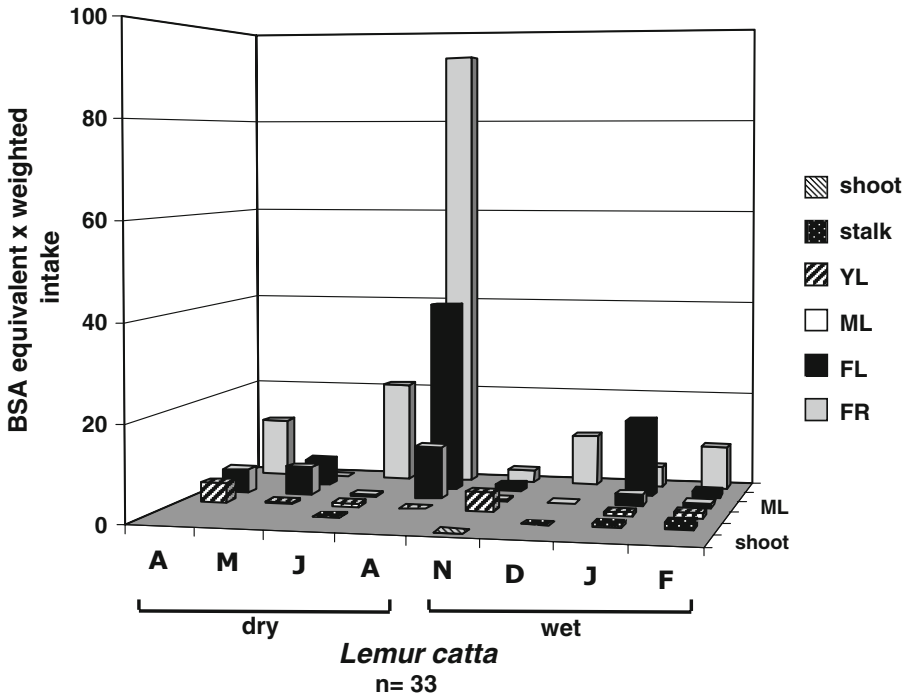


Fig. 3 Protein content in different plant parts averaged within each month from each food part tested. See Table 3 for comparisons between seasons. Note differences in scale of y-axes between graphs.

