Feeding Patterns in a Small-Bodied Nocturnal Folivore *(Avahi laniger)* and the Influence of Leaf Chemistry: A Preliminary Study

A.L. Faulkner   S.M. Lehman

Department of Anthropology, University of Toronto, Toronto, Canada

Abstract

We present data on feeding patterns in *Avahi laniger* and compare these data to temporal variations in leaf chemistry. Because *A. laniger* is one of the smallest folivorous primates and has a monogastric stomach, we hypothesized that this lemur would display behavioural adaptations to a leaf-based diet by scheduling feeding times when leaves were of highest quality. Data were collected from May to August 2004 at the Vatoharanana site in Ranomafana National Park, Madagascar. *A. laniger* fed during different time periods despite leaf carbohydrate and protein concentrations exhibiting little variation throughout the night. Although tannin concentrations exhibited temporal fluctuations, they did not covary with *A. laniger* feeding times. We suggest that *A. laniger* feeding times cannot be explained entirely by variations in leaf chemistry.

Copyright © 2006 S. Karger AG, Basel

Introduction

Studies of food quality are crucial to our understanding of primate feeding ecology. A leaf-based diet is generally characterized as low quality due to the difficulties associated with cellulose digestion, the low energy value relative to other diets and the possible presence of secondary compounds which may be toxic or reduce digestibility [Milton, 1979; Glander, 1982]. Vertebrates are not able to break down plant cell walls to extract the nutrients inside and must rely on colonies of symbiotic mi-

cro-organisms found in enlarged areas of their digestive tract to process fibrous plant material [Moir, 1965]. One of the primary morphological adaptations to a leaf-based diet is large body size. Body size is related to gastro-intestinal surface area, and therefore the larger the organism, the larger the surface area and the longer the digestion time, allowing maximum nutrient absorption [Chivers and Hladik, 1980; Kay, 1984]. Kay [1984] suggested that a leaf-based diet can only be energetically sustained by primates weighing equal to or greater than 700 g. Moreover, larger-bodied taxa are able to sustain lower-quality diets than smaller-bodied taxa in primates [Temerin et al., 1984]. For example, the large body size of gorillas (weighing 71.5–175.2 kg [Jungers and Susman, 1984]) can be seen as an adaptation to their highly fibrous, bulky diet [Milton, 1984]. Other primate folivores that exhibit morphological dietary adaptations include the colobine monkeys which have complex sacculated stomachs that are analogous to those of ruminant animals [Hladik, 1978]. Among the strepsirhine primates known to include high quantities of leaves in their diet, *Lepilemur* displays an enlarged caecum, and the Indriidae have enlarged colons [Hladik, 1978]. However, the eastern woolly lemur *(Avahi laniger)* has been documented to be almost exclusively folivorous [Ganzhorn et al., 1985; Harcourt, 1991] and, at a body size of 800–1,600 g [Glander et al., 1992; Thalmann, 2003], is one of the world's smallest folivorous primates. Despite its low-energy leaf-based diet, *A. laniger* has been shown to have the highest mean daily travel costs, both relatively and absolutely, of several nocturnal prosimians [Warren and Crompton, 1998]. Therefore, the question arises as to how this small-bodied, monogastric nocturnal lemur can subsist on a diet composed predominantly of leaves. Because *A. laniger* has such a small body size relative to the majority of other primate folivores and a simple stomach [Hladik, 1978], it is possible that *A. laniger* displays behavioural adaptations to a folivorous diet.

Many diurnal primates that include leaves in their diet schedule their leaf feeding bouts before long periods of rest or sleep, and therefore most leaf consumption occurs late in the day [Chapman and Chapman, 1991]. Explanations for this observed feeding pattern include: minimizing energy expenditure and travel time while the stomach is full of bulky leaves and minimizing the potential of encountering a higher-quality food resource at a time when it cannot be consumed [Chapman and Chapman, 1991]. However, an alternative to these explanations is that leaves themselves vary in quality in a circadian pattern, and it has been hypothesized that this temporal variation in leaf chemistry influences feeding times in folivorous primates [Ganzhorn and Wright, 1994]. As a consequence of photosynthesis, controlled laboratory tests have shown that leaves are of lowest quality (low protein and sugar concentrations) at dawn but increase in quality during the day, which could explain why diurnal primates consume leaves late in the day. Ganzhorn and Wright [1994] found that the leaves of several plant species exhibit circadian chemical property changes and suggest that these changes could coincide with a late-day leaf feeding schedule among the diurnal folivores of Madagascar. However, there have been no complementary studies on nocturnal folivores from Madagascar. *A. laniger* represents an ideal study species to test if leaf chemistry plays a role in temporal feeding patterns in nocturnal primates.

