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Diets of Two Sympatric Colobines in Zaire: More Evidence on Seed-Eating in Forests on Poor Soils

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Recent studies have shown that the so-called folivorous African colobines eat a significant amount of seeds. There is disagreement as to whether seed-eating is due to the poor quality of tree foliage, due in turn to poor soils, or to the fact that seeds are a normal part of colobine diets. To test these hypotheses, we studied feeding of red colobus monkeys, Colobus badius tholloni, *and black-and-white colobus monkeys,* Colobus angolensis angolensis, *in a tropical rain forest of Central Zaire (Salonga National Park). We conducted studies on soil properties, vegetation composition, and the availability and chemical contents of food plants simultaneously. Soils were very acid, with a high percentage of sand, very low cation exchange capacity, and very low exchangeable bases. The forest was dominated by legumes (45.6% of trees), among which the Caesalpinioideae were the best represented (85%).* C. badius *fed mostly on leaves (61%) and seeds (33%), legumes making up 65% of their diet.* C. angolensis *fed mostly on seeds (50%) and leaves (27%); 39% of their diet came from legumes. The two species tended to select items richer in crude protein or lipids or both. Total phenolics and condensed tannins were abundant in the foliage and seeds but were poor predictors of colobine choice of food. Intersite comparisons show that colobines in Zaire ate a higher proportion of seeds than all other related species so far studied in Africa and that the Salonga forest had among the poorest soils and harbored the highest percentage of Caesalpinioideae. Our results confirm that seed-eating is more common among colobines living in areas where soils are poor. They strongly suggest that this link is mediated through forest composition, especially the abundance of legumes, and that the development of seed-eating results both*

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from the high availability of nutrient-rich seeds and from the poor quality of mature tree foliage.

KEY WORDS: African colobines; *Colobus badius; Colobus angolensis;* seed-eating; poor soils; leguminosae.

INTRODUCTION

Until recently it was thought that African colobines are primarily folivorous. Recent work, however, indicates that leaf-eating varies among taxa. Within the black-and-white species group, *Colobus guereza* in Uganda eats 74% leaves annually (Oates, 1977), while *C. satanas* in Gabon ingests 26% leaves (Harrison and Hladik, 1986). Within the red colobus group, leaf-eating varies from 37% for *C. badius temminckii* Gambia (Starin, 1991) to 84% for *C. b. tephrosceles* [Uganda (Struhsaker, 1975)]. Seed-eating is reported as prevalent only in *C. b. temmickii* [Senegal (Gatinot, 1977)] and in *C. b. badius* [Sierra Leone (Davis, personal communication)], in which seeds comprise 19 and 25% of the diet, respectively. Among the black-and-white species group, seed-eating varies from 1% seeds in *C. guereza* [Uganda (Oates, 1977)] to 60% seeds in *C. satanas* [Cameroon (McKey *et al.*, 1981), Gabon (Harrison and Hladik, 1986)].

The incidence of seed-eating by *C. satanas* in Cameroon was attributed to low levels of soil nutrients, which may lead to a high investment by trees in antiherbivore defenses to protect their leaves (McKey *et al.*, 1978; Gartlan *et al.*, 1980). However, Oates *et al.*, (1990) suggested that a direct link of this type was unlikely, as seeds are a dietary item of colobines in Gabon, where the soils are higher in clay content and in pH. Our study dealt with two sympatric colobines, one black-and-white form, *C. angolensis angolensis,* and one red form, *C. b. tholloni.* These subspecies occur only on the left bank of the Zaire River, where forests grow on highly weathered, acidic white-sand soils (Evrard, 1968). The study has two main objectives: (1) to investigate the plant diets and food partitioning between these sympatric monkeys with regard to food availability and (2) to test whether there is a link among soil properties, phytochemistry, and the development of seed-eating by comparing our results with those obtained from other African sites.

STUDY SITE AND METHODS

The study site is at Botsima (1°15′S, 22°E), Salonga National Park, in the Central Zaire Basin. It is a 250-ha area within a meander of the

Lomela River. It contains patches of swamp, seasonally flooded and mainland forest habitat. Rainfall over the 12 months of the study was 1774 mm, with two dry seasons occurring around February and July. February had <50 mm of rain; 3 months (January, June, and July) had <100 mm of rain. Apart from the *Colobus,* the following monkey species occur at the site: *Cercocebus aterrimus, Cercopithecus ascanius whitesidei, C. neglectus, C. (Allenopithecus) nigroviridis,* and *C. wolfi wolfi.*

A grid of trails every 100 × 200 m allowed access to all parts of the study area, which did not suffer from hunting or logging pressure. Observations were made on one troop of *C. badius,* which comprised >60 individuals, and five troops of *C. angolensis,* whose group size varied from 3 to 7 individuals and whose home ranges covered the whole expanse used by the troop of *C. badius.* We observed all five troops of *C. angolensis* equally. Animals were habituated to the observers for 2 months; however, *Colobus angolensis* remained shier and more difficult to observe than *C. badius* was.

We collected feeding records via the frequency method (Struhsaker, 1975) but using 30-min intervals. We recorded the following items of food: young leaf (included shoots and buds), mature leaf, ripe and unripe fleshy fruit, ripe and unripe fruit with arillate seed, immature and mature seed, and flower. During analysis, we considered only consumption of ripe fleshy fruit as fruit-eating (or pulp-eating); ingestion of unripe fleshy fruit or unripe fruit with arillate seeds or immature and mature seeds from dry fruit (e.g., pods or capsules) is seed-eating. In the case of ripe fruit with arillate seeds, it was sometimes difficult to decide whether only the aril was eaten (and the seed swallowed) or both the aril and the seed were chewed (especially in the case of Myristicaceae). These cases are considered as seed-eating.

The work on *C. badius* covered one annual cycle (September 1990–September 1991; 2317 feeding records; monthly mean, 193 ± 166). We collected data on *C. angolensis* over 8 months (February 1991–September 1991; 486 feeding records; monthly mean, 60.7 ± 37). We tested differences in the diet during the 8 months common to the two species and the seasonal patterns of their diets via Wilcoxon paired ranks and Spearman rank correlation, respectively. We calculated monthly dietary diversity and the overlap index of the diets (Pianka, 1973; Holmes and Pitelka, 1968).

We recorded all trees >15 cm dbh, along a 10-km transect on a strip 2 m wide (a total area of 2 ha) to assess the botanical structure of the forest. We assessed fruit availability as follows: a 5-km trail was traveled every second week and numbers of fruiting species and of fruiting trees were noted; results are expressed as the mean monthly number of fruiting individual trees per 100 m of trail (Gautier-Hion *et al.*, 1985). We considered the availability of the following items: mature fleshy fruit, mature fruit with arillate seeds, unripe nonleguminous fruits (either fleshy fruit or fruit with arillate seeds), and unripe or ripe leguminous fruit (Gautier-Hion *et al.*, 1993).

