

The Diet of the Olive Colobus Monkey, *Procolobus verus*, in Sierra Leone

John F. Oates^{1,2}

Received November 23, 1988; revised March 15, 1989

*Observations of the feeding behavior of wild olive colobus monkeys (*Procolobus verus*) were made in southern Sierra Leone, West Africa. Most data came from systematically sampling one habituated social group, which inhabited old secondary rain forest on Tiwai Island. Olive colobus at Tiwai were highly selective feeders, obtaining most of their food from a small number of uncommon middle-canopy trees, from the forest understory, and from climbers. Mature leaf blades were largely ignored; young foliage (particularly of climbers) was a year-round dietary staple, while seeds, flowers, and mature leaf petioles were seasonally important. It is argued that this diet results largely from selection for two different attributes of food: high digestibility and physical location. Preferred foods had low fiber and tannin contents, while preferred feeding sites were in thick low growth and climber tangles. *P. verus* is the smallest extant primate species using a foregut fermentation system. Observations of its diet accord with inferences drawn from dental anatomy, digestive physiology, and considerations of body size.*

KEY WORDS: *Procolobus verus*; Colobinae; diet; feeding strategy; body size.

INTRODUCTION

The olive colobus, *Procolobus verus* (van Beneden), is the smallest of all colobine monkeys. Although its diet and feeding strategy are thus of particular interest, very little dietary information on this species is available.

¹Hunter College and the Graduate School, City University of New York, New York, New York.

²To whom correspondence should be addressed at Department of Anthropology, 695 Park Avenue, New York, New York 10021.

Here I present the first large sample of feeding data for *P. verus*. The major part of this sample came from direct observation of one well-habituated group on Tiwai Island in southern Sierra Leone during a long-term study; a few extra data were gathered from other groups on and off the island.

Average adult body weights for *P. verus* are 4.6 kg for males ($N = 22$) and 4.1 kg for females ($N = 17$) (data from wild-shot animals collated by the author). The smallest Asian *Presbytis* species average about 6 kg [e.g., *P. melalophos* (Fleagle, 1977; Bennett, 1983)]. Foregut fermentation of plant structural carbohydrates (such as occurs in colobines) is an inefficient digestive strategy in small-bodied animals (Janis, 1976; Parra, 1978). Small-bodied foregut fermenters therefore typically have diets dominated by highly digestible items with a low fiber content, have a high rate of food turnover in the fermentation chamber, and obtain substantial energy from nonfermentative digestion (Hungate *et al.*, 1959; Gaulin, 1979; Demment and van Soest, 1985). These observations could lead to the prediction that olive colobus have more fruit and less foliage in their diet than other colobines, a prediction reinforced by the observation that the species has relatively large incisors (Hylander, 1975). However, Kay (1981) has shown that *P. verus* has the thinnest enamel and relatively the highest second-molar shearing cusps of any Old World anthropoid, suggestive of a highly folivorous diet.

The olive colobus is restricted to the West African rain-forest zone between Sierra Leone and Nigeria (Oates, 1981). In much of this range it is a relatively rare animal, and where it does occur it is very difficult to observe. Only three authors have given reports on the species' diet, and two of these reports are based on an examination of stomach contents, a notoriously unreliable means of assessing primate diets (Clutton-Brock, 1977; Richard, 1985). Booth (1957) reported that all the stomachs of 33 individuals shot in Ghana contained leaves, that one contained flowers, that three (from juveniles) contained milk, and that "no remains of fruits could be definitely distinguished." In the stomachs of animals shot in Liberia, Kuhn (1964) was able to identify only small fragments of very fleshy leaves, although the mouth of a very old female whose molars were ground down to stumps contained an oil-palm fruit. In the only published study of *P. verus* containing quantified behavioral observations, Galat and Galat-Luong (1985) record 17 feeding observations from the Tai National Park, Côte d'Ivoire, over an unspecified period of time; 16 of these observations were of leaf feeding.

STUDY SITES

General Site Description

Booth (1957) described the olive colobus (in Ghana) as preferring dense, low, tangled growth, such as occurs in high forest areas where trees have

been felled or have fallen, in swampy areas, along river banks, and in abandoned cultivation. Tiwai Island, in the Moa River, supports a mosaic of vegetation including all the habitats listed by Booth. Tiwai has an area of 12 km² and is centered at approximately 7°33'N and 11°21'W. The island has sandy soils and little relief, rising from about 85 m above sea level at the Moa bank to a maximum elevation of about 120 m in the interior.

