

Nutrient Composition of Selected Plant Species Consumed by Semi Free-Ranging Lion-Tailed Macaques (*Macaca silenus*) and Ring-Tailed Lemurs (*Lemur catta*) on St. Catherines Island, Georgia, U.S.A.

Ellen S. Dierenfeld^{1*} and Colleen M. McCann²

¹Nutrition Department, Wildlife Conservation Society, Bronx, New York

²Mammal Department, Wildlife Conservation Society, Bronx, New York

Feeding behavior in two groups of semi free-ranging primates, lion tailed macaques (LTM) (*Macaca silenus*, n = 9) and ring-tailed lemurs (RTL) (*Lemur catta*, n = 13), residing on St. Catherines Island, GA, was observed seasonally at quarterly intervals for 1 year. Each group had unlimited access to native flora and fauna in addition to a daily provisioned diet; LTM were observed a total of 144 hours and RTL for 208 hours. We hypothesized that foods selected by macaques would be lower in macronutrients and higher in fiber than those consumed by lemurs owing to body size differences. Samples of plant foods observed eaten (106 samples from 30 identified species) were collected, air-dried in the field, and analyzed for macronutrient, fiber, and mineral content. Leaves and seeds were important diet components for semi free-ranging LTM most of the year, comprising 51% to 93% of observed feeding time on nonprovisioned food items, with ripe fruit a major food item (40% of observed feeding time) only during the August sampling period. In general, RTL consumed a more diverse diet of fruits and leaves during all seasons, with seeds and buds increasingly important during winter months (45% of observed feeding time). Based on the nutrient composition of different plant parts, weighted by the percentage contribution (feeding time assumed equivalent to mass of forage intake) of each part, no difference was seen in fiber (LTM 56.8 \pm 21.9% of DM, RTL 38.4 \pm 16.7% DM) or crude protein content of diets consumed (LTM 9.0 \pm 2.9% DM, RTL 11.5 \pm 6.7% DM) throughout the year. Weighted diets contained mineral concentrations meeting recommended values for non-human primates of Mg, Cu, Mn, and Zn, but were low in Na, P, and Fe, as well as Ca (LTM only). Despite wide differences in individual food items selected, overall diets were remarkably similar in macronutrient composition between these two disparate primates. Zoo Biol 18:481–494, 1999. © 1999 Wiley-Liss, Inc.

Key words: primates; nutrition; food selection; native flora

*Correspondence to: Ellen S. Dierenfeld, Nutrition Department, Wildlife Conservation Society, 2300 Southern Blvd., Bronx, NY 10460. E-mail: edierenfeld@wcs.org

Received for publication April 30, 1999; Accepted November 19, 1999.

© 1999 Wiley-Liss, Inc.

Nutrient Composition of Selected Plant Species Consumed by Semi Free-Ranging Lion-Tailed Macaques (*Macaca silenus*) and Ring-Tailed Lemurs (*Lemur catta*) on St. Catherines Island, Georgia, U.S.A.

E.S Dierenfeld, C.M. McCann. *Zoo Biology*.

Copyright©1999 Wiley-Liss, Inc. Reproduced with permission of John Wiley & Sons, Inc.

INTRODUCTION

The feeding behavior of two groups of semi free-ranging primates, lion-tailed macaques (*Macaca silenus*; body mass, 6 - 10 kg), and ring-tailed lemurs (*Lemur catta*; body mass, 2-2.5 kg), residing on St. Catherines Island Wildlife Survival Center, GA, was observed seasonally at quarterly intervals for 1 year. St. Catherines Island (SCI) is a barrier island off the coast of Georgia that covers approximately 57.8 km² and is characterized by several distinct habitats: mixed deciduous and evergreen forests, palmetto, savanna, and both fresh and saltwater marshes [Thomas, 1988]. The lion-tailed macaques were introduced onto the island in 1991 and occupy an area in the southern part of the island averaging an annual home range size of 1.2 km². Green and Minkowski [1977] reported a home range size of 5 km² for lion-tailed macaques in southern India. The ring-tailed lemurs were first released onto SCI in 1984 and now consist of three social groups inhabiting the northern part of the island. Group 1, the group in this study, has an average home range of 27.7 hectares, which is on the higher end of home range sizes reported for this species (range, 6-23 ha [Budnitz and Dainis, 1975; Sussman, 1977]). Both the lion-tailed macaques and ring-tailed lemurs have unlimited access to native flora and fauna in addition to daily provisioned diets (consisting of a commercial primate biscuit and a variety of produce) that are known to support growth and reproduction of captive groups. Thus, plant items consumed by semi free-ranging primates were considered to be preferentially selected from available forages. We hypothesized that foods selected by macaques would be lower in macronutrient concentration and higher in fiber than those consumed by lemurs owing to body size and digestive tract morphology differences between the two species.

MATERIALS AND METHODS

Subjects

The macaque group consisted of nine animals (five male, four female) ranging in age from 10 months to 24 years, whereas the ring-tailed lemur group (group 1) comprised 13 individuals (seven male, six female) ranging in age from 1 month to 9 years. The observational sampling of feeding behavior and laboratory analysis of plants followed standardized methodologies as reported in other studies of primate foraging [see Yeager et al., 1997 for details]. For purposes of calculation in this study, feeding time on plants selected was assumed equivalent to mass of forage intake.