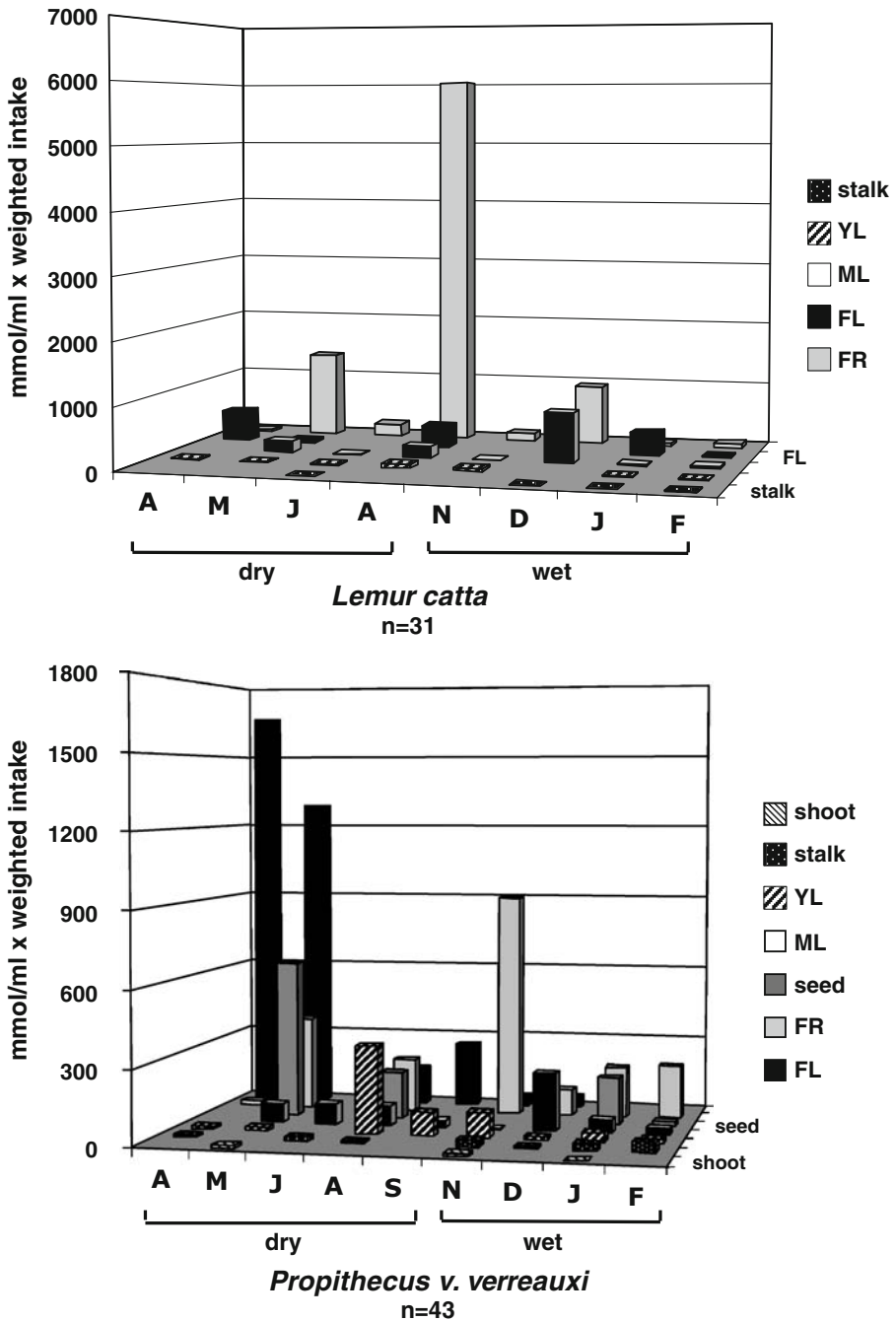
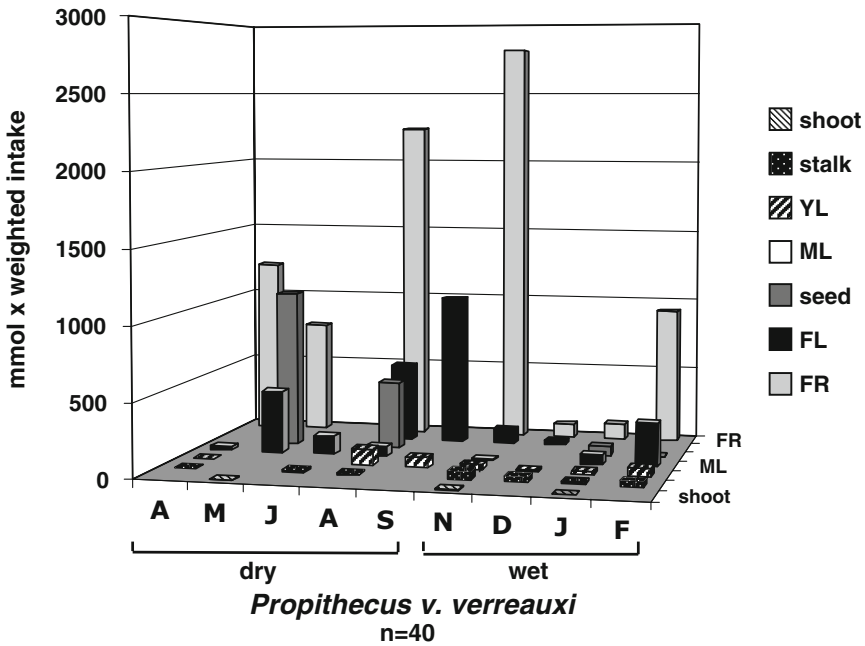
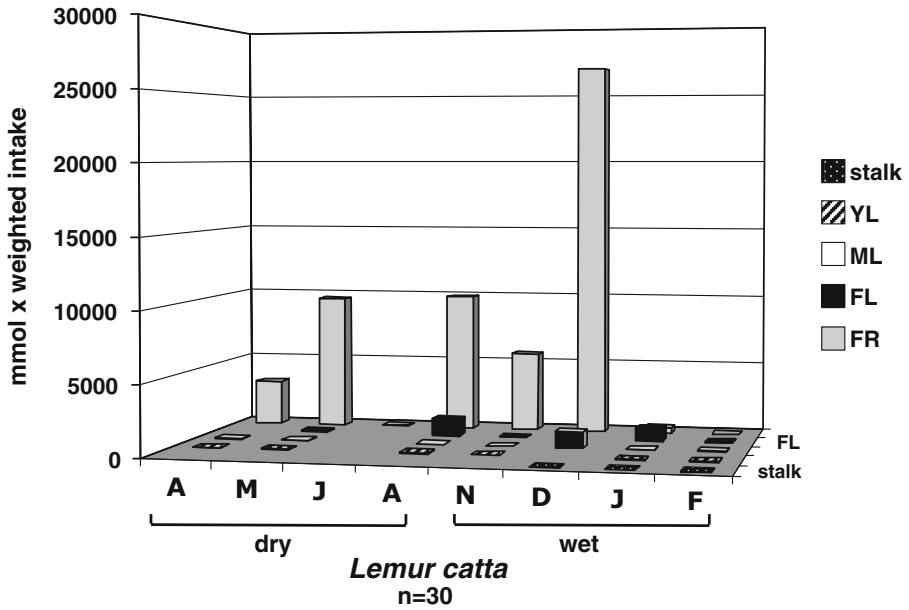


Fig. 4 Free amino acid content in different plant parts averaged within each month from each food part tested. See Table 3 for comparisons between seasons. Note differences in scale of y-axes between graphs.



**Fig. 5** Sugar (glucose) content in different plant parts averaged within each month from each food part tested. See Table 3 for comparisons between seasons. Note differences in scale of y-axes between graphs.