We collected and dried 84 plant samples and analyzed them at the Laboratory of Plant Physiology (University of Rennes) for water content, total nitrogen as crude protein (Kjeldahl method), total phenolics (Folin–Denis method), condensed tannins (proanthocyanidin method), alkaloids (Dragendorff's solution), and lipids (extracting in hexane, drying and weighing the lipids remaining).

We dug 34 soil pits throughout the study area (including flooded and mainland forest). We dried samples from them and had them analyzed for their mechanical and chemical properties at the Laboratory of Soil analysis, INRA (Arras).

RESULTS

Soil Composition

The soil was very acidic (pH 4.13), with a high percentage of sand (87%), a very low content of silt and clay, and a very low cation-exchange capacity (6.03 Cmol+/kg; Table I). Exchangeable bases are extremely low throughout the site; the soil has low levels of potassium and phosphorus and is deficient in calcium, sodium, manganese, and magnesium. All these parameters indicate a very poor soil, which is also characterized by a high level of aluminum. The very low fertility of Salonga soils is supported by evidence from ancient village sites that once areas were cleared, there was almost no regeneration, even after 15 years.

Forest Composition and Food Availability

We recorded 831 trees in the 2 ha sampled; 45.6% of them are in the Leguminosae, of which 85.2% are Caesalpinioideae, 3.1% Papilionoidae, and 0.7% Mimosoidae. The other main families are Annonaceae, Euphorbiaceae, Burseraceae, Olacaceae, and Ebenaceae (Fig. 1). The 10 most important species, half of which are Caesalpinioideae, constituted 62% of the tree population.

The availability of fruit and seeds varied seasonally (Fig. 2). Ripe fleshy fruit were especially low from November until May; maxima occurred in July and in September. Leguminous seeds (mostly Caesalpinioideae)

Table I. Soil Characteristics from Botsima, Salonga National Park

	Sample depth (cm)	
	A horizon (0–10) (N = 17)	B horizon (20–40 (N = 17)
Sand % (>50 µ–2 mm)	86.8 ±13.2 (46.6–96.7)[a]	87.98 ±14.0 (47.8–97.5)
Silt % (20–50 µm)	4.4 ±2.7 (1.8–11)	4.01 ±2.7 (1.3–10.1)
Clay % (<2 µm)	8.79 ±10.7 (1.1–42.7)	8.01 ±11.9 (1.1–42.1)
pH	4.13 ±0.4 (3.6–5.6)	5.09 ±0.7 (3.95–6.2)
% organic matter	4.5 ±4.8 (0.33–18.6)	1.6 ±3.3 (0.07–14.07)
Organic N, g/kg	1.42 ±1.26 (0.09–5.0)	0.27 ±0.3 (0.03–0.89)
Organic C, g/kg	26.21 ±28 (1.9–107.9)	9.43 ±19.27 (0.4–8.18)
C:N ratio	17.72 ±4.4 (10.4–24.6)	17.48 ±6.84 (8–34)
Available $P(P_2O_5)$, g/kg	0.012 ±0.01 (0.002–0.028)	0.003 ±0.004 (0.002–0.017)
CEC, Cmol+/kg	6.03 ±6.11 (0.7–22.6)	2.78 ±5.8 (0.1–24.6)
Ca^{2+}, g/kg	0.011 ±0.002 (0.01–0.02)	0.01
Na^{+}, g/kg	0.005 ±0.006 (0.002–0.027)	0.003 ±0.002 (0.001–0.009)
Mn^{2+}, g/kg	<0.5	<0.5
Mg^{2+}, g/kg	0.006 ±0.03 (0.001–0.015)	0.001 ±0.002 (0.001–0.008)
K^{+}, g/kg	0.023 ±0.015 (0.001–0.053)	0.008 ±0.024 (0–0.1)
Al, Cmol+/kg	1.241 ±1.47 (0.01–4.5)	0.936 ±1.65 (0.01–6.7)
Total P %	0.029 ±0.027 (0.01–0.1)	0.182 ±0.02 (0–0.07)

[a] Plus/minus SD; range in parentheses.

were abundant from July to October. Mature fruit with arillate seeds (mostly Annonaceae) showed two peaks of abundance, in April–May and in August. Unripe nonleguminous fruit were available from December until March (mostly Annonaceae) and from June to August (mostly Olacaceae).

Of fruit types, 10% of tree bore arillated seeds, 22% bore fleshy fruit, and 53% bore dry seeds (pods and capsules).

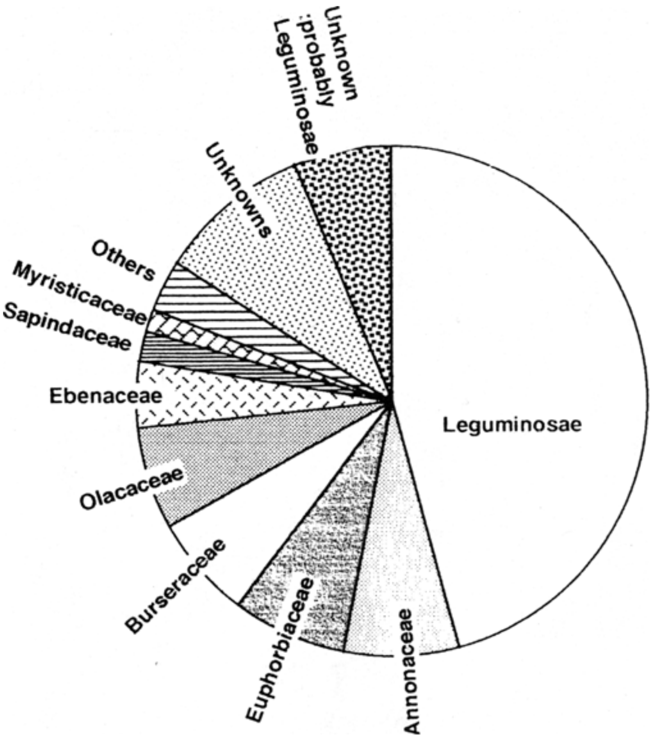

Fig. 1. Proportion of trees in the different plant families.

Quantitative Composition of Plant Diets and Seasonal Variations

C. badius concentrated on leaves (60.5%) and on seeds (a total of 31%; Table II). They were primarily folivorous from December to July (80%) and primarily seed-eaters from August to November (65–75%; Fig. 3). The pulp of ripe fleshy fruit complemented their diet from September to December. *C. angolensis* were mainly seed-eaters (50%) and leaf-eaters (27.5%). Fleshy fruit and flowers constituted 23% of their diet (Table II). They were successively leaf eaters (53% in February), seed-eaters (50 and 40% in April and May respectively), pulp-eaters (56% in June), and again seed-eaters (70 and 88% from July to September; Fig. 3). During the 8 common months, *C. badius* ate significantly more leaves than *C. angolensis* did ($P = 0.008$). *C. angolensis* ate more seeds ($P = 0.018$), more arillate seeds ($P = 0.004$), and more ripe fleshy fruit ($P = 0.039$, from February to August).