When primate studies began on Tiwai in 1982, approximately 60% of the island was covered by old secondary forest estimated to be 40–60 years old. The remainder of the island's vegetation consisted of palm swamp, river-fringing forest, a few active farms and "farmbush" (young second-growth forest on recently abandoned farms, <20 years old). Hunting pressure on the island had been light. In 1982 hunting was prohibited on the orders of local chiefs, and in 1987 Tiwai was declared a Game Sanctuary under Sierra Leone law.

Most of the data in this paper come from one group of olive colobus living in an area on the east side of Tiwai island. Between May 1983 and October 1985 this study group used 113 50 × 50-m cells of a trail grid (28.25 ha). Twenty-two of these cells bordered on the Moa River bank, and 17 contained some farmbush growing on land cleared in 1980 and abandoned in 1981. The remainder of the group's range lay within old secondary forest. The upper canopy of this forest lies between 15 and 25 m, with scattered large emergents rising to over 40 m. The upper canopy varies in continuity, with frequent gaps present as a result of windfalls, soil conditions, and scattered tree cutting. Lianas are abundant in this forest.

In the study area, all trees with a diameter at breast height (dbh) of at least 40 cm and/or an estimated height of at least 20 m were measured, mapped, and identified ($N = 1192$). Smaller trees were enumerated in a stratified random sample of 62 25 × 2-m plots ($N = 360$). By combining data from these two samples (taking care not to score any individual tree more than once), the basal area per hectare of all tree species in the study area was estimated. Basal areas are considered to be a useful measure of relative biomass and productivity (Whitmore, 1975). Table I shows the estimated basal areas/ha for the top 20 tree species in the east study area on Tiwai.

Olive colobus share the old forest habitat on Tiwai with nine other primate species: the red colobus, *Procolobus badius*; the black-and-white colobus, *Colobus polykomos*; three species of *Cercopithecus*; the sooty mangabey, *Cercocebus atys*; chimpanzees, *Pan troglodytes*; and two species of prosimian. Population densities are reviewed by Whitesides *et al.* (1988).

At only one of the sites outside Tiwai where I observed olive colobus did I obtain more than a single feeding record. This was along the Makibi stream on the edge of Pujehun town (7°21'N, 11°43'W). Here, olive colobus were observed in a strip of riverine forest which extended 15–20 m to either side of a 4-m-wide perennial stream. The maximum height of trees in this forest was 20–25 m. Beyond the forest lay farmland and young second-

growth forest. Other primates seen at the Pujehun site were red and black-and-white colobus and two *Cercopithecus* species.

Climate and Seasons on Tiwai

Tiwai, like other parts of southern Sierra Leone, has a very high annual rainfall which is markedly seasonal. Annual rainfall recorded on the western side of Tiwai was 3046 mm in 1983, 2417 mm in 1984, and 3108 mm in 1985. Most of this rain falls in a pronounced wet season extending from May through October (Fig. 1). Very little rain falls between December and the end of March, while April and November are transitional months, with moderate rainfall. Over the year, daily maximum shade temperatures average 32°C and minimum temperatures average 23°C.

The wet season on Tiwai may be divided into three phases: early, middle, and late. In the middle of the wet season (July and August), rain usually falls almost every day and the average daily maximum temperature is close to or below 30°C. The early dry season (December and January) is relatively cool, with below-average maximum temperatures and nighttime minima as low as 14°C; at this time of year the dust-laden Harmattan wind often blows off the Sahara (Gwynne-Jones *et al.*, 1978). Temperatures rise during February; in March the highest daily maxima are attained, and occasional days reach 40°C.

The vegetation on Tiwai responds to this seasonal climate through variation in the production of foliage and fruit. However, this response is not

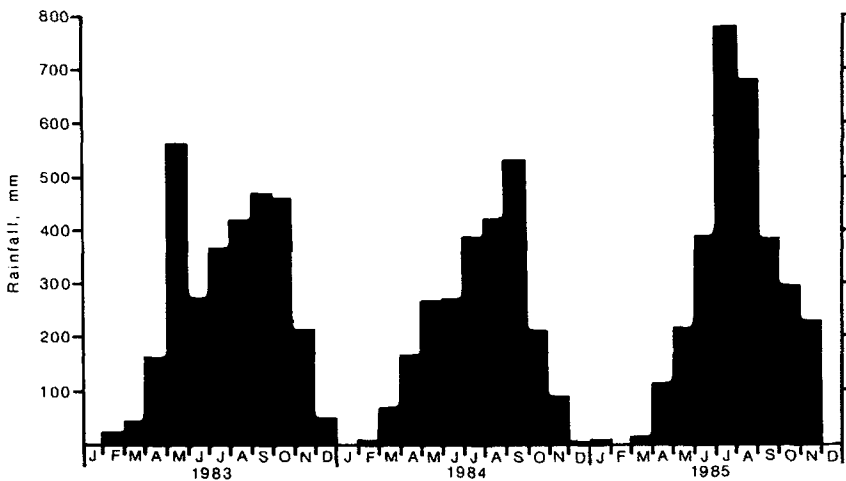


Fig. 1. Monthly rainfall at west camp, Tiwai Island, 1983-1985.