Diets comprising approximately 100 or 50 g (for macaques and lemurs, respectively) high-fiber primate biscuits (HMS High Fiber Primate Diet, Bluffton, IN) and 200 or 400 g raw produce (63% vegetables, 37% g fruit) per adult individual were distributed to each group at midday. Diets were designed to meet the calculated energy needs of the species (500 and 275 kcal, respectively) and were generally completely consumed. Nutrient contributions of provisioned diets were excluded from this analysis. Fresh water was freely available at all times.

Behavioral Observation

Sampling of feeding behavior for this study consisted of three 2-day observation periods per species during 1 month each season (February, May, August, November) over 1 year (May 1996 through February 1997). A 2-day observation period

consisted of 2 consecutive days of sampling from 06:30 to 10:30 and from 16:00 to 20:00. Selection of observation periods was based on prior reports of peak feeding activity. Instantaneous scan samples of each group were taken every 10 minutes during the sample period [Altmann, 1974], and the following data were recorded: activity of each individual (specifically actively feeding or not); if feeding, the plant species, plant part being eaten, and feeding height.

Additionally, continuous focal animal observation (at 20-minute intervals) was employed to determine the duration of feeding bouts [Altmann, 1974]. The order of animals observed was randomized so that each animal was observed during each block of the entire sampling period to minimize time biases. During focal observations the following data were recorded when the focal animal was observed actively feeding: the time, the plant species, plant part being eaten, feeding height, and the time when feeding stopped.

Plant Analyses

Based on feeding observations, representative samples were manually collected from three to five individual plants per species. We attempted to obtain 50 to 100 g (wet weight) of material for subsequent chemical assay. Samples were weighed to the nearest 0.1 g, dried in a forced-draft oven at $<60^{\circ}\text{C}$ until constant weight to determine moisture content, ground through a 2-mm screen in a laboratory mill, and kept at room temperature until analysis. Absolute dry matter (DM) was measured by drying samples at 100°C , and all analytical data were corrected to a 100% DM basis.

Crude protein content was calculated as total nitrogen $\times 6.25$ using a macro-Kjeldahl method with a Cu catalyst [Cunniff, 1996]; bound protein was determined on leaf and woody plant materials (twigs, branches, bark) as acid-detergent crude protein [Yeager et al., 1997]. Detergent fiber analyses (neutral detergent fiber [NDF], acid detergent fiber [ADF], and sulfuric acid lignin) were conducted on all plant samples collected, using the methods of Van Soest et al. [1991]. Soluble carbohydrates were evaluated in fruit and seed samples only using a phenol/sulfuric acid colorimetric assay [DuBois et al., 1956] as modified by Strickland and Parsons [1972]. Crude fat was measured in seeds only [Cunniff, 1996]. Macromineral concentrations (Ca, Mg, Na, P) and trace elements (Cu, Fe, Mn, Zn) were assayed by spectroscopy according to standard methodology [Cunniff, 1996].

RESULTS

Data are based on 144 hours of observation (36 hours/season) for the liontailed macaques and 208 hours of observation (52 hours/season) for ring-tailed lemurs. One hundred six samples from 30 identified plant species were collected for chemical analysis over the course of this study. Non-plant materials (insects, soils) observed eaten by study animals were excluded from this analysis. Both the proportion of total observation time spent feeding and the food items selected for consumption appeared to vary by primate species.

Seasonal feeding activity was lowest for both species in the May sampling period ($<10\%$ of observation time, see Table 1). Macaques spent more than twice as much time feeding as lemurs in August, and the opposite behavior pattern was noted in February. The number of food plants consumed by both primate species was highest during the August sampling period (Table 1) and dropped during colder months.

TABLE 1. Seasonal differences in feeding activity of semi free-ranging primates on St. Catherines Island, GA, U.S.A.

	% of total observation time			
	Feb	May	Aug	Nov
Foraging activity				
Lion-tailed macaques	16.0	9.7	26.1	22.9
Ring-tailed lemurs	35.8	4.6	10.2	28.3
Number of plant species consumed				
Lion-tailed macaques	5	11	20	7
Ring-tailed lemurs	14	14	22	13

Lion-tailed macaques (*Macaca silenus*) were observed a total of 144 hours, and ring-tailed lemurs (*Lemur catta*), 208 hours.

(February, November), particularly for the macaques. Leaves and seeds (combined) were important diet components for semi free-ranging lion-tailed macaques most of the year (Table 2), comprising 51% to 93% of observed feeding time on non-provisioned food items, with ripe fruit a major food item (40% of observed feeding time) only during the August sampling period. In general, ring-tailed lemurs consumed a more diverse diet of fruits and leaves during all seasons (see Table 3 for detailed list of plants and plant parts consumed), with seeds and buds increasingly important during winter months (>45% of observed feeding time, Table 2). Food sources belonging to five key genera, *Quercus*, *Tillandsia*, *Pinus*, *Vitis*, and *Arundinaria*, contributed >70% to the diet selected by the macaques, whereas a different five genera, *Persea*, *Melia*, *Celtis*, *Sabel*, and *Juniperus*, were important for the lemurs.

The crude protein content of plant parts eaten was highest in the early growing season (February and May for fruits, buds, and some leaves, see Tables 4 and 5) and reflected the seasonal trend in protein content of selected foods consumed by the ring-tailed lemurs. Only bud samples (n = 5) contained mean crude protein levels considered adequate for meeting the dietary needs of non-human primates (16.7% of DM [NRC, 1978]). With the exception of acorns consumed in August, all foods were moderately (30–50% of DM) to highly (>50% of DM) fibrous. Fruits (soluble carbohydrates) and seeds (fats) were seasonal primary calorie sources for both species.