This paper seeks to answer three questions: (1) does *A. laniger* display variation in feeding amounts between time periods throughout the night, (2) do the leaves consumed by *A. laniger* display circadian fluctuations in soluble carbohydrate, crude

protein and condensed tannin levels, and (3) is there a relationship between the times when *A. laniger* feeds on leaves and the times when leaves are of highest quality (high protein and carbohydrate to tannin levels)?

Methods

Study Site

Ranomafana National Park (40,000 ha) is located in south-east Madagascar (21°02'–21°25' S and 47°18'–47°37' E [Hemingway, 1998]). The study was carried out from the end of May to August 2004 at Vatoharanana, a 5-km^2 satellite site within the national park located 7 km south of the Centre Valbio research station [Overdorff, 1991]. Vatoharanana is a minimally disturbed high montane rain forest at an altitude of 1,125 m [Overdorff, 1991]. Temperature varied throughout the study period; average nighttime temperature was 8.4°C (range 4–12°C), and average daytime temperature was 22.3°C (range 15–26°C). The site receives approximately 2,300–2,700 mm of rain annually [Overdorff, 1991; Hemingway, 1998] and, although data were collected during what is considered the cold, dry season, 514 mm of rain fell during the study period.

Behavioural Data Collection

Each night *A. laniger* individuals or groups were located by walking the trail system at Vatoharanana with the aid of headlamps. Data were collected in 6-hour intervals throughout the study period so that all times of the night when *A. laniger* was active were represented (sunset–midnight, 21.00–3.00 h, or midnight–sunrise). Behavioural data on *A. laniger* were collected using focal-animal sampling [Altmann, 1974] in 5-min sample periods that focused on behaviour durations. *A. laniger* groups or individuals were encountered on 31 nights, and 26 h and 15 min of focal data were collected. When an animal was seen feeding, the plant species and part were noted. Tree species were recorded by local name in the field, and species designations were later determined following Turk [1995].

Leaf Collection

Over several nights near the end of the study period, leaf samples were collected from the 5 most commonly consumed species and part (as of July 18, 2004) using a pruning pole to cut down tree branches. Only one sample of each plant type at each time was collected. However, an effort was made to control for possible non-circadian variation by collecting from feeding trees when possible, in addition to collecting from several individual trees of the feeding species [for a review, see Chapman et al., 2003]. Leaves were collected at 18.00, 22.00, 2.00 and 6.00 h and were dried immediately upon collection in a metal container over a paraffin stove and then transferred to a drying stove kept at 40°C to ensure complete dryness for preservation. The leaf samples were then stored in sealed plastic bags and taken back to the University of Toronto Botany Laboratory and the Liquor Control Board of Ontario Quality Assurance Laboratory for analysis.

Leaf Chemistry Analysis

Dried leaf samples were ground using a Thomas-Wiley Intermediate Mill 3383-L10 Series (Arthur H. Thomas Co., Philadelphia, Pa., USA) to pass through a 40-mesh filter screen. Soluble carbohydrate content was determined following Dubois et al. [1956]. 0.5 g of each sample was added to 20 ml of a 60% ethanol solution and allowed to sit for 24 h. The solutions were then filtered, and 0.05 ml of each of the extracts were added to 1.95 ml of deionized water, 0.05 ml of phenol and 5 ml of sulphuric acid to determine the optical density of absorption of the solution. Optical density of absorption was measured using a Novaspec II Spectrophotometer (Biochrom Ltd., Cambridge, UK) read at 490 µl (Hexos) and fitted to a calibration curve to assess the amount of soluble carbohydrate per sample. Protein (nitrogen) content was determined using a Costech Carbon and Nitrogen Analyzer (Elemental Combustion System 4010, Costech Analytical Technologies Inc., Valencia, Calif., USA). After measuring the total nitrogen content of a sample, crude protein values were assessed by multiplying by the standard