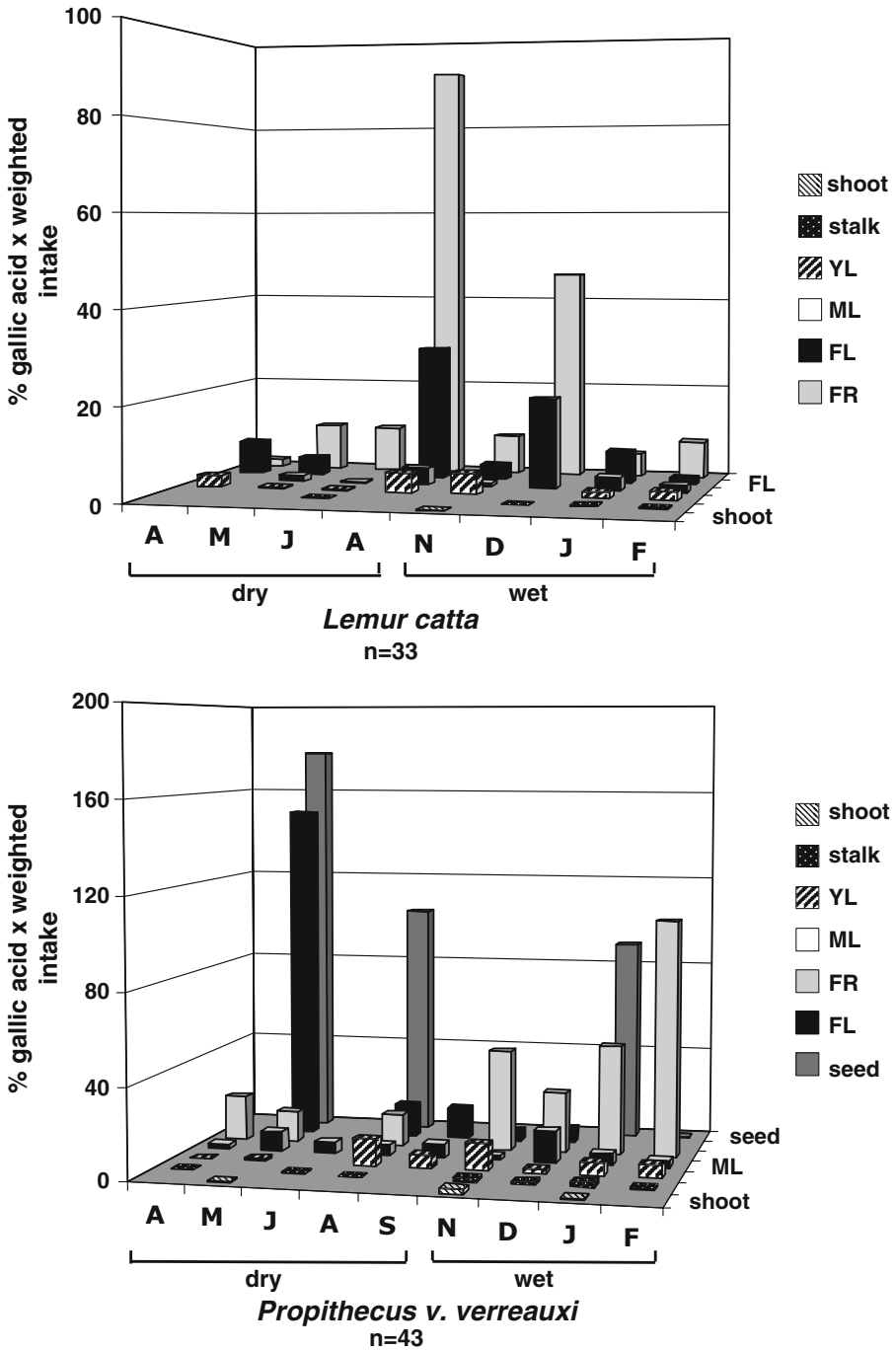
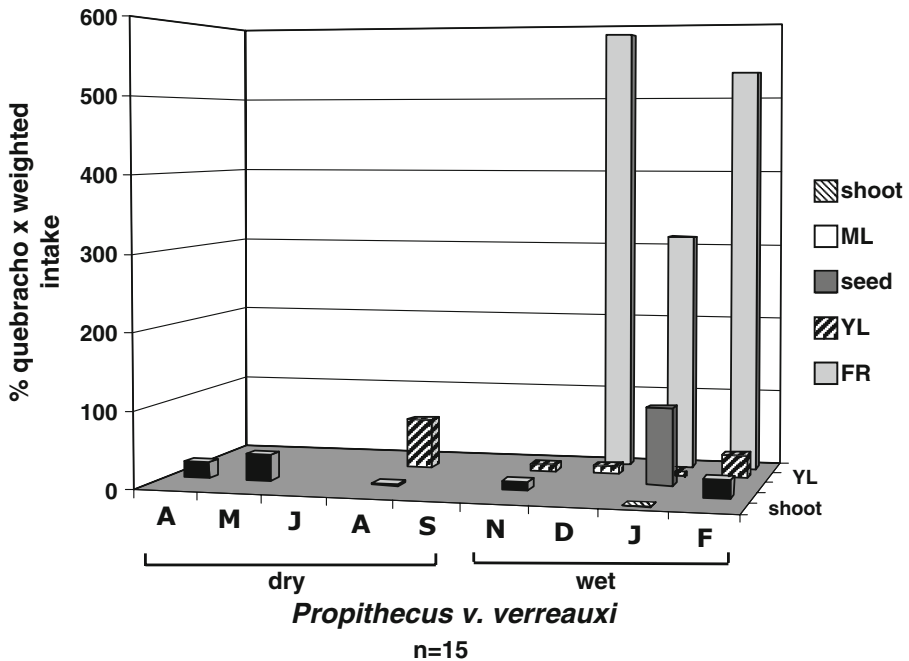


Fig. 6 Phenolic content in different plant parts averaged within each month from each food part tested. See Table 3 for comparisons between seasons. Note differences in scale of y-axes between graphs.