Mineral content of foods eaten by both macaques and lemurs ranged widely both within and among food categories (Table 6), hence median values were used as a better descriptive statistic than means. All food categories had median values indicating low Na and P content. Overall, seeds (as a category) were low in Ca, Na, and P, and fruits appeared low in Ca (with some individual exceptions). Trace mineral needs for Cu, Mn, and Zn could likely be met by any of the general food categories defined in this study; however, Fe may be limiting compared with published primate dietary recommendations (196 mg/kg DM [NRC, 1978]). Only dry woody samples (n = 5) and a single leafy species (n = 2) contained Fe levels that would appear to be adequate in this survey.

In general, individual plants, as well as the overall weighted averages of forages consumed by macaques contained lower protein and higher fiber levels than foods eaten by lemurs (Tables 4, 5, and 7), but differences were not statistically significant. Foods selected by macaques (weighted by percentage of observed feeding time) were low in Ca and may have been marginal in Cu content compared with

TABLE 2. Seasonal differences in feeding choices of semi free-ranging primates on St. Catherines Island, GA, U.S.A.

Food category	% of total feeding time observed							
	Feb		May		Aug		Nov	
	LTM	RTL	LTM	RTL	LTM	RTL	LTM	RTL
Fruit		23.0		79.2	40.2	66.0		37.7
Seeds	58.5	15.4			13.1	1.0	83.7	44.2
Leaves	26.7	16.2	89.1	11.9	37.9	28.1	9.1	18.2
Wood ^a	14.8		10.9		8.7	4.9	7.1	
Buds		45.3		8.9				

^aWood, bark, twigs, and branches.

Lion-tailed macaques (*Macaca silenus*) (LTM) were observed a total of 144 hours, and ring-tailed lemurs (*Lemur catta*) (RTL), 208 hours.

those selected by lemurs. Na and P levels were low in diets consumed by both species, and Fe concentration was only one third to one half that recommended for nonhuman primates [NRC, 1978].

DISCUSSION

Although studies have been conducted detailing behaviors in the feeding ecology of both lion-tailed macaques [Kumar, 1987; Kurup and Kumar, 1993; Menon and Poirier, 1996] and ring-tailed lemurs [Sussman, 1977; Rasamimanana and Rafidinarivo, 1993] in their native habitats, few data exist on chemical composition of foods eaten by, or digestive physiology of, either species. Both species are considered opportunistically omnivorous, but plants comprise the vast majority of the diet. Hence, recognition and utilization of available plant resources become a critical component of species conservation. It is difficult, however, to compare directly feeding choices of free-ranging primates to those of provisioned animals (termed *semi free ranging* in this study) because nutritional considerations that may underlie food choices in native habitats can be altered by the provisioning (food availability).

For example, Menon and Poirier [1996] reported that lion-tailed macaques in a fragmented forest in India spent 18% of the time actively feeding, which is similar to our average observation of 19% of the time feeding. These authors, however, found that foraging behavior (the process of actively hunting for food) contributed a greater proportion (24%) to the time budget of macaques in their study group, with a significant seasonal influence owing to food availability. We specifically documented feeding behavior (rather than foraging activity) to determine preferential selection of native flora, because our study groups had ready access to a prepared diet designed to meet nutritional needs.

Feeding activity in our macaque group was lowest in May, but highest in August, which were both periods of increased forage species diversity (and inferentially a measure of food availability) compared with winter months. The foods eaten differed considerably between these months, however, with high-moisture (low nutrient density) grapes a major food item in August and high-fat (high nutrient density) seeds consumed in winter months, hence the food selection observed appeared to follow nutrient density rather than plant species density per se. Although foraging

TABLE 3. Plants eaten by semi free-ranging primates on St. Catherines Island, GA, U.S.A., 1996–97^a

Species	Common name	Plant part	Eaten by ring-tailed lemur ^b	Eaten by lion-tailed macaque ^b
<i>Arundinaria gigantea</i>	Giant cane	Leaves	N	M,A
		Stem, dead shoot	A	A
<i>Bumelia tena</i>	Buckthorn	Leaves	A	
		Berries	A	
<i>Carya ovalis</i>	Small pignut	Leaves	A	
		Insect galls	M	
<i>Celtis laevigata</i>	Sugarberry	Leaves	M, A, N	
		Twig		N
<i>Celtis occidentalis georgiana</i>	Hackberry	Leaves	A	
		Buds	F	
		Insect galls	A	
<i>Chenopodium ambrosioides</i>	Mexican tea	Leaves	M	
<i>Cornus florida</i>	Flowering dogwood	Buds	N	
<i>Diospyros virginiana</i>	Persimmon	Fruit	A, N	
<i>Ilex opaca</i>	American holly	Leaves		M
		Berries	F	N
<i>Ilex vomitoria</i>	Yaupon	Leaves	F	
		Berries	N	
<i>Juniperus silicicild</i>	Red cedar	Bark	A, N	
		Berries	A	A
<i>Magnolia grandiflora</i>	Southern magnolia	Leaves	M	
		Flower buds	M	M
<i>Melia azedarach</i>	Chinaberry	Leaves	A	
		Twig	A	
		Berries	M, A, N	
<i>Myrica cerifera</i>	Southern bayberry/wax myrtle	Leaves	M, F	A
<i>Parthenocissus quinquefolia</i>	Virginia creeper	Leaves	M	A
		Vine		A

Nutrient Composition of Selected Plant Species Consumed by Semi Free-Ranging Lion-Tailed Macaques (*Macaca silenus*) and Ring-Tailed Lemurs (*Lemur catta*) on St. Catherines Island, Georgia, U.S.A.