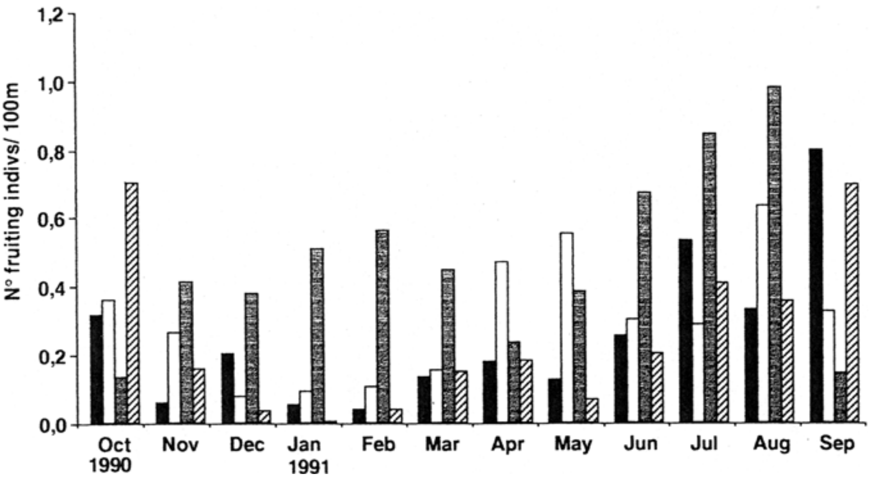

Fig. 2. Seasonal availability of fruits and seeds. (■) Mature fleshy fruits; (☐) mature fruit with arillate seeds; (▩) unripe nonleguminous fruit; (▨) ripe and unripe leguminous fruit.

Qualitative Composition of Plant Diets

Of all items eaten annually by *C. badius*, 65% were in the Leguminosae, including leaves (45%), seeds (19%), and flowers (1%). Of the diet of *C. angolensis*. 40% were from legumes, including leaves (18%), seeds (16%), and flowers (6%). Nearly 75% of leaves and 62% of seeds eaten by *C. badius* are from legumes (Table III); of these, Caesalpinioideae contributed the most (>85 % for both leaves and seeds); while Mimosaceae were used mainly for their leaves and Papilionoideae for their seeds. *C. angolensis* took 65% of leaves and 31% of seeds from legumes; both the Caesalpinioideae and the Mimosoideae contributed significantly to the leaf diet (58 and 40%, respectively), while 64% of the legume seeds eaten are from Papilionoideae (Table III).

Leguminous species rank both first and second in the diet of *C. badius* during 8 months of the year and either first or second all year (Table IV). The most commonly consumed leguminous leaves are from Caesalpinioideae. The most commonly eaten leguminous seeds are from three species of Caesalpinioideae and one species of Papilionoideae (Table IV). Arillate seeds are mainly from Annonaceae and Myristicaceae, while other seeds from unripe fleshy fruit mainly consist of drupes from Olacaceae.

C. angolensis foraged leaves from Mimosoideae and Caesalpinioideae, as well as from Clusiaceae and Olacaceae (Table V). Their most commonly

Table II. Percentage of Plant Foods Eaten by *C. badius tholloni* and *C. angolensis angolensis*

Species	*N*	Young leaves	Mature leaves	Seeds from legumes	Seeds from unripe fleshy fruit	Arillate seeds	Pulp from ripe fleshy fruit	Flowers
C. badius (12 mos)	2317	54.3	6.4	19	6.3	5.5	7.1	1.4
C. badius (8 mos)	2079	58.7	9.5	12.4	8.6	6.5	3.2	1.1
C. angolensis (8 mos)	486	21.0	6.4	15.7	18.2	16.0	16.8	5.9

Table III. Percentage of Leaves and Seeds Eaten that Are from the Leguminosae, and Contribution of the Three Subfamilies (Caesalpinioideae, Mimosoideae, Papillionoideae) to This Figure[a]

Monkey species	Leaves				Seeds			
	All legumes	Caesalp.	Mimos.	Papillio.	All legumes	Caesalp.	Mimos.	Papillio.
C. badius (12 mo)	74.5	85.2	9.7	0.9	61.7	86.8	3.1	7.9
C. badius (8 mo)	72.4	83.4	10.7	1.4	45.1	68.6	11.6	19.0
C. angolensis (8 mo)	65.3	58.1	39.7	1.7	31.5	31.8	4.4	63.7

[a] Items of unknown subfamily are included under "all legumes."