conversion factor of 6.25 [Quarmby and Allen, 1989]. Condensed (procyanidin) tannin concentrations (along with total phenolics) were measured from an extract taken from 0.1 g of ground leaf sample in a 1-ml solution of 50% ethanol and 50% water [Oates et al., 1980] after sitting for 48 h for maximum extraction. Using a Waters 717 plus autosampler, the extract was injected into a Waters high-pressure liquid chromatograph 616 pump interfaced to a Waters 996 photodiode array detector (Waters Corp., Milford, Mass., USA). The column used was a stainless-steel reverse-phase ACE 3 C18, 15.0 × 4.6 cm (Mac-Mod Analytical Inc., Chadds Ford, Pa., USA) [Goldberg et al., 1996].

Descriptive and Statistical Analysis

Variations in feeding proportion and in leaf chemistry between time periods over the night were identified using a descriptive approach. To control for differences in the amount of behavioural data collected between time periods, feeding duration amounts are expressed as a proportion of all behaviours observed within each time period. Statistical analysis was done using SPSS 12.0.1 (SPSS Inc., Chicago, Ill., USA). Non-parametric Kendall's tau correlation was used to determine the relationship between feeding pattern (measured as the sum of the duration of feeding bouts within each time period) and leaf chemistry values. Correlation coefficients were calculated for all feeding species samples combined and separately. The significance level was set at 0.05.

Results

The majority of the *A. laniger* nightly activity was dedicated to resting (table 1). Feeding times were highest just after *A. laniger* became active for the night (in the period from 16.00 to 20.00 h), followed by a second peak in feeding in the middle of the night (0.00–4.00 h). *A. laniger* reduced the amount of time spent feeding between 20.00 h and midnight, and was observed to spend the least amount of time feeding during the last part of the night (4.00–8.00 h; table 2). Leaves from 9 different plant species were the only food items consumed, with young leaves making up over 98% of the diet (table 3).

Soluble carbohydrate, crude protein and condensed tannin concentrations of each leaf species sample from the different time periods throughout the night are presented in table 4. Table 5 shows the average leaf chemistry patterns, which includes combined values from the young leaf samples of *Harungana madagascariensis*, *Syzygium* sp., *Erythroxylum sphaeranthum*, *Dombeya pubescens* and *Canthium* sp.; these were the most commonly consumed species and part at the time of collection (later young leaves from *Alberta humblotii* made up more of *A. laniger*'s diet than *Canthium* sp.). Descriptive analysis revealed that although soluble carbohydrate concentrations increased throughout the night, there was no major variation between the time periods (carbohydrate concentration differences between time periods are less than 0.01 g). Likewise, there was likely no biologically significant variation in protein levels between time periods, as there is less than a maximum of 2% difference in protein concentration between time periods. Condensed tannin concentrations displayed a large peak at 22.00 h, and the large standard deviation from this time was due to the high tannin level of *H. madagascariensis* (the most commonly consumed species).

There were no observable or statistical relationships between carbohydrate or protein concentrations and feeding amounts in the different time periods, which may be due to carbohydrate and protein values remaining almost constant throughout the night (table 6). There was no correlation between tannin levels and feeding

Table 1. Activity budget for *A. laniger*

Behaviour	Duration, %
Inactive	82.25
Travelling	1.83
Feeding	5.39
Autogroom	1.05
Allogroom	0.23
Vocalization	0.00
Out of sight	9.25
Total	100.00

Table 2. Proportion of time spent feeding by *A. laniger* by time period

Time	Feeding proportion, %
18.00 h (16.00–20.00)	8.64
22.00 h (20.01–0.00)	3.54
2.00 h (0.01–4.00)	7.31
6.00 h (4.01–8.00)	0.90