E.S Dierenfeld, C.M. McCann. *Zoo Biology*.

Copyright©1999 Wiley-Liss, Inc. Reproduced with permission of John Wiley & Sons, Inc.

<i>Persea borbonia</i>	Red bay	Leaves	A, N	M
		New growth		M
		Fruit	A, N	
<i>Phoradendron flavescens</i>	Mistletoe	Berries	F	
<i>Pinus taeda</i>	Loblolly pine	Branches, bark	A	A
		Seeds		N, F
<i>Polypodium polyploides</i>	Resurrection fern	Whole		A
<i>Prunus caroliniana</i>	Carolina cherry laurel	Fruit	F	
		Flower buds	F	
<i>Quercus virginiana</i>	Live oak	Leaves	A, F	M, A, N, F
		Buds	F	
		Bark, twigs, wood	M	M, A, F
		Acorn	N	A, N, F
<i>Rubus betuifolius</i>	Blackberry	Berries	M	M
<i>Sabel palmetto</i>	Cabbage palm	Berries	A, N, F	A
<i>Smilax laurifolia</i>		Leaves		A
		Vine	F	
<i>Solanum nigrum</i>	Common nightshade	Berries	N	
<i>Tillandsia usneoides</i>	Spanish moss	Leaves	A, F	M, A, N
<i>Vaccinium arboreum</i>	Sparkleberry	Leaves	A	
		Berries	F	
<i>Vitis cinerea</i>	Nut muscadine	Fruit	A	A
<i>Vitis rotundifolia</i>	Muscadine grape	Leaves	M	M, A
		Bark		A
		Fruit	A, N	A
		Vine		N
<i>Zanthoxylum clava-herculis</i>	Hercules' club	Flower buds	M	
		Leaves	M	
	Unknown grass sp	Leaves	M	M, A, F
	Mushrooms (unknown spp)	Whole	F	A

^aPlant taxonomy after Coile and Junes, 1988.

^bMonth of collection: F, February; M, May; A, August; N, November.

TABLE 4. Proximate composition of foods eaten seasonally by semi free-ranging lion-tailed macaques (*Macaca silenus*) on St. Catherines Island, GA, U.S.A.

Month	Fruits	Seeds	Leaves	Wood ^a
Crude protein (%)				
February		10.1 ± 6.5 (2)	9.2 ± 0.1 (2)	3.9 ± 1.2 (3)
May			9.8 ± 3.7 (7)	9.7 ± 6.4 (4)
August	6.9 ± 3.8 (3)	3.0	9.6 ± 3.1 (10)	2.8 ± 1.2 (4)
November	4.9	11.1 ± 8.8 (2)	6.9 ± 3.9 (2)	2.9 ± 1.1 (3)
Cell wall fiber (NDF), (%)				
February		53.7 ± 35.9	61.7 ± 22.6	71.4 ± 5.8
May			63.2 ± 15.2	62.1 ± 17.0
August	44.8 ± 29.6	8.9	61.7 ± 14.1	83.6 ± 9.0
November	54.4	53.7 ± 30.0	64.6 ± 13.4	73.8 ± 4.2
Water-soluble carbohydrates (%) ^b				
February		7.7 ± 9.0		
May				
August	16.5 ± 24.5	21.3		
November	17.6	6.3 ± 6.7		
Crude fat (%) ^c				
February		17.1 ± 2.0		
May				
August		12.4		
November		23.8 ± 7.1		

^aWood, bark, twigs, and branches.^bWater-soluble carbohydrates analyses performed on fruit and seed samples only.^cCrude fat analyses performed on seed samples only.

Data are presented as means ± SD on a dry basis, with number of samples analyzed in parentheses.

time is clearly an important component to document, at least initially, in primate release or re-introduction programs, as animals are becoming familiar with their environment, the use of chemical data to determine nutrient resources can also provide guidelines for habitat assessment.

Contrary to the macaques, the ring-tailed lemurs increased feeding activity considerably during winter months. Although forage species diversity did not change, plant phenology did. Lemurs relied far more heavily on seeds in November and shifted to buds and fruits (less nutrient dense food resources) by February. Macaques and lemurs on SCI appear to utilize different feeding strategies and select different available foods, with little dietary overlap. The provisioned diet may have alleviated or minimized the need for increased feeding by macaques during cooler months on SCI, but seasonal usage of the provisioned diets has not been detailed for either species. Furthermore, plant diversity indices on the different parts of the island inhabited by the two primate species have not yet been completed.

Macaques in our study group consumed a rather limited number of food plants compared with numbers previously reported in India (81 species in the annual diet [Kumar, 1987], 42 species [Menon and Poirier, 1996]). Conversely, lemurs in our study (average annual feeding time 20% of observations) and those of Ganzhorn [1986] in a similar climate, ate a more diverse array of plant species than reported in studies in Madagascar, where eight species made up >70% of the diet at two different sites [Sussman, 1977; Rasamimanana and Rafidinarivo, 1993]. These differences may be a function of habitat diversity among study sites but need to be evaluated in

Nutrient Composition of Selected Plant Foods 489

TABLE 5. Proximate composition of foods eaten seasonally by semi free-ranging ring-tailed lemurs (*Lemur catta*) on St. Catherines Island, GA, U.S.A.