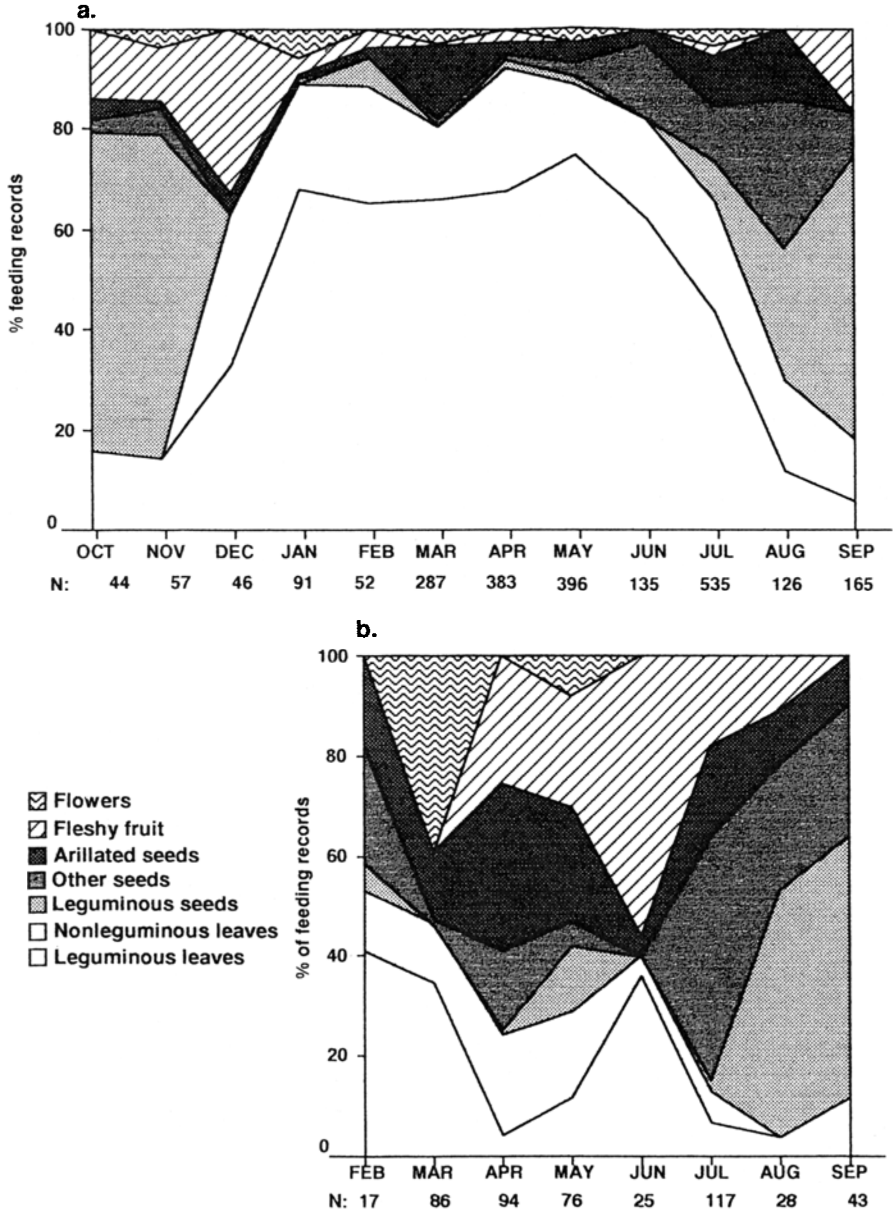

Fig. 3. Seasonal variations of diets: (a) *C. badius*; (b) *C. angolensis*.

Table IV. The Top 10-Ranking Plant Species in the Diet of *C. badius*[a]

Rank	October	November	December	January	February	March	April	May	June	July	August	September
1	Caesalp., *Guibourtia demeusei:* 34.1%; US	Caesalp., *D. pynaertii:* 45%; US	Clusiaceae, *Symphonia globulifera:* 21.7%; P	Caesalp., *C. pedicellata* 23.1%; YL	Caesalp., *G. dewevrei* 23%; YL	Mimosoid., *P. africanum* 20.5%; YL	Caesalp., *C. hankeii* 18.2%; ML/YL	Caesalp., *G. dewevrei* 32.3%; YL	Caesalp., *C. pedicellata* 13.3%; YL	Caesalp., *G. dewevrei* 11.7%; YL & Fl	Olacaceae, *S. tetranda* 20.7%; US	Caesalp., *D. pynaertii* 6.1%; US
2	Caesalp., *Dialium sp.:* 15.9%; US	Caesalp., *G. demeusei:* 15.8%; US	Caesalp., *Cynometra pedicellata:* 15.2%; YL	Unknown: 17.6%; YL	Caesalp., *G. demeusei* 19.2%; YL	Caesalp., *Dialium sp.* 15.7%; YL	Caesalp., *C. pedicellata* 10.2%; YL	Caesalp., *C. hankei* 13.2%; YL	Caesalp., *G. demeusei* 10.4%; YL	Caesalp., *Dialium sp.* 8.4%; YL	Caesalp., *D. pynaertii* 12.7%; US	Olacaceae, *S. tetranda* 18.7%; P/RS
3	Caesalp., *Daniellia pynaertii:* 11.4%; US	Caesalp., *Dialium sp.:* 14.0%; YL	"Boona" 15.2%; YL	Caesalp., *G. demeusei* 11%;YL	Unknown: 11.5%; YL	Annonaceae, *X. aethiopica* 12.1%; Ar & YL	Caesalp., *G. demeusei* 9.4%; YL/US	Caesalp., *M. pteridophyll.* 9.1%; YL & ML	Caesalp., *G. dewevrei* 9.6%; YL	Olacaceae, *Strombosia/ Strombosinopsis* 8.2%; YL/US	Myristica, *C preussi* 7.1%; Ar	Papillion., *Millettia* 15.7%; US/RS
4	Caesalp., *Dialium sp.:* 11.4%; YL	Olacaceae, *O. gore:* 8.8%; P	Caesalp., *Monopetalanthus pteridophyllus:* 8.7%; YL	Mimosoid., *Albizzia sp.* 9.9%; YL	Caesalp., *Dialium sp.* 9.6%; YL	Caesalp., *C. hankei* 6.6%; YL	Caesalp., *Dialium sp.* 9.1%; YL	Olacaceae, *Strombosia/ Strombosiopsis* 8.6%; YL/US	*M. pteridophyl,* 9.6%; YL/ML	Caesalp., *M. pteridophyl.* 7.9%; YL/ML	Clusiaceae, *S. globulifera* 7.1%; YL/RS	Caesalp., *Dialium sp.* 12.1%; US
5	Unknown: 9.1%; P	Unknown: 5.3%; S	Caesalp., *Gilbertiodendron dewevrei:* 6.5%; YL	Caesalp., *G. dewevrei* 8.8%; YL	Liane sp. 7.7%; YL	*C. pedicellata* 6.6%; YL	Olacaceae, *Strombosia/ Strombosiopsis* 7.8%; YL	Mimosoid., *P. africanun* 7.8%; ML	*Scorodophleus zenkeri* 8.9%; ML	Myristica, *C. preussi* 7.8%; Ar	Olacaceae, *Strombosia/ Strombosiopsis* 6.3%; US/YL	Euphorbia., "Boliankenge" 5.4%; YL
6	Caesalp., *Aphanocalyx marginervata:* 4.54%; YL	"Boseki": 3.5%; Fl	Scytopetalum *pierranun:* 6.5%; YL	Caesalp., *A. marginervata* 4.4%; YL	Mimosoid *Piptadeniastrum africanun* 5.8%; US	Caesalp., *M. pteridophyllus* 6.2%; YL & ML	Caesalp., *G. dewevrei* 7.3% YL	Caesalp., *G. demeusei* 5%; YL/ML	Olacaceae, *Strombosia/ Strombosiopsis* 8.2%; YL/US	Euphorbia "Boliankenge" 5%; YL	Caesalp., *Brachystegia laurentii* 5.5%; YL	Myristica, *P. angolensis* 3.5%; ML
7	Ebenaceae, *Diospyros sp.* 2.3% P	Caesalp., *Dialium sp.* 3.5%; P	Connarac., *Connarus sp.* 4.3%; Ar	Caesalp., *D. pynaertii* 4.4%; YL	Mimosoid., *Albizzia sp.* 3.8%; YL	Myristica., *Pycnanthus angolensis* 3.5%; Ar	Caesalp., *M. pteridophyl.* 4.5%; YL	Annonac., *X. aethiopica* 2.8%; Ar & YL	Clusiaceae, *S. globulifera* 6.7%; US	*Albizzia sp.* 4.7%; YL/ML/RS	Caesalp., *Dialium sp.* 4.8%; US	Clusiac., *M. africana* 3%; US
8	Olacaceae, *Ongokea gore:* 2.3%; P	Caesalp., *T. lescrauwaetii* 1.7%; S.	Rosaceae, *Parinari congensis* 4.3%; YL	Caesalp., *M. pteridophyl* 2.2%; YL	Polygalac., *Carpolobia glabrescens* 3.8% P	Olacaceae, *Strombosiopsis tetranda* 3.1%; YL	Papilion., *Pterocarpus sp.* 3.9%; YL	Caesalp., *C. pedicellata* 2.3%; YL	Caesalp., *C. pedicellata* 5.2%; YL	Burserac., *Santiria sp.* 4.5%; US/YL	Olacaceae, *O. gore* 4.8%; YL	Unknown 3%; YL
9	Caesalp., *Tessmania lescrauwaetii:* 2.3%; S	Unknown: 1.7%; P	Unknown: 4.3%; P	*Schotia romii* 2.2%; YL	Caesalp., *Cynometra hankeii* 1.9%; YL	Caesalp., *G. dewvrei* 2.4%; YL	Clusiaceae *S. globulifera* 3.1%; YL	Caesalp., *Dialium sp.* 2.2%; YL & ML	Sp. 320, 3.3%; RS	Caesalp., *G. demeusei* 4.3%; YL/ML	Myristica., *P. angolensis* 4.8%; Ar	Arecaceae, *Oncocalamus acanthocnemis* 2.4%; P
10	Annonac., *Xylopia aethiopica* 2.3%; Ar		Caesalp., *G. demeusei:* 2.2%; YL	Clusiaceae, *S. globulifera* 2.2%; P	"Ekongoko" 1.9%; YL	Clusiaceae, *S. globulifera* 2.4% YL & US	Mimosoid., *P. africanum* 2.8%; YL	Myristica., *Coelocaryon preussi:* 2%; ML & Ar	Euphorbia., "Boliankenge" 3.7%; YL	*Cryptosepalum congolanum* 3.7%; US	Caesalp., "Ekongoko" 3.1%; YL	Mimosoid., *Parkia sp.* 1.8%; P
Total	95.4	100	88.9	85.8	88.2	79.1	76.3	85.3	80	66.2	76.9	91.8