Table 3. Tree species exploited as food resources by *A. laniger*

Species name	Feeding time, %		
	ML	YL	total
Harungana madagascariensis	1.46	48.51	49.97
Syzygium sp.	0.00	19.03	19.03
Erythroxylum sphaeranthum	0.00	12.52	12.52
Dombeya pubescens	0.00	5.85	5.85
Alberta humblotii	0.00	4.95	4.95
Canthium sp.	0.00	4.72	4.72
Protorhus sp.	0.00	1.95	1.95
Tongoalahy (local name)	0.00	0.64	0.64
Oncostemum botryoides	0.27	0.10	0.37
Total	1.73	98.27	100.00

ML = Mature leaves; YL = young leaves.

proportion either; even though the condensed tannin concentration of *H. madagascariensis* peaked at 22.00 h, feeding amount at that time was in the middle range. To try to clarify some of these relationships and to address the high standard deviations when all species were examined together, the chemical and feeding values were also analysed for each species separately, although this did not reveal any significant relationships either.

Discussion

A. laniger was often resting during sampling. However, the study animals were unhabituated and uncollared which may have biased observational sampling towards resting, and the majority of the times the animals went out of sight they had

Table 4. Leaf chemistry pattern for *A. laniger* food items

Time	Species	Soluble carbohydrate, g	Crude protein, %	Condensed tannins, g/100 g
18.00 h	*Harungana madagascariensis*	0.047	11.781	0.055
18.00 h	*Syzygium* sp.	0.038	10.319	0.087
18.00 h	*Erythroxylum sphaeranthum*	0.037	16.931	0.012
18.00 h	*Dombeya pubescens*	0.026	20.638	0.034
18.00 h	*Canthium* sp.	0.112	14.325	0.033
22.00 h	*Harungana madagascariensis*	0.075	13.219	0.528
22.00 h	*Syzygium* sp.	0.034	10.563	0.024
22.00 h	*Erythroxylum sphaeranthum*	0.032	16.575	0.027
22.00 h	*Dombeya pubescens*	0.028	28.000	0.021
22.00 h	*Canthium* sp.	0.103	15.269	0.052
2.00 h	*Harungana madagascariensis*	0.054	13.300	0.028
2.00 h	*Syzygium* sp.	0.040	11.600	0.204
2.00 h	*Erythroxylum sphaeranthum*	0.040	16.700	0.007
2.00 h	*Dombeya pubescens*	0.036	22.938	0.043
2.00 h	*Canthium* sp.	0.105	13.181	0.040
6.00 h	*Harungana madagascariensis*	0.061	12.919	0.169
6.00 h	*Syzygium* sp.	0.024	13.738	0.008
6.00 h	*Erythroxylum sphaeranthum*	0.068	17.119	0.017
6.00 h	*Dombeya pubescens*	0.035	23.544	0.026
6.00 h	*Canthium* sp.	0.100	13.425	0.015

Table 5. Leaf chemistry patterns in food items eaten by *A. laniger* (means ± 1 SD)

Time	Soluble carbohydrate, g	Crude protein, %	Condensed tannins, g/100 g
18.00 h	0.052 ± 0.034	14.799 ± 4.124	0.044 ± 0.028
22.00 h	0.054 ± 0.033	16.725 ± 6.700	0.131 ± 0.223
2.00 h	0.055 ± 0.029	15.544 ± 4.532	0.064 ± 0.079
6.00 h	0.058 ± 0.030	16.149 ± 4.452	0.047 ± 0.069

just started travelling. Our first question asked was if *A. laniger* displays variation in feeding amounts between time periods throughout the night. There was an observable trend in the feeding pattern of *A. laniger* throughout its nightly activities. *A. laniger* spent the greatest amount of time feeding just after becoming active for the night, which may be explained by the need to replenish energy, protein and other nutrient stores that depleted during sleep. Feeding amounts decreased after this initial peak, perhaps to allow for digestion following the first feeding bout, and then increased again in the middle of the night between midnight and 4.00 h. *A. laniger* was observed to spend the least amount of time feeding in the time before returning to its sleep site. These preliminary data indicate that not all primate folivores sched-

Table 6. Kendall's tau correlation coefficients between feeding proportions and leaf chemistry in *A. laniger* food items (n = 4 for all correlations)