Month	Fruits	Seeds	Leaves	Wood ^a	Buds
Crude protein (%)					
February	15.0 ± 12.8 (5)	5.5	15.3 ± 13.7 (4)		18.2 ± 11.7 (3)
May	13.7 ± 5.6 (2)		14.4 ± 5.9 (6)		17.2 ± 9.3 (2)
August	9.2 ± 4.7 (10)	3.0	11.6 ± 4.6 (8)	3.0 ± 1.0 (5)	
November	8.4 ± 3.9 (9)	4.9	11.7 ± 0.9 (4)		10.3
Cell wall fiber (NDF) (%)					
February	40.6 ± 16.7	28.4	38.1 ± 16.1		36.5 ± 13.8
May			45.5 ± 14.2		41.7 ± 20.7
August	41.0 ± 22.0	8.9	47.2 ± 19.6	82.5 ± 9.1	
November	47.4 ± 11.5	32.5	41.8 ± 26.6		52.0
Water-soluble carbohydrates (%) ^b					
February	22.2 ± 2.9				
May	12.8 ± 0.6				
August	17.5 ± 18.1				
November	17.4 ± 12.0	11.1			
Crude fat (%) ^c					
February					
May					
August					
November		18.8			

^aWood, bark, twigs, and branches.

^bWater-soluble carbohydrates analyses performed on fruit and seed samples only.

^cCrude fat analyses performed on seed samples only.

Data as means ± SD on a dry basis, with number of samples analyzed in parentheses.

more detail, including chemical comparison of the food and nutrient resources available and/or utilized.

Body size and gut morphology differences between the two primates in our study were originally hypothesized to underlie possible differences in food selectivity noted. Smaller species require more energy per unit body metabolic body size; other nutrients supplied proportional to energy intake (which drives intake) are then, by inference, found in higher dietary concentrations or made available by faster throughput. The hindgut of lemurs (particularly the colon) has been shown to be anatomically simpler than that of macaques [Stevens and Hume, 1995], and the fermentative capability of the lemurs appears limited owing to rapid passage [Cabre-Vert and Feistner, 1995]. For these reasons, macaques were expected to be able to utilize foods containing a higher level of fiber compared with the lemurs on SCI. Differences between the species, however, were not significant, and both species ate native forages that contained much higher levels of cell wall constituents (NDF) compared with domestic produce and commercial primate diets. Mass-specific differences in energy needs between these two species were likely not great enough to have an effect (calculated 145 kcal/kg metabolic body size [MBS] for a 3-kg lemur vs. 140 kcal/kg MBS for 7-kg macaques). Cecal specializations found in lemurs may partially compensate for the colonic haustrations of macaques, but direct comparisons of passage and fiber fermentation have not been made between these species. Compared with the fiber content of foods eaten by the primates in this study, fiber fermentation capabilities of either species have probably not been challenged by diets previously reported in the literature.

Nutrient Composition of Selected Plant Species Consumed by Semi Free-Ranging Lion-Tailed Macaques (*Macaca silenus*) and Ring-Tailed Lemurs (*Lemur catta*) on St. Catherines Island, Georgia, U.S.A.

E.S Dierenfeld, C.M. McCann. *Zoo Biology*.

Copyright©1999 Wiley-Liss, Inc. Reproduced with permission of John Wiley & Sons, Inc.

TABLE 6. Median and range (min-max) in mineral content of foods eaten by free-ranging lion-tailed macaques (*Macaca silens*) and ring-tailed lemurs (*Lemur catta*) on St. Catherines Island, GA, U.S.A.

	Fruits (n = 26)	Seeds (n = 5)	Leaves (n = 37)	Wood ^a (n = 15)	Buds (n = 6)	Primate dietary recommendation ^b
Ca (%)	0.31 (0.11–1.50)	0.07 (0.04–0.10)	0.73 (0.04–3.99)	0.78 (0.12–2.90)	0.66 (0.34–3.41)	0.54
Mg (%)	0.27 (0.06–0.99)	0.19 (0.08–1.00)	0.32 (0.14–1.11)	0.51 (0.01–0.78)	0.25 (0.16–0.33)	0.16
Na (%)	0.04 (0.02–0.27)	0.02 (0.01–0.02)	0.04 (0.01–0.78)	0.04 (0.01–1.67)	0.03 (0.02–0.04)	0.20
P (%)	0.20 (0.05–0.57)	0.12 (0.06–0.43)	0.15 (0.04–0.62)	0.03 (0.01–0.51)	0.42 (0.24–0.77)	0.43
Cu (mg/kg)	11.1 (2.0–38.4)	10.6 (7.6–14.4)	5.6 (1.5–24.8)	7.7 (1.0–11.5)	15.2 (10.2–28.8)	10
Fe (mg/kg)	44.3 (12.9–137.5)	34.5 (22.6–108.8)	84.2 (22.0–786.2)	51.4 (21.6–831.5)	56.1 (32.9–92.1)	196
Mn (mg/kg)	23.3 (3.7–199.5)	61.5 (23.1–133.6)	114.4 (17.8–494.1)	34.2 (4.3–449.5)	33.0 (8.3–117.8)	30
Zn (mg/kg)	19.5 (7.1–121.3)	15.1 (5.8–59.9)	24.1 (8.9–224.6)	16.8 (3.1–79.9)	41.9 (20.9–69.3)	11

^aWood, bark, twigs, and branches.^bNational Research Council, 1978; Oftedal and Allen, 1996.

Data are presented on a dry matter basis.