Table 1. Relative Biomass of the Top 20 Tree Species in *Procolobus verus* Study Area, Tiwai Island (Excluding Trees <5 cm in Diameter at Breast Height or <5 m in Maximum Height)

Species	Family	Phenology ^a	BA/ha ^b	% of total BA/ha
<i>Pentaclethra macrophylla</i>	Mimosaceae	E	38,839	15.0
<i>Uapaca guineensis</i>	Euphorbiaceae	E	32,788	12.7
<i>Funtumia africana</i>	Apocynaceae	E	21,493	8.3
<i>Piptadeniastrum africanum</i>	Mimosaceae	D	14,775	5.7
<i>Dialium guineense</i>	Caesalpiniaceae	E	12,539	4.8
<i>Plagiosiphon emarginatus</i>	Mimosaceae	E	10,559	4.1
<i>Vitex micrantha</i>	Verbenaceae	E	8,389	3.2
<i>Diospyros thomasii</i>	Ebenaceae	E	6,591	2.6
<i>Myrianthus libericus</i>	Moraceae	E	6,237	2.4
<i>Pycnanthus angolensis</i>	Myristicaceae	E	5,539	2.1
<i>Afrosersalisia afzelii</i>	Sapotaceae	E	4,404	1.7
<i>Hannoa klaineana</i>	Simaroubaceae	E	4,360	1.7
<i>Caloncoba echinata</i>	Flacourtiaceae	E	3,916	1.5
<i>Erythrophleum ivorense</i>	Caesalpiniaceae	D?	3,262	1.3
<i>Parkia bicolor</i>	Mimosaceae	D	3,082	1.2
<i>Cathormion altissimum</i>	Mimosaceae	D?	3,072	1.2
<i>Cynometra leonensis</i>	Caesalpiniaceae	D	2,979	1.2
<i>Samanea dinklagei</i>	Mimosaceae	D	2,434	0.9
<i>Dialium dinklagei</i>	Caesalpiniaceae	D	2,271	0.9

^aD, deciduous; E, evergreen (represents behavior observed during study; in some parts of Sierra Leone seasonal behavior may differ, according to notes of Savill and Fox, 1967).

^bBA, basal area (in cm²).

simple, given the diversity of the forest vegetation and the variability of the climate from year to year. The most obvious seasonal response involves the shedding of old foliage by a number of deciduous tree and liana species. At least 10% of large trees in the olive colobus study area (in terms of basal area) are deciduous (Table I). Many of these are emergents (e.g., *Piptadeniastrum africanum* and *Daniellia ogea*), which typically shed their foliage early in the dry season and soon replace it with a fresh leaf crop. Some medium-sized species of the main canopy may also replace all or most of their leaves at this time, although they are not truly deciduous (e.g., *Pentaclethra macrophylla*, *Dialium guineense*, *Sapium aubrevillei*). On the other hand, a few deciduous canopy species remain leafless for many weeks, from the middle of the dry season until the beginning of the rains. One of these trees is *Terminalia ivorensis*, an important olive colobus food species. Most of the canopy trees are evergreens; these species (e.g., *Funtumia africana* and *Uapaca guineensis*) produce some young leaves in most months but typically show a peak of foliage production early in the wet season (May–June). The great majority of understory trees is evergreen too; those studied on Tiwai produce few young leaves in the dry season but show a fairly steady production of young leaves the rest of the year. Lianas have most young leaves in the early wet season. The result of these different cyclical patterns is that some young

leaves are present in the forest all year, but peaks of abundance typically occur in December–January (early in the dry season) and May–June (the early wet season) with a marked scarcity in March (late dry season). A peak of tree flowering also occurs early in the dry season, followed by a peak of fruiting.

METHODS

Study Periods

I observed olive colobus at Pujehun in August 1979 and January 1980 and at Tiwai in 21 months spread between June 1982 and January 1987. One social group on Tiwai ("PF" group) was habituated to close observation by being followed on many days in March–May 1983. Subsequently, feeding records were collected on this group in the course of 11 3-day dawn-to-dusk sample periods, as follows (numbers of 3-day samples in each month in parentheses): June 1983 (1), July 1983 (2), August 1983 (1), January 1984 (2), June 1984 (1), February 1985 (1), March 1985 (1), and October 1985 (2). Some additional feeding observations on a second Tiwai olive-colobus group (which was not well habituated) were obtained in February 1983.