**Fig. 7** Tannin content in different plant parts averaged within each month from each food part tested. See Table 3 for comparisons between seasons.

## Nutrient Patterns

The foods that the lemurs consumed contained nutrients that are balanced between seasons in contrast to marked environmental seasonality. Nutrient levels across months are generally stable (Figs. 3, 4 and 5). For example, several different plant parts contribute proteins and FAAs to the diets of both lemur species throughout the year (Figs. 3 and 4). Sugar content is almost wholly derived from fruit flesh in ring-tailed lemurs, but, in sifakas, from combinations of fruits, flowers, and mature leaves and seeds (Fig. 5). The 2 lemur species are not constrained nutritionally by their environment, at least not in a manner that directly parallels availability of specific plant parts that fluctuate seasonally. Even though consumption of young leaves and fruits tracks their abundance (Table 1), the lemurs compensate nutritionally by eating other plant parts or by increasing total feeding time within each month (*Lemur catta*: 25.2% wet, 30.2% dry; *Propithecus verreauxi verreauxi*: 42.8% wet, 53.2% dry).

The large differences in scale between lemur species for the chemicals assayed are related to the disproportionate feeding times devoted to specific foods. Sifakas ate flowers and seeds of unripe fruit, in particular, in large quantities when they were available (Figs. 1, 3, 4, 5, 6 and 7), and the fruit of *Tamarindus indica* (*kily*) was a dietary staple for the ring-tailed lemurs.

The finding of nutrient balance is somewhat surprising given the extremely seasonal environment that the 2 species share and that constrains their reproductive schedules to strict seasonal breeding (Gould *et al.* 2003; Richard *et al.* 2002). Both species mate and gestate in the dry season, give birth at the end of the season, and lactate and wean with the beginning of the rains. During the dry season, *Lemur catta* reduce an already low basal metabolic rate versus that of other primates (Müller 1985; Pereira 1993; Wright 1999; Young *et al.* 1990) by limiting the costs of living and using fat stores that were deposited in the wet season as food intake is reduced (Pereira *et al.* 1999). Kurland and Pearson (1986) considered their seasonal hypometabolism to be related to a poorer quality diet in the dry season. Similarly, female *Propithecus verreauxi verreauxi* decrease body mass throughout the dry season by using stored fat acquired in the wet season (Richard *et al.* 2002).

Researchers have argued that the period of lactation and weaning in the wet season may be more energetically stressful than in the dry season when females are gestating (Ganzhorn 2002; Gould *et al.* 2003; Pereira *et al.* 1999; Richard *et al.* 2002; Wright 1999). For the nutritional data to be consistent with the hypotheses, we would expect to see elevations in nutrient intake during the wet season or lack of nutrients in the dry season, or both. Though there is variability in seasonal nutrient intake, the relative stability of nutrients across the year does not offer strong support for nutrient packing in the wet season, either in anticipation of food shortage in the dry season or to support seasonal increases in reproductive energetics. Curtis (2004) likewise found little interseasonal nutritional difference for *Eulemur mongoz* in a seasonally dry forest in northwestern Madagascar. However, though nutrient levels appear relatively balanced between seasons, absolute food abundances decrease in the dry season (Fig. 2; Sauter, 1998). The weight loss in both species during the dry season indicates the lemurs being in negative energy balance. Knott (1998) reported fluctuations in orangutan caloric intake that corresponded directly with fruit availability. Similarly, though the lemurs may be maintaining a balance of nutrients between seasons, at least for the nutrients assayed, they are most likely not taking in sufficient calories in the dry season as changes in body mass and fat storage preceding the dry season indicate (Pereira *et al.* 1999; Richard *et al.* 2002).

### Interspecific Comparisons of Nutrients and Deterrents

Though most of the interspecific comparisons of dietary chemicals are not statistically different, it is significant that protein and, to a lesser extent, phenolics (and tannins, which were not present in appreciable quantities in ring-tailed lemur diets) were different (Table 2). While the choice of solvent (Hagerman 1988) may have reduced the sensitivity of the tannin test, the relative differences between the sympatric lemur species would probably not have been altered.

One could relate the differences between the 2 species in consumption of the chemicals to different tolerances for the secondary plant metabolites associated with beneficial nutrients or to different metabolic needs. *Lemur catta* are generalist herbivores, while *Propithecus verreauxi* are obligate folivores. Yearly consumption of leaf material based on time spent feeding is 38% for ring-tailed lemurs and 64% for sifakas. Fruit consumption is 31% and 12%, respectively (Fig. 1). In terms of