Macaque Nutritional Considerations

Fruits, seeds, and flowers (the latter particularly during periods of low food availability) are reported as staple foods of lion-tailed macaques in India [Menon and Poirier, 1996], whereas leaves and seeds were the most important food categories selected by macaques on SCI. Fruits (grapes, *Vitis* sp) were only available during the August sampling period but were quite seasonally favored. These differences in food categories consumed can have a substantial impact on overall nutrition of primates. Fruits, in general, are lower in protein than seeds or leaves, although the acorns (*Quercus* sp) consumed only contained 3.0% crude protein. A mixture of fruits and seeds, as analyzed in this study, contained approximately the same protein content as a leaf-based diet. Leaves were available year-round and readily abundant. A mixture of acorns with pine seeds (*Pinus* sp) in winter months provides higher protein, higher fat foods to the macaques in much the same manner as they did as a dietary staple for Native Americans [Fowler, 1986]. Specific requirements have not been established for this species but have been established for other members of the genus *Macaca* [NRC, 1978]. The recommended dietary protein concentration for Old World primates at all physiological stages (16.7% of DM [NRC, 1978] is higher than in foods consumed by the macaques eating native vegetation on SCI. The macaques may be dependent on their provisioned diet (biscuits containing 26.3% crude protein), particularly seasonally, to meet dietary needs of this nutrient. Conversely, adult humans need only approximately 9.5% dietary protein on a DM basis [NRC, 1989], thus protein content of native vegetation may not be particularly deficient for adult individuals if considered on an annual basis.

The fiber (NDF) content of leaves and woody plant parts eaten by macaques

Nutrient Composition of Selected Plant Species Consumed by Semi Free-Ranging Lion-Tailed Macaques (*Macaca silenus*) and Ring-Tailed Lemurs (*Lemur catta*) on St. Catherines Island, Georgia, U.S.A.

E.S Dierenfeld, C.M. McCann. *Zoo Biology*.

Copyright©1999 Wiley-Liss, Inc. Reproduced with permission of John Wiley & Sons, Inc.

Nutrient Composition of Selected Plant Foods 491

TABLE 7. Nutrient composition of foods eaten by free-ranging lion-tailed macaques (*Macaca silenus*) and ring-tailed lemurs (*Lemur catta*) on St. Catherines Island, GA, U.S.A.

	Lion-tailed macaque (n = 45)	Ring-tailed lemur (n = 61)	Primate dietary recommendation ^a
Crude protein (%)	9.00 ± 2.87	11.52 ± 6.74	16.7
NDF (%)	56.84 ± 21.85	38.38 ± 16.73	10 to 20
Ca (%)	0.38 ± 0.25	0.63 ± 0.19	0.54
Mg (%)	0.28 ± 0.26	0.35 ± 0.29	0.16
Na (%)	0.05 ± 0.04	0.08 ± 0.04	0.20
P (%)	0.18 ± 0.05	0.25 ± 0.04	0.43
Cu (mg/kg)	8.09 ± 2.57	13.59 ± 6.00	10
Fe (mg/kg)	85.52 ± 30.13	65.03 ± 20.19	196
Mn (mg/kg)	106.45 ± 15.59	48.60 ± 18.63	30
Zn (mg/kg)	28.41 ± 14.98	35.42 ± 4.03	11

^aNational Research Council, 1978; Oftedal and Allen, 1996.

Data, based on percent feeding time, are presented as weighted means ± SD on a dry basis. Samples were collected over four seasons (number of plant samples analyzed in parentheses).

on SCI in May was higher than reported in leaves consumed by Japanese macaques (*Macaca fuscata yakui*) in April (5–35%, wet matter basis [Hill and Lucas, 1996]), much higher than found in commercially manufactured primate diets (14–26%, DM basis [Oftedal and Allen, 1996]), and more similar to foods eaten by folivorous colobine monkeys [Yeager et al., 1997]. Even fruits and seeds were high (although quite variable) in total cell wall content. Japanese macaques were found to select against toughness in food choices; however, the index of toughness was independent of plant fiber content [Hill and Lucas, 1996]. Although fiber-digesting ability of the lion-tailed macaque has not been reported, adult males were able to maintain body weight when fed a diet containing approximately 30% NDF in a controlled trial [Lessnau et al., 1998]. *Macaca* species have a simple stomach, a relatively short small intestine, and a haustrated colon, presumably adapted for hindgut fermentation of their herbivorous diet [Stevens and Hume, 1995]. These and other mid-sized primates appear to readily tolerate a medium- to high-fiber diet [Conklin-Brittain et al., 1999] and may benefit from increased fiber in captive diets.

Foods (weighted seasonally by percentage of feeding time) consumed by macaques in this study were found to be low in Ca, Na, P, and Fe relative to dietary recommendations for non-human primates [NRC, 1978]. Fruits and seeds are notoriously poor sources of mineral nutrition, particularly Ca, Na, and P. In contrast, leaves and woody plant parts (twigs, bark) are better sources of Ca; a combination may have balanced out some of the lack of Ca in other dietary ingredients. We noted some chewing of limestone on occasion by the macaques, perhaps in an attempt to meet Ca needs; however, we assume that mineral needs of the group are met by the provisioned diet. Clinical mineral deficiencies or imbalances have not been documented in this study group, and detailed examination of mineral and vitamin status is currently underway [Eidlin et al., unpublished data]. Na was remarkably low in all foods analyzed, and we noted many instances of primates licking the outside of plants, perhaps in an attempt to obtain more Na deposited from the marine environment. An external salt source would be required for primates to meet nutrient needs in this habitat without a provisioned diet.

Regarding trace mineral nutrition, native plants consumed by macaques may

have been marginal in Cu content, although no signs of deficiency have been noted in this group. Acorns analyzed were low in Fe, Mn, and Zn, whereas pine seeds were high in all these minerals, hence the mixture of pine seeds and acorns consumed by the macaques may have been nutritionally beneficial.