[a] Plant part is indicated: Ar, arillated seed; ML, mature leaf; P, fruit pulp; RS, ripe seed; S, seed of unknown age; US, unripe seed; YL young leaf. Caesalp., Caesalpinoideae; Euphorbia., Euphorbiaceae; Mimosoid., Mimosoideae; Myristica., Myristicaceae; Papilion., Papilionoideae; Polygalac., Polygalaceae.

Table V. The Top 10-Ranking Plant Species in the Diet of *C. angolensis*[a]

Rank	February	March	April	May	June	July	August	September
1	Mimosoid., *Piptadeniastrum africanum* 23.5%; YL/US	Papilion., *Angylocalyx pynaertii* 39.5%; Fl	Myristica., *Pycnanthus angolensis* 24.5%; Ar	Olacaceae, *Ongokea gore* 22.4%; P	Olacaceae, *O. gore* 56%; P	Clusiaceae, *Symphonia globulifera* 13.7%; US	Papilion., *Millettia sp.* 35.7%; US	Papilion *Millettia sp.* 39.3%; US & YL
2	Annonac., *Xylopia aethiopica* 23.5%; US	Caesalp., *Dialium sp.* 20.9%; YL	Olacacea, *O. gore* 21.3%; P	Anonac., *X. aethiopica* 17.1%; Ar	Mimosoid., *Albizzia sp.* 24%; ML	Myristica., *C. preussi* 12.8%; Ar	Olacaceae, *Strombosiopsis tetranda* 25%; US	Caesalp., *Guibourtia demeusei* 16.4%; US
3	Myristica, *Coelocaryon sp.*17.6%; Ar	Caesalp., *Gilbertiodendron dewevrei* 5.8%; YL	*Liane sp. a.* 8.5%; YL	Papilion., *A. pynaertii* 13.1%; US & RS	Caesalp., *Dialium sp.* 12%; YL	Olacaceae, *O. gore* 12.8%; P	Caesalp., *G. demeusei:* 14.3%; US	Olacaceae *S. tetranda* 14%; US
4	Caesalp, *G. demeusei* 11.8%; YL	Annonac., *X. aethiopica* 4.7%; Ar & YL	*Liane sp. b.* 7.4%; US	Clusiaceae, *S. globulifera* 7.8%; YL, Fl & US	*Clusiac., sp.* 1 4%; YL	Olacaceae, *Strombosia/ Strombosiopsis* 11.1%; YL/US/UP	Arecaceae, *Raphia* sp. 10.7%; Ar	Olacaceae, *O. gore* 11.6%; US
5	Unknown 11.8%; YL	Mimosoid., *Albizzia sp* 4.6%; YL	Annonac., *X. aethiopica* 7.4%; Ar	Caesalp., *Daniellia pynaertii:* 5.3%; Fl	Annonac., *X. aethiopica* 4%; Ar	Burseraceae, *Santiria sp.* 7.7%; US	Euphorbia., *Uapaca guineensis* 7.1%; P	Myristica, *Staudtia stipitata* 9.3%; Ar
6	Mimosoid., *Albizzia sp.* 5.9%; YL	Myristica., *Coelocaryon preussi* 4.6%; Ar	Sp. 47 5.3%; RS	Olacaceae, *Strombosia/ Strombosiopsis* 5.3%; ML		Olacaceae, *S. tetranda* 6%; US	Caesalp., *G. demeusei* 3.6%; YL	Caesalp., *D. pynaertii* 4.6%; US
7	Caesalp., *Dialium sp.* 5.9%; YL	Caesalp., *Cynometra pedicellata:* 3.5%; YL	Tiliaceae, *Grewia sp.* 4.2%; P	Myristica., *P. angolensis* 3.9%; Ar		Caesalp., *Scorodophleus zenkeri* 5.1%; YL & ML	Euphorbiaceae, *Macaranga sp.* 3.6%; P	Caesalp., *Dialium sp.* 2.3%; US
8		Olacaceae, *O. gore* 3.5%; YL	Olacaceae, *Strombosia/ Strombosiopsis* 4.2%; YL	Caesalp., *S. zenkeri* 3.9%; ML		Sp. 446 4.3%; RS		*M. pteridophyllus* 2.3%; ML
9		Myristicac., *P. angolensis* 3.5%; Ar	Ebenaceae, *Diospyros sp.* 2.1%; YL	Fern sp. 2.6%; ML		Myristica., *S. stipitata.* 3.4%; Ar		
10		Annonac., *Annonidium mannii* 2.3%; YL Clusiaceae, *S. globulifera* 2.3%; YL	Unknown 2.1%; YL	Liane sp. 2.6%; YL		Annonac., *X aethiopica* 3.4%; US		
Total	100	95.2	87	84	100	80.3	100	99.8

[a] Plant part is indicated: Ar, arillated seed; ML, mature leaf; P, fruit pulp; RS, ripe seed; S, seed of unknown age; US unripe seed; YL young leaf. Caesalp., Caesalpinoideae; Euphorbia, Euphorbiaceae; Mimosoid, Mimosoideae; Myristica., Myristicaceae; Papilion., Papilionoideae; Polygalac. Polygalaceae.

eaten legume seeds are from Papilionoideae and Caesalpinioideae. As in *C. badius*, most of the arillate seeds are from the Myristicaceae and Annonaceae and other seeds are mainly those of the Olacaceae. Finally, the only ripe fleshy fruit consumed in any quantity by both species are those of Olacaceae and Clusiaceae.