Table 4 FAAs by month<sup>a</sup>

	Apr	May	June	Aug	Sept	Nov	Dec	Jan	Feb	Annual total
<i>Lemur catta</i>										
ala	97.40 <sup>b</sup> (0.05)	42.59 (0.01)	60.02 (0.26)	3416.83 (0.10)	0.00 (0.00)	41.61 (0.06)	164.72 (0.09)	151.45 (0.20)	77.21 (0.17)	4051.82
arg	159.40 (0.07)	68.60 (0.01)	0.00 (0.00)	3617.68 (0.11)	1.00 (0.03)	88.14 (0.13)	336.89 (0.19)	29.20 (0.04)	0.97 (0.00)	4301.87
asp	158.33 (0.07)	127.23 (0.02)	17.47 (0.08)	6433.78 (0.19)	0.00 (0.00)	256.73 (0.38)	32.04 (0.02)	244.68 (0.33)	9.17 (0.02)	7279.40
cys	37.03 (0.02)	64.31 (0.01)	0.00 (0.00)	449.81 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.50 (0.00)	551.64
glu	8.05 (0.00)	11.57 (0.002)	0.00 (0.00)	545.48 (0.02)	24.50 (0.62)	75.24 (0.11)	32.54 (0.02)	70.47 (0.09)	142.90 (0.31)	910.74
gly	—	—	—	—	—	—	—	—	—	0.00
his	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	15.28 (0.03)	15.28
ile	2.32 (0.00)	74.44 (0.01)	0.00 (0.00)	362.54 (0.01)	0.00 (0.00)	1.68 (0.00)	0.00 (0.00)	16.93 (0.02)	0.00 (0.00)	457.90
leu	43.35 (0.02)	0.00 (0.00)	0.00 (0.00)	362.54 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	405.89
lys	37.87 (0.02)	0.00 (0.00)	0.00 (0.00)	3098.38 (0.09)	0.00 (0.00)	115.20 (0.17)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	3251.45
met	22.83 (0.01)	147.43 (0.02)	54.28 (0.24)	5.50 (0.00)	2.50 (0.06)	0.00 (0.00)	0.00 (0.00)	10.03 (0.01)	9.68 (0.02)	252.24
phe	41.03 (0.02)	189.34 (0.03)	0.00 (0.00)	722.46 (0.02)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	952.83
pro	1231.85 (0.57)	1885.27 (0.26)	95.26 (0.41)	11036.07 (0.32)	3.00 (0.08)	54.97 (0.08)	1010.91 (0.57)	76.00 (0.10)	59.68 (0.13)	15453.00
ser	63.55 (0.03)	0.00 (0.00)	0.00 (0.00)	97.88 (0.00)	0.00 (0.00)	0.00 (0.00)	3.00 (0.00)	25.66 (0.03)	67.38 (0.15)	257.47
thr	143.61 (0.07)	2235.53 (0.307)	0.00 (0.00)	0.00 (0.00)	6.00 (0.15)	0.00 (0.00)	105.16 (0.06)	106.58 (0.14)	75.34 (0.16)	2672.20
tyr	67.33 (0.03)	63.99 (0.01)	1.50 (0.01)	1944.36 (0.06)	0.00 (0.00)	49.24 (0.07)	30.54 (0.02)	0.00 (0.00)	0.00 (0.00)	2157.45
val	35.82 (0.02)	2458.65 (0.33)	1.27 (0.01)	1927.98 (0.06)	2.50 (0.06)	1.72 (0.00)	52.83 (0.03)	16.93 (0.02)	0.00 (0.00)	4497.68



*Propithecus verreauxi verreauxi*

<b>ala</b>	67.36 (0.04)	755.17 (0.15)	12.26 (0.03)	327.27 (0.14)	31.90 (0.04)	280.25 (0.07)	75.34(0.16)	886.68 (0.43)	371.68 (0.41)	2807.91
<b>arg</b>	21.95 (0.01)	156.53 (0.03)	15.35 (0.04)	121.60 (0.05)	84.88 (0.10)	781.28 (0.19)	0.00 (0.00)	21.57 (0.01)	0.00 (0.00)	1203.16
<b>asp</b>	282.13 (0.16)	225.58 (0.04)	37.87 (0.11)	302.08 (0.13)	0.00 (0.00)	94.62 (0.02)	66.59 (0.14)	72.90 (0.04)	0.00 (0.00)	1081.74
<b>cys</b>	11.20 (0.01)	134.83 (0.03)	0.00 (0.00)	97.21 (0.04)	37.12 (0.04)	63.34 (0.02)	10.68 (0.02)	24.39 (0.01)	0.00 (0.00)	378.76
<b>glu</b>	0.00 (0.00)	847.67 (0.17)	30.15 (0.08)	527.67 (0.23)	446.23 (0.50)	1729.63 (0.41)	60.41 (0.13)	203.09 (0.10)	66.03 (0.07)	3910.89
<b>gly</b>	—	—	—	—	—	—	—	—	—	0.00
<b>his</b>	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	142.16 (0.07)	0.00 (0.00)	142.16
<b>ile</b>	14.41 (0.01)	0.00 (0.00)	0.00 (0.00)	39.65 (0.02)	12.93 (0.01)	40.68 (0.01)	0.50 (0.00)	0.21 (0.00)	1.00 (0.00)	109.38
<b>leu</b>	7.20 (0.00)	0.00 (0.00)	0.00 (0.00)	24.45 (0.01)	11.59 (0.01)	21.00 (0.01)	0.50 (0.00)	23.27 (0.01)	57.58 (0.06)	145.60
<b>lys</b>	0.00 (0.00)	0.00 (0.00)	5.03 (0.014)	26.80 (0.01)	0.00 (0.00)	86.96 (0.02)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	118.78
<b>met</b>	2.00 (0.00)	607.48 (0.12)	18.26 (0.05)	36.48 (0.02)	37.55 (0.04)	50.14 (0.01)	0.22 (0.00)	80.11 (0.04)	1.99 (0.00)	834.23
<b>phe</b>	0.79 (0.00)	42.15 (0.01)	7.04 (0.02)	49.64 (0.02)	45.62 (0.05)	0.00 (0.00)	0.00 (0.00)	34.09 (0.02)	0.00 (0.00)	179.33
<b>pro</b>	1251.34 (0.70)	1474.19 (0.29)	70.02 (0.19)	377.90 (0.16)	57.82 (0.07)	602.35 (0.14)	134.17 (0.28)	447.54 (0.22)	349.78 (0.39)	4765.10
<b>ser</b>	6.37 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.90 (0.00)	24.12 (0.01)	3.24 (0.00)	34.62
<b>thr</b>	59.50 (0.03)	185.08 (0.04)	6.99 (0.02)	66.57 (0.03)	38.67 (0.04)	29.28 (0.01)	111.47 (0.23)	7.31 (0.00)	44.80 (0.05)	549.66
<b>tyr</b>	1.00 (0.00)	235.05 (0.05)	23.64 (0.07)	59.18 (0.03)	12.79 (0.01)	298.93 (0.07)	5.22 (0.01)	91.31 (0.04)	2.00 (0.00)	729.10
<b>val</b>	73.03 (0.04)	394.86 (0.08)	134.24 (0.37)	280.97 (0.12)	70.90 (0.08)	106.49 (0.03)	8.34 (0.02)	3.86 (0.00)	0.50 (0.00)	1073.18