Lemur Nutritional Considerations

Natural feeding behavior of the ring-tailed lemur is a combination of frugivory and folivory, although some flowers, bark, dead wood, and sap are also reported consumed [Sussman, 1977; Rasamimanana and Rafidinarivo, 1993]. Young and mature leaves of the leguminous *Tamarindus indica* (tamarind tree), important in the diet of lemurs and other African primates, are high in nitrogen (crude protein) as well as fiber [Mowry et al., 1996]. Indeed, fruits and leaves consumed by lemurs on SCI were higher in crude protein content than equivalent foods eaten by macaques, and buds eaten in spring months contained the highest protein level of all food categories sampled. As suggested previously by Ganzhorn [1986] in his study of provisioned lemurs at Duke University Primate Center, selected plant materials may have contributed little to overall protein nutrition owing to heavy contribution from the commercial biscuits. Nonetheless, the overall diet consumed by lemurs tended to be higher in protein than that eaten by macaques, reflecting either a better selective ability of the ring-tailed lemur, perhaps a higher physiological requirement for this nutrient, or different plant species to select from on their portion of the island.

Lemur catta also feeds on more fibrous foods and has a slower gut passage time than some of the more frugivorous lemur species such as *L. fulvus* [Ganzhorn, 1986] or *Varecia variegata* [Cabre-Vert and Feistner, 1995], thus may have a more developed gastrointestinal tract for dealing with plant fibers. All foods eaten by ringtailed lemurs on SCI contained fiber levels well above those presented as general primate dietary recommendations (10–20% NDF, dry basis [Ofstedal and Allen, 1996]), and considerably higher than found in most domestic produce utilized as substitute foods in managed feeding programs. Nonetheless, the minimal residence time of food in the digestive tract [1.5 to 6.5 hr; Cabre-Vert and Feistner, 1995] is unlikely to provide sufficient time to allow significant fermentation of plant cell wall constituents, and the readily-digestible soluble carbohydrates in fruits consumed on a year-round basis (or fat in acorns eaten in November) were more reliable sources of energy to meet the needs of the lemurs.

Buds, as a food category, were important sources of both Ca and P relative to other foods, and foods selected by the lemurs on an annual basis were higher in both these nutrients compared with macaques. As in other studies of free-ranging herbivores, Na appeared to be limiting in the environment. Observed licking of tidalsaturated plants and/or soil ingestion may have been sources of Na for lemurs at SCI, with a possible substantial contribution from the provisioned diet. Trace mineral concentrations in native vegetation appeared adequate to meet estimated dietary needs. It is possible that Fe content of plants consumed by lemurs may be a better reflection of physiological requirement for this species than the current NRC dietary recommendations. Spelman et al. [1989] found that captive lemurs were extremely susceptible to excess iron deposition (hemosiderosis) in organs and attributed the disease to a diet high in Fe and ascorbic acid, and low in tannins. Lower Fe levels, as well as higher levels of dietary fiber and tannins [Mowry et al., 1997] in foods con-

sumed by the lemurs on SCI, may be beneficial in managing this disease, hence these data may provide some practical guidelines.

CONCLUSIONS

Provisioned diets known to support growth and reproduction of lion-tailed macaques and ring-tailed lemurs in zoos were provided to supply basic nutritional needs of these two primate species on St. Catherines Island, GA. Hence, foods selected by these semi free-ranging primates, observed over the course of 1 year, were assumed to be representative of preferred forages and plants that could be physiologically utilized. With no consideration of the contribution of the provisioned diet, behavioral and chemical differences were noted:

1. Although the annual feeding time was identical between the two primate species (18.7% and 19.7% of observation time), wide seasonal variations existed in individual feeding activities.
2. Ring-tailed lemurs had a much higher diet diversity compared with the liontailed macaques.
3. The lion-tailed macaque staple food selections comprised leaves and seeds, with fruits eaten only seasonally, whereas fruits and leaves were primary food items for the ring-tailed lemur, with buds and seeds eaten seasonally.
4. Overall, forages selected (both seasonally as well as annual means weighted by seasonal intake) were low in protein and high in fiber, relative to estimates of dietary requirements for non-human primates.
5. Annual weighted means of forages selected met Ca requirements for the ring-tailed lemur, but not the lion-tailed macaque, and were low in Na, P, and Fe for both species.
6. Despite differences in food items selected, the nutrient composition of forages consumed was notably similar between these disparate primates.

ACKNOWLEDGMENTS

This project was funded by a Wildlife Conservation Society's Species Survival Fund grant to CMM. Several individuals helped with the data collection and analyses in this study. We especially appreciate the efforts of R. Lessnau in coordinating the field data collection staff: L. Cordy, R. Jackson, J. Savage, J. Hinely, J. Warlikowski, A. Jolliffe, and S. Silber for assistance with the data collection. M. Fitzpatrick, S. Vitazkova, L. Egol, M. Pozzuoli, L. Pearson, and H. Cantor provided laboratory analytical assistance, and J. Quispe and N. Morabito assisted greatly in the behavioral data summaries. The St. Catherines Island (SCI) Foundation contributed logistical support for this study, particularly R. Hayes, who provided his assistance and valuable information about SCI.