Feeding proportions of plant species	Leaf chemistry		
	soluble carbohydrate	crude protein	condensed tannins
Total species	–0.667	–0.667	–0.333
Harungana madagascariensis	–0.667	0.000	–0.333
Syzygium sp.	0.548	0.183	0.548
Erythroxylum sphaeranthum	0.236	–0.236	–0.707
Dombeya pubescens	0.548	0.183	0.183
Canthium sp.	0.707	0.236	–0.236

All p values >0.1.

ule leaf feeding bouts before long periods of rest or sleep [Chapman and Chapman, 1991]. This finding also differs from previous studies by Ganzhorn et al. [1985] and Harcourt [1991], which found that *A. laniger* also had high feeding scores in the last 1–2 h of the night; however, this may be due to differences in data collection methodology (in both sampling method and technology) and in sample size. Further research is required to clarify the feeding patterns of *A. laniger*, especially long-term studies that cover all seasons of the year.

Our second question asked was if the leaves consumed by *A. laniger* display circadian fluctuations in soluble carbohydrate, crude protein and condensed tannin levels. Very little variation in soluble carbohydrate and crude protein from leaves similar to the ones consumed by *A. laniger* was observed between time periods of the night. Condensed tannin concentrations did display large fluctuations between time periods, especially in *H. madagascariensis* and *Syzygium* sp. (the most commonly consumed species); however, greater sample sizes are required to support these findings both statistically and biologically. High levels of variation in leaf chemistry throughout the night might not be expected, as a previous study by Ganzhorn [1995] demonstrated a correlation between sunlight irradiance and carbohydrate, protein and tannins; this relationship between sunlight exposure and relative leaf quality was both a circadian and a seasonal phenomenon. Because the present study was carried out at night, sunlight may have a negligible effect on leaf chemistry, and further research will be needed to identify the factors that influenced the variation in leaf chemistry that was observed at night.

When examining between-species variation in leaf chemistry, it should be noted that crude protein levels of leaves from *D. pubescens* and soluble carbohydrate levels of leaves from *Canthium* sp. were consistently elevated at all times during the night relative to the young leaves from the other samples that were collected (table 4). Further research will clarify why these seemingly high-quality leaves make up considerably less of *A. laniger*'s diet than leaves from *H. madagascariensis*, *Syzygium* sp. and *E. sphaeranthum*.

Our third question asked was if a relationship exists between the times when *A. laniger* feeds on leaves and the times when leaves are of highest quality (high protein

and carbohydrate to tannin levels). Although the general feeding times of diurnal folivores may be related to circadian patterns in leaf chemistry, the relationship does not hold for *A. laniger*. However, *A. laniger* does appear to manage a highly folivorous diet in other ways. This study, as well as the studies by Ganzhorn et al. [1985] and Harcourt [1991] found that *A. laniger* dedicated the majority of its nightly activity budget to resting, which may be adaptive for digestion and energy conservation [Ganzhorn et al., 1985]. *A. laniger* is also highly selective about the leaves it consumes. During this study, *A. laniger* was observed to feed on the leaves from only 9 different tree or plant species, with more than 80% of the diet being comprised of 3 species. In addition, 98% of *A. laniger*'s diet was made up of young leaves, which have higher protein and protein-to-fiber ratios – and are therefore of higher quality – than mature leaves [Milton, 1979; Yeager et al., 1997; Chapman et al., 2004]. Previous studies have also shown that *A. laniger* exhibits a selective diet [Ganzhorn, 1988; Ganzhorn et al., 1985], and *A. occidentalis* has been documented to repeatedly exploit rare food sources [Thalmann, 2001]. *A. laniger* has been observed to exploit higher-quality (high protein, low alkaloid) foods than *Lepilemur mustelinus*, another nocturnal lemur that includes high quantities of leaves in its diet [Ganzhorn, 1988]. Furthermore, *A. laniger* has been found to select leaves with high quantities of protein and sugar, and avoids leaves with high alkaloid concentrations [Ganzhorn et al., 1985].