*ala*=alanine; *arg*=arginine; *asp*=aspartic acid; *cys*=cysteine; *glu*=glutamic acid; *gly*=glycine; *his*=histidine; *ile*=isoleucine; *leu*=leucine; *lys*=lysine; *met*=methionine; *phe*=phenylalanine; *pro*=proline; *ser*=serine; *thr*=threonine; *tyr*=tyrosine; *val*=valine. Essential amino acids are in bold.

<sup>a</sup> Monthly totals calculated by summing each FAA and multiplying by volume/mass of samples and weighted intake average (explanation in text).

<sup>b</sup> Monthly totals (% within month).

**Table 5** Intraspecific correlations of dietary nutrients and deterrents<sup>a</sup>

<i>Lemur catta</i>	Proteins ( <i>n</i> )	FAAs ( <i>n</i> )	Sugar ( <i>n</i> )	Phenolics ( <i>n</i> )
FAAs	0.522** (31)			
Sugar	0.309 (30)	0.781**** (28)		
Phenolics	0.545*** (33)	0.874**** (31)	0.745**** (30)	
<i>Propithecus verreauxi</i>				
FAAs	0.806**** (43)			
Sugar	0.759*** (40)	0.899**** (40)		
Phenolics	0.884**** (43)	0.889**** (43)	0.838**** (40)	
Tannin	0.679** (15)	0.646** (15)	0.704** (15)	0.736** (15)

<sup>a</sup> Spearman correlation coefficients ( $r_s$ ).

\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ , \*\*\*\* $p < 0.0001$ .

nutrients, this translates into more sugar and less phenolics (and tannins) in ring-tailed lemur diets and more protein in sifaka foods. Sifakas obtain major quantities of proteins from seasonally occurring flowers and seeds. The interspecific similarities in body mass would appear to preclude size as an explanation for differences in nutrient content and secondary plant compounds in the diet. However, the 2 species belong to morphologically distinct families. Food choice and nutrient intake may reflect an interplay between digestive physiology and morphology that can constrain (or divert) types of nutrients that are efficiently or readily digested (Milton 1981).

Ring-tailed lemurs possess a large, sacculated cecum (Campbell *et al.* 2000) that suggests a seasonal diet high in leaf materials, and, indeed, young and mature leaves are major components of their diet (Fig. 1). However, phenolics occur at much lower levels than in sifaka diets, though both species obtain protein from leaves. Ring-tailed lemurs may have a lower tolerance for secondary plant compounds and avoid leaves with high levels. Ring-tailed lemurs in Berenty in southern Madagascar had lower percentages of phenolics and alkaloids in their diets versus sympatric sifakas (Simmen *et al.* 1999).

The enlarged cecum also suggests the presence of bacterial symbionts to aid in processing leaves (Campbell *et al.* 2000). However, Campbell *et al.* (2004a) found that digesta passage rates in *Varecia variegata*, a frugivore that also has an enlarged cecum, and *Eulemur fulvus* were probably too rapid for significant fermentation to occur, and neither species processes fiber efficiently compared to *Propithecus verreauxi* (Campbell *et al.* 2004b). *Eulemur fulvus* has a mixed herbivorous diet similar to that of confamilial *Lemur catta*, and if their digestive morphologies and retention times are also similar, then significant cecal fermentation may not be occurring in *L. catta*. Leaf material by itself then probably does not supply *Lemur catta* with sufficient nutrients, which they must obtain from other sources.

In contrast, the relatively high occurrence of deterrents in the sifaka diet and their significant correlations with nutrients (Table 5) indicate a high tolerance for

deterrents when they occur in the same foods. Other indriids tolerate tannins at high levels (Ganzhorn 1988; Powzyk and Mowry 2003; Simmen *et al.* 1999).