Dietary Diversity and Intraspecific Dietary Overlap

The diet of *C. badius* included 84 plant species during the annual cycle and 80 species during the 8 months of the study in common with *C. angolensis*. During this same period, *C. angolensis* ate 46 species. In all but 1 month (August), a single food item comprised >60% of the diet of *C. badius*. This was the case for *C. angolensis* during only 2 months (August and September). On an 8-month basis, the top species in the diet of *C. badius* made up 12.2% of records vs 15.2% for the top species for *C. angolensis*, and the top five species made up 40.5 and 42.5%, respectively (Tables IV and V).

The diets of both colobines showed a broadly similar pattern of seasonal variation of specific diversity, with the highest index during the dry season (July; Fig. 4). In terms of items, the diversity of *C. angolensis* is strongly seasonal, with a peak in April–May, while it remained relatively constant over the year for *C. badius*. The diet of *C. badius* is more diverse in terms of species than that of *C. angolensis* ($P = 0.008$), while the diet of *C. angolensis* is more diverse in terms of items ($P = 0.013$ from February until July). The intraspecific dietary overlap, in terms of items, between neighboring months, is 30% on average for *C. badius* (maxima in October–November and June–July) and 24% for *C. angolensis* (maxima in April–May and in August–September; Fig. 4). The mean percentage overlap between all pairs of months is 18.2% for *C. badius* and 11.24% for *C. angolensis*. The interspecific dietary overlap (monthly mean, 21%) has the highest values in February–March and from July until September (Fig. 4).

Food Selection in Relation to Food Availability

The three legume subfamilies (Caesalpinoideae, Papillionoidae, and Mimosoidae) comprise, respectively, 85, 3.1, and 0.7% of the leguminous tree population. The two colobines differed in the number of items eaten and the selection of items within these subfamilies. First, *C. badius* ate legume leaves more frequently than nonlegume leaves ($P = 0.019$), but *C. angolensis* ($P = 0.098$) did not. Second, *C. badius* relied more on the most abundant leaves of Caesalpinioideae (85% of legume leaves eaten), while

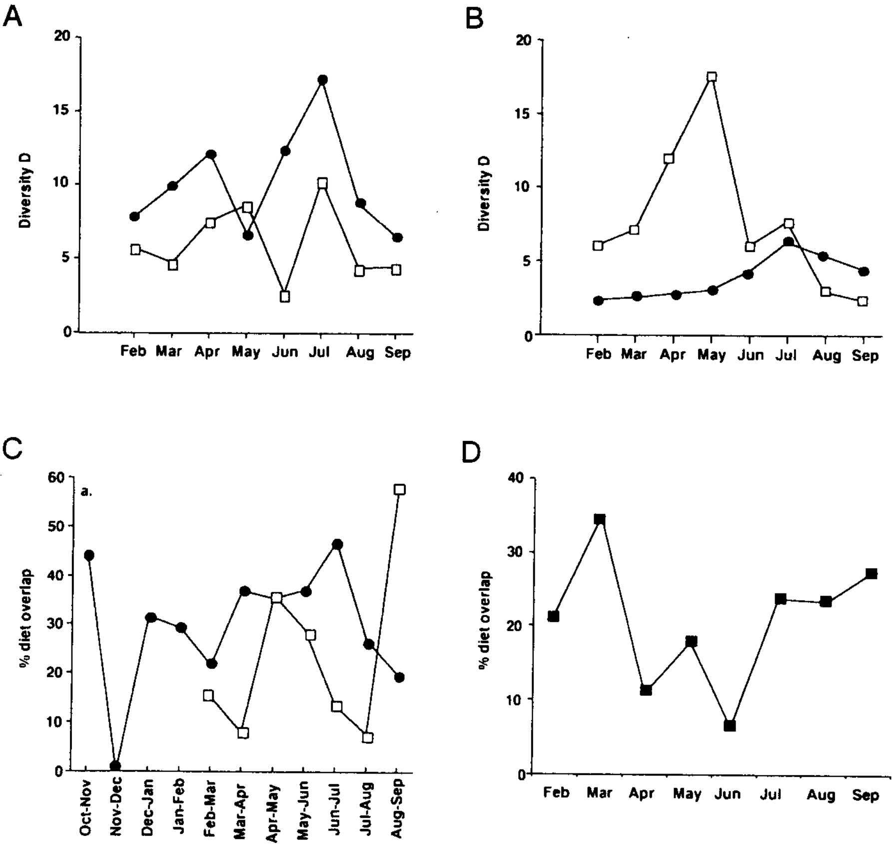

Fig. 4. Dietary diversity in terms of plant species (A) and plant categories (B); intraspecific dietary overlap between neighboring months (C); *C. badius* (●); *C. angolensiso* (☐)*; and interspecific dietary overlap [in terms of plant species items (D)].*

C. angolensis ate leaves of both Caesalpinioideae (58%) and Mimoisoideae (40%). For both species, there is no significant difference between the consumption of legume and that of nonlegume seeds ($P = 0.4$ and $P = 0.08$, respectively). However, while *C. badius* relied mainly on the most abundant seeds of Caesalpinioideae (87% of legume seeds eaten), *C. angolensis* ate seeds of both Caesalpinioideae and Papilionoideae (32 and 64%).

The consumption of legume seeds is correlated with their availability in terms of fruiting trees and fruiting species for *C. badius* ($P = 0.017$ and $P = 0.014$, respectively) but not for *C. angolensis* ($P = 0.2$ and $P = 0.14$, respectively). Consumption and availability of trees bearing unripe nonlegume, nonarillate seeds are also correlated for *C. badius* ($P = 0.009$) but not for *C. angolensis* ($P = 0.5$). Finally, the availability of mature fleshy fruit, and of all arillate seeds is not significantly correlated with consumption for either species. In sum, *C. badius* appeared to rely more on the most abundant plants than do *C. angolensis*, which are more selective in terms of plant family and plant species.