REFERENCES

- | | |
|---|---|
| Altmann J. 1974. Observational study of behavior: sampling methods. <i>Behaviour</i> 49:227–85. | Cabre-Vert N, Feistner ATC. 1995. Comparative gut passage time in captive lemurs. <i>Dodo, J. Wildl Preserv Trust</i> 31:76–81. |
| Budnitz N, Dainis K. 1975. <i>Lemur catta</i> : ecology and behavior. In: Tattersall I, Sussman RW, editors. <i>Lemur biology</i> . New York: Plenum Press. p 219–35. | Coile NC, Jones Jr SB. 1988. Checklist of the vascular flora of St. Catherines Island, Georgia. <i>Am Museum</i> 2920:1–14. |

Nutrient Composition of Selected Plant Species Consumed by Semi Free-Ranging Lion-Tailed Macaques (*Macaca silenus*) and Ring-Tailed Lemurs (*Lemur catta*) on St. Catherines Island, Georgia, U.S.A.

E.S Dierenfeld, C.M. McCann. *Zoo Biology*.

Copyright©1999 Wiley-Liss, Inc. Reproduced with permission of John Wiley & Sons, Inc.

- Conklin-Brittain NL, Wrangham RW, Hunt KD. 1999. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *Int J Primatol* 19:971–99.
- Cunniff, PA, editor. 1996. Official methods of analysis of AOAC International, 16th ed. Gaithersburg, MD: AOAC International (CD-ROM).
- DuBois M, Gilles KA, Hamilton JK, Rebers PA, Smith F. 1956. Colorimetric method for determination of sugars and related substances. *Anal Chem* 28:350–6.
- Fowler CS. 1986. Subsistence. In: Sturtevant WC, D'Azevedo WL, editors. *Handbook of North American Indians*. Volume 11: Great Basin. Washington, DC: Smithsonian Institution Press. p 64–97.
- Ganzhorn JU 1986. Feeding behavior of *Lemur catta* and *Lemur fulvus*. *Inter J Primatol* 7:17–30.
- Green S, Minkowski K. 1977. The lion-tailed monkey and south Indian rainforest habitat. In: Prince Rainier III, HRH, Bourne GH, editors. *Primate conservation*. New York: Academic Press. p 290–338.
- Hill DA, Lucas PW. 1996. Toughness and fiber content of major leaf foods of Japanese macaques (*Macaca fuscata yakui*) in Yakushima. *Am J Primatol* 38:221–31.
- Kumar A. 1987. The ecology and population dynamics of the lion-tailed macaque (*Macaca silenus*) in south India [Ph.D. dissertation]. Cambridge: Cambridge University.
- Kurup GU, Kumar A. 1993. Time budget and activity patterns of the lion-tailed macaque (*Macaca silenus*). *Int J Primatol* 14:27–39.
- Lessnau RG, Obrock, CH, Dierenfeld ES, McCann CM. 1998. Food intake and fat-soluble vitamin status in captive lion-tailed macaques (*Macaca silenus*) [abstract]. *Proc Am Primatol Soc* 45:192.
- Menon S, Poirier FE. 1996. Lion-tailed macaques (*Macaca silenus*) in a disturbed forest fragment: activity patterns and time budget. *Int J Primatol* 17:969–85.
- Mowry CB, Decker BS, Sure DJ. 1996. The role of phytochemistry in dietary choices of Tana River red colobus monkeys (*Procolobus badius rufomitatus*) *Int J Primatol* 17:63–84.
- Mowry CB, McCann C, Lessnau R, Dierenfeld E. 1997. Secondary compounds in foods selected by free-ranging primates on St. Catherines Island, GA. *Proc AZA Nutr Adv Group Conf*, Fort Worth, TX.
- Mowry CB. 1998. Feeding ecology of *Lemur catta*: implications for captive populations [abstract]. XVII Congress of the International Primatology Society, Antananarivo, Madagascar.
- National Research Council. 1978. Nutrient requirements of nonhuman primates. Washington, DC: National Academy Press. 83 p.
- National Research Council. 1989. Recommended dietary allowances, 10th rev ed. Washington, DC: National Academy Press. 302 p.
- Oftedal OT, Allen ME. 1996. The feeding and nutrition of omnivores with emphasis on primates. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S, editors. *Wild mammals in captivity*. Chicago: University of Chicago Press. p 148–57.
- Rasamimanana HR, Rafidinarivo E. 1993. Feeding behavior of *Lemur catta* in relation to their physiological state. In: Kappeler PM, Ganzhorn JU, editors. *Lemur social systems and their ecological basis*. New York: Plenum Press. P 123–33.
- Spelman LH, Osborn KG, Anderson KG. 1989. Pathogenesis of hemosiderosis in lemurs: role of dietary iron, tannin, and ascorbic acid. *Zoo Biol* 8:239–51.
- Stevens CE, Hume ID. 1995. Comparative physiology of the vertebrate digestive system, 2nd ed. Cambridge: Cambridge University Press. 300 p.
- Strickland JDH, Parsons TR. 1972. A practical handbook of seawater analysis. Ottawa: Fisheries Research Board of Canada. 167 p.
- Sussman RW. 1977. Feeding behavior of *Lemur catta* and *Lemur fulvus*. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys, and apes*. London: Academic Press. p 1–37.
- Thomas DH. 1988. St. Catherines: an island in time. Atlanta: University of Georgia Press. 82 p.
- Van Soest PJ, Robertson JB, Lewis BA. 1991. Methods for dietary fiber, neutral detergent fiber and nonstarch polysaccharides in relation to animal nutrition. *J Dairy Sci* 74:3583–97.
- Yeager CP, Silver SC, Dierenfeld ES. 1997. Phytochemical comparison of leaves from food and nonfood plants of proboscis monkeys (*Nasalis larvatus*). *Am J Primatol* 41:117–28.