It will be necessary to conduct long-term studies on the feeding ecology of *A. laniger*. Most studies of *A. laniger* dietary patterns have been conducted during the dry season [Ganzhorn et al., 1985; Harcourt, 1991], which may have implications for our current understanding of the dietary composition of *A. laniger*, as well as the quality of the food it consumes. For example, Ganzhorn [1992] noted that leaf quality (measured as protein-to-fiber ratios) covaries with seasonality and rainfall. Additionally, 2 species of sifaka that are sympatric with *A. laniger (Propithecus edwardsi* and *Propithecus diadema)* greatly increase their consumption of leaves during the dry season [Arrigo-Nelson, 2005; Irwin, 2005] and even become more selective about the plant species included in their diet by reducing dietary diversity [Irwin, 2005].

Research on diet quality has often focused on protein-to-fiber ratios, carbohydrates and a few secondary compounds [Milton, 1979, 1998; Oates et al., 1980; Ganzhorn et al., 1985; Ganzhorn, 1988, 1992, 1995, 2002; Wasserman and Chapman, 2003]. However, temporal variations in protein, carbohydrate and condensed tannin concentrations (or lack thereof) do not explain how *A. laniger* can subsist on a diet of leaves. Some folivores, such as *A. laniger*, might be selecting leaves for components other than or in addition to protein, carbohydrates and tannins. Further research that examines the circadian patterns of leaf chemistry between food and nonfood species as well as measuring other dietary components such as vitamins, minerals, lipids and other secondary compounds such as saponins and cyanogenic glycosides may provide additional insight into understanding the nutritional requirements of small-bodied folivores.

Acknowledgments

References

Altmann J (1974). Observational study of behavior: sampling methods. *Behaviour* 49:227–267.

Arrigo-Nelson SJ (2005). The impact of habitat disturbance on fruit consumption by the Milne-Edwards' sifaka *(Propithecus edwardsi)* in Ranomafana National Park, Madagascar. *American Journal of Physical Anthropology* 126:66.

Chapman CA, Chapman LJ (1991). The foraging itinerary of spider monkeys: when to eat leaves? *Folia Primatologica* 56:162–166.

Chapman CA, Chapman LJ, Naughton-Treves L, Lawes MJ, McDowell LR (2004). Predicting folivorous primate abundance: validation of a nutritional model. *American Journal of Primatology* 62:55–69.

Chapman CA, Chapman LJ, Rode KD, Hauck EM, McDowell LR. (2003). Variation in the nutritional value of primate foods: among trees, time periods, and areas. *International Journal of Primatology* 24:317–333.

Chivers DJ, Hladik CM (1980). Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. *Journal of Morphology* 166:337–386.

Dubois M, Gilles KA, Hamilton JK, Rebers PA, Smith F (1956). Colorimetric method for determination of sugars and related substances. *Analytical Chemistry* 28:350–356.

Ganzhorn JU (1988). Food partitioning among Malagasy primates. *Oecologia* 75:436–450.

Ganzhorn JU (1992). Leaf chemistry and the biomass of folivorous primates in tropical forests: test of a hypothesis. *Oecologia* 91:540–547.

Ganzhorn JU (1995). Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. *Ecology* 76:2084–2096.

Ganzhorn JU (2002). Distribution of a folivorous lemur in relation to seasonally varying food resources: integrating quantitative and qualitative aspects of food characteristics. *Oecologia* 131:427–435.

Ganzhorn JU, Abraham JP, Razanahoera-Rakotomalala M (1985). Some aspects of the natural history and food selection of *Avahi laniger. Primates* 26:452–463.

Ganzhorn JU, Wright PC (1994). Temporal patterns in primate leaf eating: the possible role of leaf chemistry. *Folia Primatologica* 63:203–208.

Glander KE (1982). The impact of plant secondary compounds on primate feeding behavior. *Yearbook of Physical Anthropology* 25:1–15.

Glander KE, Wright PC, Daniels PS, Merenlender AM (1992). Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. *Journal of Human Evolution* 22:1–17.

Goldberg DM, Tsang E, Karumanchiri A, Diamandis EP, Soleas G, Ng E (1996). Method to assay the concentrations of phenolic constituents of biological interest in wines. *Analytical Chemistry* 68:1688–1694.