Study Groups

In April 1983, the PF group in the east study area on Tiwai contained two adult males, five adult females, one juvenile, and three infants. Thereafter, group size declined, reaching a minimum size of three in November 1985: one adult male, one adult female, and one juvenile. The average number of individuals in the group on each of the 3-day sample periods was 2 adult males, 3.5 adult females, 1.6 juveniles, and 1.4 infants. The second Tiwai group, observed in February 1983 in the west study area, comprised one adult male, one adult female, and an infant. In January 1980 the Pujehun group was estimated to contain at least eight individuals, with at least one infant.

General Observational Techniques

Olive colobus are highly cryptic, and thus extremely difficult to observe. They are drably colored; they make few loud vocalizations; they spend long periods inactive in thick vegetation; they typically associate closely with so-

cial groups of other monkey species (especially *Cercopithecus* spp.), in which they become hidden; and they frequently disperse when feeding.

On Tiwai, observation of monkeys was facilitated by a grid of trails cleared through the forest undergrowth on N-S, E-W compass bearings at 50-m intervals in both the east and the west study areas. In the east area additional trails were cut at 25-m intervals in the central part of the PF-group range. I observed monkeys with 10 × 40 binoculars and recorded observations in handwritten form in notebooks and on prepared data sheets. Even with habituated animals and a good trail system, I was rarely able to keep more than a few group members under observation at one time; the rate of data collection was therefore low.

Sampling of Feeding Behavior

Observation at Pujehun and on the small Tiwai group in the west study area were made unsystematically—i.e., on an *ad libitum* basis. I made similar *ad lib.* observations on the PF group in the east study area outside the periods of systematic sampling.

The main systematic sample of feeding behavior was collected during the 11 3-day sample periods listed above, following the procedure used by Struhsaker (1975) in his study of red colobus (*Procolobus badius tephrosceles*) in the Kibale Forest. In this procedure, “events” of feeding on particular food items are recorded, with one feeding event operationally distinguished from another by the following criteria: (1) a different individual monkey eating the same food item (e.g., young leaf blades of *Terminalia ivorensis*); (2) the same individual eating a different part (e.g., mature leaf petioles) of the same food species or eating a different species; or (3) the same monkey eating the same item at least 1 hr after any previous record for that item. Feeding included the gathering, processing, and/or ingestion of food. Essentially the same procedure was used by Oates (1977) in studies of *Colobus guereza*, by McKey (1978) and Harrison (1986) in studies of *C. satanas*, and by Marsh (1981) in studies of the Tana River red colobus. Data presented here may therefore be compared directly with the results of these other colobus studies.

Categories of food item (e.g., young vs mature leaves, ripe vs unripe fruit) were distinguished on the basis of gross physical appearance: size, coloration, and (in the case of leaves) translucence and turgidity. Olive colobus often consumed opening buds and young leaves in the same feeding bout, and these items have therefore been lumped together in this analysis.

The event method of sampling food consumption (sometimes called the “frequency” method) was found by Oates (1977) and Marsh (1981) to produce much the same results as methods that estimate the time spent feeding on

Table II. Comparison of Results from Scan and Event Sampling of *Procolobus verus* Diet at Tiwai Island: Data from 11 Three-Day Sample Periods, 1983–1985

Food species	Food part ^a	Scan method			Event method		
		<i>N</i>	%	Rank	<i>N</i>	%	Rank
<i>Terminalia ivorensis</i>	YL	28	12.9	1	58	12.2	1
<i>Sapium aubrevillei</i>	YL	20	9.2	2	33	6.9	2
<i>Acacia pennata</i>	YL	11	5.1	3.5	23	4.8	4
<i>Sapium aubrevillei</i>	MLP	11	5.1	3.5	25	5.3	3
<i>Lovoa trichiloides</i>	FL	10	4.6	5.5	17	3.6	6
<i>Plagiosiphon emarginatus</i>	YS	10	4.6	5.5	11	2.3	10
<i>Funtumia africana</i>	MS	7	3.2	7.5	22	4.6	5
<i>Parkia bicolor</i>	YL	7	3.2	7.5	10	2.1	11
<i>Myrianthus libericus</i>	YL	6	2.8	9	14	2.9	8
<i>Pterocarpus santalinoides</i>	YL	5	2.3	10	13	2.7	9
<i>Xylopia quintasii</i>	MLP	4	1.8	11	16	3.4	7
Other species		82	37.8		208	43.7	