Both colobines select the food items in a similar way. They shift from leaf-eating to seed-eating when seeds become available, as indicated by the fact that the consumption of young leaves and seeds is negatively correlated for both species ($P = 0.003$ for *C. badius* and $P = 0.039$ for *C. angolensis*). Both ate buds and young leaves more frequently than mature leaves (54.3 vs 6.4%, *C. badius*; 21 vs 6.4%, *C. angolensis*; Table II). This choice is especially obvious for young leaves of Caesalpinioideae, which comprise approximately 89% of all Caesalpinioideae leaves eaten. Among the fleshy fruit, both monkeys ate the yellow drupes of *Ongokea gore* only when ripe, they ate those of *Strombosiopsis tetrandra* (both Olacaceae) either unripe or almost ripe. They consumed all other fruit species when unripe. They ate fruit with arillate seeds both unripe and ripe. For unripe arillate fruit, monkeys consumed the aril plus the seed (dehiscent drupes of Myristicaceae) or the whole fruit (mericarp of *Xylopia aethiopica*, Annonaceae).

Food Selection in Relation to Plant Chemistry

Young leaves, seeds, and unripe fruit are the items highest in crude proteins (14.75, 12.7, and 13.5%; $n = 22$, 16, and 7, respectively), and in condensed tannins (6.1, 5.2, and 5.1%, respectively). Young leaves contain significantly more crude proteins, more condensed tannin, and more water than mature leaves do ($n = 13$; 14.75 vs 10.9%, 6.1 vs 3.7%, and 71.5, vs 55.6%, respectively; $P < .05$ for all tests; Mann–Whitney U test). Seeds contain significantly more lipids than young leaves do (9.03 vs 3.8%) and more water than mature leaves do (68.4 vs 55.6%; $P < 0.05$ for both tests). Unripe fruit contain significantly more water than mature leaves and seeds (83.6 vs 55.6 and 68.4%, respectively; $P < 0.05$). Total phenolics do not vary significantly among the categories.

We found no significant differences for any phytochemical parameter (secondary compounds included) when comparing leguminous items and nonleguminous ones. However, when we rank items in terms of their crude protein, there are 7 Leguminosae in the top 10 young leaves, 5 in the top 10 mature leaves, and 5 in the top 10 seeds. Furthermore, young Caesalpinioideae foliage ($n = 13$) contains significantly more water and more crude protein (71.4 and 16%, respectively) than mature foliage of Caesalpinioideae does ($n = 6$; 50.5 and 9%, respectively; $P < 0.05$ and $P < 0.001$, respectively). They do not differ significantly in condensed tannins (4.4 vs 3.4%) and total phenolics (6.75 vs 5.8%).

When we divided the data set into items eaten and those avoided by colobines, we obtained the following results: Leaves that were eaten ($N = 25$) were significantly younger ($P < 0.0001$) and contained more condensed tannins, more water, and fewer lipids ($P < 0.05$ for all three tests) than eschewed leaves did ($N = 10$). We tested a subset of 10 tree species for which data are available for both mature and young leaves and whose young leaves are all eaten by colobines (Wilcoxon paired ranks test). These species include 6 of the 10 most common trees and altogether represent 43% of the total number of trees in the habitat. Their young leaves contain higher levels of protein and water than mature leaves do ($P < 0.01$ for both); however, there is no difference for total phenolics or condensed tannins. Seeds eaten ($N = 14$) are lower in condensed tannin content ($P < 0.02$) than the two avoided species that are the top-ranking in terms of condensed tannin. Finally, fruit eaten ($N = 12$) have a lower total phenolic content ($P < 0.0.05$) than those avoided do ($N = 5$).

In sum, both colobines selected for more succulent items—young leaves and immature fruits—and for items richer in proteins or lipids or both—young leaves and seeds—even if their amounts of total phenolics or condensed tannins or both are higher than those of uneaten items; however, they tend to avoid the species which contain very high levels of tannins and phenolics.

DISCUSSION

Diets and Food Partitioning

The diets of the two monkeys differ significantly in their level of folivory and the diversity of species eaten, which are higher in *C. badius*, and in the level of seed-eating and the diversity of the food items, which are higher in *C. angolensis*, which also tended to eat more fleshy fruit. Both species select for young leaves, but this tendency was more pronounced in *C. badius*. In both species, the number of fleshy fruit species eaten is small; one of the most important species is *O. gore* (Olacaceae), a fleshy drupe that was not eaten by *Cercopithecus* spp. in the Salonga (personal observation) or in Gabon (Gautier-Hion *et al.*, 1985). The two colobines have different feeding tactics. The wide-ranging red colobus rely mainly on legumes and on a wide range of the dominant species of Caesaepinoideae, from which they eat seeds and young leaves. The black-and-white colobus are more selective, relying less on legumes and eating not only seeds and leaves of Caesalpinioideae but also leaves of Mimosoideae, which are less abundant but potentially more nutritious (Waterman, 1994), and seeds of Papilionoideae. Finally, the overlap between the diets of the two colobines reaches an annual mean of 21%. This is much higher than the overlap observed at Kibale between *C. b. tephrosceles* and *C. guereza* [mean, 7%, (Struhsaker and Oates, 1975)].

C. b. tholloni fall within the range of folivory of other subspecies of *C. badius*, although they eat a relatively low percentage of fruit pulp and a higher proportion of seeds (37 versus 1–25%; Table VI). Their diet is more diverse than that of most red colobus, as indicated by the number of species eaten and by the contribution to the diet of the top species (Table VI). They also differ from other species in their strong preference for young leaves and their dependence upon Caesalpinioideae. However, Oates *et al.* (1990) noted that trees Caesalpinioideae are prominent in the diet of the red colobus at Tiwai.

C. angolensis in Salonga consume less leaf material and more seeds than any other species of black-and-white colobus (Table VII). Their leaf consumption is similar to that of the black colobus in Gabon, while their consumption of seeds is very close to that observed in this species in Gabon and in Cameroon. They ate a similar number of plant species to *C. polykomos* and *C. guereza* and more than *C. angolensis* did in Kenya but a lower number of species than *C. satanas* did. If the contribution of the top species eaten is considered, *C. angolensis* in Zaire show dietary diversity similar to that of *C. satanas* and *C. polykomos* and greater than the monotonous diet of *C. guereza*. In sum, the diet of *C. angolensis* in Salonga most closely resembled that of black colobus.