Leaf parts provide sifakas with a steady supply of nutrients, which is consistent with their anatomical specializations. Sifakas are morphological folivores that possess specializations of the dentition and gastrointestinal tract—sacculated cecum, spiral colon, elongated tract—for hindgut fermentation. The cecum contains symbiotic bacteria that break down otherwise indigestible cellulose and hemicellulose in leaf material to digestible fatty acids (Campbell *et al.* 2000; Chivers and Hladik 1980; Lambert 1998). Coupled with the ability to process fibrous leaf material efficiently for specialists is the ability to tolerate high amounts of secondary plant compounds. *Propithecus verreauxi* has the typical slow metabolism of folivores (Dasilva 1992; McNab 1978; Müller 1985), which constrains its diet and the manner in which the digesta is metabolized (Richard and Nicoll 1987). McNab (1978) tied a slow metabolism to the presence of food toxins; longer processing time is coupled with detoxification in addition to extraction of nutrients. The specializations of the sifaka tract are related to increased retention times and a greater ability to absorb structural carbohydrates versus that of some lemurids (Campbell *et al.* 2004a, b).

Researchers have found similar patterns of maximizing protein intake while simultaneously ingesting high levels of secondary compounds in the diets of howlers (Milton 1979), cercopithecines (Conklin-Brittain *et al.* 1998; Wrangham *et al.* 1998), and colobine folivores (Chapman and Chapman 2002; Davies *et al.* 1988; Oates *et al.* 1980; *cf.* McKey *et al.* 1981). The secondary compounds do not appear to act as effective deterrents in the amounts consumed. If anything, monkeys appear most constrained by the amount of fiber in plant parts that limit digestibility. While I did not report fiber content, I examined toughness values for sifaka diets with data taken concurrently with the chemical data set (Yamashita 2002; Yamashita *et al.* 2001). Quantifying toughness is a direct measure of the mechanical challenge of breaking down foods, in this case, leaf material. Leaf toughness is generally conferred by the composition of the midrib and secondary veins (Lucas *et al.* 1991). For sifakas, leaves adjacent to those actually eaten are tougher, which suggests that leaf toughness acts as an indicator of food quality. In contrast, western lowland gorillas eat fruits without regard to tannin or fiber content (Remis *et al.* 2001).

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## Appendix: Plant Parts Tested

Vernacular name	Plant part tested	No. of times tested per month										Scientific name	Family	
		Apr	May	June	Aug	Sept	Nov	Dec	Jan	Feb				
<i>Lemur catta</i>														
Adranahaka	Stalk			1									<i>Commelina</i> sp.	Commelinaceae
Bageda	ML		1											
Bea	ML			2	1									
Beandahiny	ML								1					
Bokabe	Stalk										1		<i>Marsdenia cordifolia</i>	Asclepiadaceae
Bokabe	YL									3				
Clematis vine	ML				1									
Dango	Stalk									4	2		<i>Talinella dauphinensis</i>	Portulacaceae
Dango	YL		1					1						
Dango	ML		2											
Famata	Stalk									1			<i>Euphorbia tirucalli</i>	Euphorbiaceae
Fatra	FR										1		<i>Terminalia fatraea</i>	Combretaceae
Fatra	FL										1			
Filofilo	FR								3				<i>Azima tetracantha</i>	Salvadoraceae
Filofilo	YL							1						
Forimbitike	YL										1			Verbenaceae
Forimbitike	ML										3			
Katrafay	YL							4			1		<i>Cedrelopsis grevei</i>	Meliaceae
Katrafay	ML								1					
Katrafay	Shoot								2					
Kililo	ML	2	5		7					6	1		<i>Metaporana parvifolia</i>	Convolvulaceae
Kililo	Stalk											1		
Kililo	YL									4				
Kily	YL	2						7					<i>Tamarindus indica</i>	Fabaceae
Kily	ML								3	1				
Kily	FR-unripe			4	3							1		
Kily	FR-ripe	3	3		1		1	1	3					
Kily	FL		2					1						
Lisinambo	ML									1	2			
Malimatse	FR	2											<i>Grewia</i> sp.	Tiliaceae
Mantsake	ML										1		<i>Enterospermum pruinosum</i>	Rubiaceae
Mantsake	YL									1				
Mantsake	FR		3											
Oxiala	ML										1		<i>Dioscorea</i> sp.	Dioscoreaceae
River vine	FR	1	1											
Sasavy	YL		1	1				1					<i>Salvadora angustifolia</i>	Salvadoraceae
Sasavy	ML			2										