Harcourt C (1991). Diet and behaviour of a nocturnal lemur, *Avahi laniger*, in the wild. *Journal of Zoology* 223:667–674.

Hemingway CA (1998). Selectivity and variability in the diet of Milne-Edwards' sifakas *(Propithecus diadema edwardsi)*: implications for folivory and seed-eating. *International Journal of Primatology* 19:355–377.

Hladik CM (1978). Adaptive strategies of primates in relation to leaf-eating. In *The Ecology of Arboreal Folivores* (Montgomery GG, ed.), pp 373–395. Washington, Smithsonian Institution Press.

Irwin MT (2005). The lean season lasts all year: diademed sifakas *(Propithecus diadema)* in forest fragments show reduced dietary diversity and rely heavily on parasitic mistletoes. *American Journal of Physical Anthropology* 126:120.

Jungers WL, Susman RL (1984). Body size and skeletal allometry in African apes. In *The Pygmy Chimpanzee* (Susman RL, ed.), pp 131–177. New York, Plenum Press.

Kay RF (1984). On the use of anatomical features to infer foraging behavior in extinct primates. In *Adaptations for Foraging in Nonhuman Primates* (Rodman PS, Cant JGH, eds.), pp 21–53. New York, Columbia University Press.

Milton K (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *American Naturalist* 114:362–378.

Milton K (1984). The role of food-processing factors in primate food choice. In *Adaptations for Foraging in Nonhuman Primates* (Rodman PS, Cant JGH, eds.), pp 249–279. New York, Columbia University Press.

Milton K (1998). Physiological ecology of howlers *(Alouatta)*: energetic and digestive considerations and comparison with the Colobinae. *International Journal of Primatology* 19:513–548.

Moir RJ (1965). The comparative physiology of ruminant-like animals. In *Physiology of Digestion in the Ruminant* (Dougherty RW, Allen RS, Burroughs W, Jacobson NL, McGilliard AD, eds.), pp 1–14. Baltimore, Waverly Press.

Oates JF, Waterman PG, Choo GM (1980). Food selection by the South Indian leaf-monkey, *Presbytis johnii* in relation to leaf chemistry. *Oecologia* 45:45–56.

Overdorff DJ (1991). *Ecological Correlates to Social Structure in Two Prosimian Primates:* Eulemur fulvus rufus *and* Eulemur rubriventer *in Madagascar.* Dissertation, Ann Arbor, UMI Dissertation Services, Bell and Howell Company.

Quarmby C, Allen SE (1989). Organic constituents. In *Chemical Analysis of Ecological Materials* (Allen SE, ed.), 2nd ed., pp 160–200. Oxford, Blackwell Scientific Publications.

Temerin LA, Wheatley BP, Rodman PS (1984). Body size and foraging in primates. In *Adaptations for Foraging in Nonhuman Primates* (Rodman PS, Cant JGH, eds.), pp 217–248. New York, Columbia University Press.

Thalmann U (2001). Food resource characteristics in two nocturnal lemurs with different social behavior: *Avahi occidentalis* and *Lepilemur edwardsi. International Journal of Primatology* 22:287–324.

Thalmann U (2003). *Avahi*, woolly lemurs, *avahy, fotsy-fe, ampongy, tsarafangitra, dadintsifaky.* In *The Natural History of Madagascar* (Goodman SM, Benstead JP, eds.), pp 1340–1342. Chicago, University of Chicago Press.

Turk D (1995). *A Guide to Trees of Ranomafana National Park and Central Eastern Madagascar.* Washington, United States Agency for International Development.

Warren RD, Crompton RH (1998). Diet, body size and the energy costs of locomotion in saltatory primates. *Folia Primatologica* 69:86–100.

Wasserman MD, Chapman CA (2003). Determinants of colobine monkey abundance: the importance of food energy, protein, and fibre content. *Journal of Animal Ecology* 72:650–659.

Yeager CP, Silver SC, Dierenfeld ES (1997). Mineral and phytochemical influences on foliage selection by the proboscis monkey *(Nasalis larvatus). American Journal of Primatology* 41:117–128.