Soils, Vegetation, Phytochemistry, and Diets

Table VIII is a comparison of the properties of soils from five sites where colobines have been studied. We identify three broad categories. (1) Soils from Salonga, Douala-Edea and Tiwai are characterized by the highest percentage of sand, the lowest percentage of silt and clay, a low pH, and low values of exchangeable bases. Among these sites, Salonga soils have values for mechanical properties similar to the minimum values found at Douala-Edea and values for mineral nutrients similar to the minimum values found at Tiwai. Thus, they can be considered as the poorest soils. (2) Soils from Kibale have the highest percentage of silt and clay; they are the least acidic soils and they possess the highest content of exchangeable

Table VI. Diets of Red Colobus Monkeys (%)

								% diet in top	
Red colobus[a]	Young leaves	Mature leaves	Seeds	Fruit Pulp	Flowers	Others	No. of species eaten	First species	Five species
C. b. tholloni (1)	54.3	6.4	30.8	7.1	1.4		84	11.35	38.6
C. b. badius (2)	31.7	20.2	25.3	5.9	16.1				
C. b. rufomitrata (3)	52.4	11.5	0.9	24.1	6.2	4.9	22	29.4	78
C. b. temminckii (4)	41.5	5.4	19.2	16.8	8.71	8.01	44	43.9	77.5
C. b. temminckii (5)	26.0	11.1	18.0	30.0	8.5	6.4	89		
C. b. tephrosceles (6)	34.8	44.1	2.8	8.5	6.8	2.9	60	15.4	52
C. b. tephrosceles (7)	50.6	33	0.8	4.8	11.8		68	15.4	55.9

[a](1) Zaire (this study); (2) Sierra Leone (G. Davies, personal communication); (3) Kenya (Marsh, 1981); (4) Senegal (Gatinot, 1977); (5) The Gambia (Starin, 1991); (6) Tanzania (Cluton-Brock, 1975); (7) Uganda (Struhsaker, 1975).

Table VII. Diets of Black-and-White Colubus (%)

								% diet in top	
Black-and-White colubus and black colubus[a]	Young leaves	Mature leaves	Seeds	Fruit pulp	Flowers	Others	No. of species	First species	Five species
C. angolensis (1)	21.2	6.4	49.9	16.8	5.9		46	15.2	42.4
C. angolensis (2)	67.9[b]		10.7	21.4			28		
C. guereza (3)	61.7	12.4	1	12.6	2.1	10.2	43	50.1	66
C. polykomos (4)	29.9	26.7	33.3	3.2	2.7	4.7	46	16.1	39.3
C. satanas (5)	23	19	58				100	10.9	38.9
C. satanas (6)	23	3	60.1	4.1	5.3	4.4	65	14	37.8

[a](1) Zaire (this study); (2) Kenya (Moreno-Black and Maples, 1977); (3) Uganda (Oates, 1977); (4) Sierra Leone (Dasilva, 1989); (5) Cameron (McKey et al., 1981; McKey and Waterman, 1982; (6) Harrison and Hladik, 1986; Harrison, personal communications

[b]Young leaves and mature leaves.

Table VIII. Properties of Soils from Salonga (Zaïre; This Study), Tiwai (Sierra Leone), Douala-Edea (Cameroon), Kibale [Uganda; from Oates *et al.* (1990)], and Lopé [Gabon; from Harrison (personal communication)][a]

Sample depth, cm N	Sites				
	Salonga	Tiwai	Douala-Edea	Lopé	Kibale
	0–10	0–20	0–5 (10–20*)	0–10	0–5 (38–45**)
	17	22	34	32	3, 15[a]
Sand, %	87.0	77.1	84.8	51	15.6
Silt, %	4.4	14.3	11.8	21	39.1
Clay, %	8.8	8.7	3.3	28	45.3
pH	4.13	4.3	3.4	4.5	6.0
P (mg/kg)	12.0	4.5	22.4	4.0	16.0
K (mmol/kg)	0.59	0.17	2.5	1.1	3.15
Ca (mmol/kg)	0.55	1.97	2.49*	1.3	22.75**
Mg (mmol/kg)	0.50	0.22	1.42*	1.1	9.17**

[a] Sample size was 3 for chemistry and 15 for sand–silt–clay.
*Figures at 10–20 cm depth.
**Figure at 38–45 cm depth.

bases. (3) The Lope soils have intermediate values for their mechanical properties and low levels of exchangeable bases.

Two parameters that influence diets vary with soil properties: the species composition of vegetation and the food quality. Legumes that can adapt to low-nutrient conditions are often abundant on poor acidic soils (Gartlan *et al.*, 1986; Newbery *et al.*, 1988; Oates *et al.*, 1990; Maisels and Gautier-Hion, 1994). In the Salonga and Tiwai, where the poorest soils occur, legumes account for about 45% of tree populations (Dasilva, 1989; this study), while a minimum of 2.8% of legumes exists on the richest soils of Kibale (Struhsaker, 1975). Intermediate values occur in Douala-Edea [17% (McKey *et al.*, 1981)] and Lopé [28% (Harrison, personal communication)]. Thus, the relative abundance of legumes roughly increases with increasing soil poverty. The increasing representation of legumes, which raises the availability of nutrient-rich seeds, should further the development of seed-eating by either the red colobus, the black-and-white colobus, or the black colobus (Tables VI and VII).

Differences in nutrient or toxic-compound content of the vegetation or both have been related to differences in soil quality (McKey, 1978). For example, on the poor soils of Tiwai, the mature foliage (20 tree species) is characterized by higher levels of condensed tannins than those of Douala-Edea or Kibale are but by higher ratio of protein to fiber than Douala-Edea is (Oates *et al.*, 1990). In fact, these differences may be attributed more directly to differences in the vegetation composition, especially the relative abundance of legumes, than to differences in soil conditions. Leaves and seeds of legumes tend to contain higher crude protein levels than nonlegumes, while they often contain alkaloids and other toxins as well as high levels of condensed tannins (Waterman, 1984, 1994; Oates *et al.*, 1990; this study).

Condensed tannins (and other toxins as well) do not seem to act as efficient feeding deterrents for colobines at Salonga, though they avoided two food species with very high levels of toxins. While some toxins (e.g., alkaloids) can be detoxified by gut microflora (McKey, 1978), this seems less likely for condensed tannins. Tannins can form insoluble complexes with proteins. Thus, feeding supplemental protein may saturate the tannins and reduce their toxic effect (McKey, 1978). We suggest that in forests rich in legumes, the high amount of protein-rich seeds and young leaves available to animals could help both to saturate the tannins and to feed them.

Our results confirm that forests rich in legumes are suitable habitat for colobines as shown at Tiwai (Oates *et al.*, 1990) and in Southeast Asia, where the biomass of *Presbytis* spp., which rely heavily on leguminous seeds, is positively correlated with legume abundance (Davies, 1984; Davies *et al.*, 1988).

In conclusion, the apparent relation between the amount of seed-eating and the poverty of soil is mediated through the composition of plant communities that are adapted to unfertile soils. The link between poor soils and seed-eating should result from the combination of the high availability of nutrient-rich seeds, due in part to the dominance of legumes and of the low food value of the mature foliage. Seed-eating by colobines must be viewed as a positive, adaptive strategy, as suggested by an increasing body of evidence for the so-called leaf-eaters in the Neotropics, Asia, and Africa (Van Roosmalen *et al.*, 1988; Davies *et al.*, 1988; Oates *et al.*, 1990; Dasilva, 1992; Harrison (personal communication).

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