Sasavy	FR								1											
Sarirotsy	FR								1											
Tainajajamena	ML											1			<i>Acalypha decaryana</i>	Euphorbiaceae				
Tanjaka	FR											2			<i>Anacolosia pervilleana</i>	Olacaceae				
Taritarike	FL											3			<i>Combretum albiflorum</i>	Combretaceae				
Teloravy	ML												2							
Trataborondreo	FR	1													<i>Grewia leucophylla</i>	Tiliaceae				
Tratriotse	YL												1							
Tratriotse	ML												1		<i>Acacia bellula</i>	Fabaceae				
Tsipoteke	ML												3							
Tsiridambo	Stalk																			
Tsompia	ML	1													<i>Pentopetia</i> sp.	Asclepiadaceae				
Valiandro	FL														<i>Quivisiaanthepapinae</i>	Meliaceae				
Velae	FL																			
Voamaea	FR	1	2												<i>Vitex beravinensis</i>	Verbenaceae				
Voafogna	FR														<i>Antidesma petiolare</i>	Euphorbiaceae				
Unknown shoot	FL																			
Unknown vine	YL																			
Unknown vine	ML												1							
<i>Propithecus verreauxi verreauxi</i>																				
Akaly	ML	1													<i>Crateva excelsa</i>	Capparaceae				
Andriambolafotsy	ML														<i>Tabernaemontana koffeoides</i>	Apocynaceae				
Angalora	YL														<i>Secamone</i> sp.	Asclepiadaceae				
Avoha	YL													6	1	11	<i>Dichrostachys humbertii</i>	Fabaceae		
Avoha	FR																			
Avoha	ML		2																	
Bea	ML																			
Bokabe	YL														1		<i>Marsdenia cordifolia</i>	Asclepiadaceae		
Bokabe	ML		2												1	1				
Dango	Stalk															2	<i>Talinella dauphinensis</i>	Portulacaceae		
Dango	ML		2																	
Dango	YL														1					
Dango	FL														1					
Daro	ML															1	<i>Commiphora aprevalii</i>	Burseraceae		
Daro	YL																			
Darosike	FL															1	<i>Gonocrypta grevei</i>	Asclepiadaceae		
Darosike	YL															1				
Fadriandambo	YL														2	1	2	<i>Physena sessiliflora</i>	Capparaceae	
Fadriandambo	ML		2	1	5	1	1	2												
Famata	YL	1															1	<i>Euphorbia tirucalli</i>	Euphorbiaceae	
Famata	Stalk	2		3	1		1	3	3	5										
Famata	FR																			
Fatra	ML	2	3															<i>Terminalia fatraea</i>	Combretaceae	
Filofilo	FR														2			<i>Azima tetraacantha</i>	Salvadoraceae	
Hafotse ampelam.	YL																	1	<i>Acacia</i> sp.?	Fabaceae

Halimboron'ala	YL				1	1			<i>Albizia</i> sp.	Fabaceae
Hary	YL				2				<i>Bridelia pervilleana</i>	Euphorbiaceae
Hary	ML				2					
Hazombalala	FR					1			<i>Suregada chauvetiae</i>	Euphorbiaceae
Karimbola mitsy	YL				1				<i>Dialium madagascariense</i>	Fabaceae
Katrafay	Stalk				2				<i>Cedrelopsis grevei</i>	Meliaceae
Katrafay	YL				1	1	3	1		
Katrafay	Shoot				2		2			
Katrafay	FL				2					
Kililo	ML	6	1	1			3	1	<i>Metaporana parvifolia</i>	Convovulaceae
Kililo	YL				1		3			
Kily	Unripe	1		1			4		<i>Tamarindus indica</i>	Fabaceae
Kily	FR									
Kily	Seed	1		1			2	1		
Kily	ML			1			1			
Kily	YL						1			
Kily	FL	1			4	1				
Kompitse	ML	2	2				1	1	<i>Gonocrypta grevei</i>	Asclepiadaceae
Kompitse	YL				1		1			
Kotipoke	YL				1		2	3	<i>Grewia grevei</i>	Tiliaceae
Kotipoke	ML	1					1			
"Lance leaf"	ML							1		
Latex vine	ML	1						1		
Lisinambo	ML							1		
Maintyfototse	YL				2		1		<i>Grewia</i> sp.	Tiliaceae
Maintyfototse	ML	1		1						
Malimatse	FR	1							<i>Grewia</i> sp.	Tiliaceae
Pira	YL				2				<i>Landolphia</i> sp.	Apocynaceae
Robontsy	YL			4	3	2	1	2	<i>Acacia rovuuae</i>	Fabaceae
Roi	YL					1	1	1	<i>Acacia</i> sp.	Fabaceae
Roi	FL						2			
Roimaintyfototse	ML	3		1						
Roimaintyfototse	YL	1								
Sabonto	ML						4	3	<i>Roupellina boivinii</i>	Apocynaceae
Sagnira	ML	2							<i>Phyllanthus seyrigii</i>	Euphorbiaceae
Sele bohoke	ML							1	<i>Grewia grandidieri</i>	Tiliaceae
Sele	ML	4	2					3	<i>Grewia triflora</i>	Tiliaceae
Talifatra	YL					1				
Talivorokoko	YL				1	1			<i>Terminalia seyrigii</i>	Combretaceae
Talivorokoko	ML					1				
Tamboro be	ML	1								Asclepiadaceae
Tamboro	ML	2								
Tamenake	Stalk			1					<i>Combretum</i> sp.	Combretaceae
Tanjaka	ML	3		1					<i>Anacolosia pervilleana</i>	Olacaceae
Tanjaka	FR						1	2		
Taraby	YL				2				<i>Commiphora brevicalyx</i>	Burseraceae
Taly	FR					1	1	1	<i>Terminalia mantaly</i>	Combretaceae
Taly	ML			6						
Taly	YL					1				

Tratriotse	YL		3		1	<i>Acacia bellula</i>	Fabaceae
Tratriotse	ML	1			1		
Tratriotse	FL		2				
Tsianagnampo	ML	3					
Tsingatse	FR	2				<i>Commiphora simplicifolia</i>	Burseraceae
Tsiongake	ML		1	2	2	<i>Rhopalocarpus lucidus</i>	Sphaerosepalaceae
Tsiongake	YL			1	2		
Tsipoteke	ML				1	<i>Achyranthes aspera</i>	Acanthaceae
Tsompia	ML	2			1	<i>Pentopetia</i> sp.	Asclepiadaceae
Valiandro	ML	2				<i>Quivisanthe papinae</i>	Meliaceae
Valiandro	FL		4	1			
Varo	FL				1		
Voamena	ML	1	2				
Voamena	YL	2					
Unknown tree	ML						
Unknown tree	YL	1		1			
Unknown vine	ML				1		

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