^aYL, young leaves and leaf buds; MLP, mature leaf petioles; YS, immature seeds; MS, mature seeds; FL, flowers and floral buds. Only food items where both species and part were identified are included.

different food items. The same finding was made in this study, in which food consumption was also recorded during scan sampling of the PF group during 3-day samples. In 5-min scans separated by 15-min intervals, the behavior of clearly visible individuals was noted; if the behavior was feeding, food species and part were also noted. Table II compares data on predominant food items in the olive-colobus diet on Tiwai as collected by the two different methods. Of the top 10 items identified by each technique, 9 are listed in the top 10 found by the other technique, and the rank orders of the items are significantly correlated ($r_s = .74$, $p < .01$).

Inevitably, these feeding data have biases. During scan sampling, an average of only 1.5 olive colobus was seen per 5-min scan across all 33 sample days. Much feeding was therefore missed, and what was seen is probably biased further by the monkeys' proclivity for foraging in low, dense vegetation, where observation was difficult. All observational studies of forest primates suffer from a similar bias, although in this instance the degree of bias may be greater than usual. However, I believe that the data presented here are the best obtainable for this species in a habitat of this type. They reflect the relative importance of different items in the olive colobus diet at Tiwai, although not too much weight should be placed on their precise numerical values.

Plant Chemistry

Fresh samples of major olive colobus food items were collected on Tiwai together with samples of abundant potential food items that were not con-

sumed (i.e., mature leaves from the tree species with the highest biomass in the study area). These samples were dried in the sun, then sealed in plastic bags for later analysis. Analyses were performed in the laboratory of Professor Peter G. Waterman at the University of Strathclyde, using methods described by Oates *et al.* (1980) and Waterman *et al.* (1983).

RESULTS

Tiwai: All Observations

Table AI (Appendix) lists all the plant species and parts on which *P. verus* was observed to feed at Tiwai. At least 50 species were recorded. Olive colobus were never seen to search for or intentionally ingest any insects or other animal material; undoubtedly they occasionally ingested small amounts of animal matter along with plant foods, but I believe that this was accidental and of little nutritional significance. Soil eating has been observed in a number of wild colobine populations (Davies and Baillie, 1988) but was not seen at Tiwai.

Tiwai: Systematic Sample

The event method yielded a total of 587 feeding records from the PF group during 11 3-day sample periods. Table III displays the complete sample, by species and plant part. In 364 cases the food plant was identified as a tree, and in 136 cases a climber; in a further 87 cases (many of them observations during foraging in low, thick growth) the plant type could not be identified with confidence. The predominant food species were the trees *Terminalia ivorensis* (19% of those records where the plant type was identified) and *Sapium aubrevillei* (17%) and the thorny climber *Acacia pennate* (8%).

Young foliage (59% of records) dominates the sample of 521 identified plant parts. Mature leaf consumption was restricted largely to petioles (9% of records); blades were rarely eaten (2%). The total contribution of fruit and fruit parts to the sample was 19%, most of which was seeds (14%). The seeds eaten were mostly small or medium-sized; large seeds (e.g., of *Pentaclethra macrophylla*) were eaten infrequently. *Pentaclethra* seeds (4–5 cm in diameter) are contained in a very large (30- to 40-cm), woody pod; olive colobus were apparently unable to chew through the unopened pod and ate only seeds from ripe pods after their dehiscence. Fruit pericarps were rarely eaten; when consumed, pericarps were unripe and green (i.e., relatively leaf-like).

Table III. Observations of Food Choice by *Procolobus verus* (PF Study Group) on Tiwai Island During 11 Three-Day Sample Periods, Based on Feeding Events

Plant species	YL ^a	MLL	MLP	UL	FL	YF	YS	MS	UF	UN	Total
Trees											
<i>Terminalia ivorensis</i>	58	1			2					7	68
<i>Sapium aubrevillei</i>	33	1	25			2					61
<i>Funtumia africana</i>						2	1	22	1		26
<i>Xylopia quintasii</i>	2	1	16							2	21
<i>Plagiosiphon emarginatus</i>	1				6	1	11		1		20
<i>Lovoa trichiloides</i>					17						17
<i>Myrianthus libericus</i>	14			1						1	16
<i>Vitex micrantha</i>	6		4			3				3	16
<i>Pterocarpus santalinoides</i>	13										13
<i>Dialium guineense</i>								10		1	11
<i>Eugenia</i> sp.					1		10				11
<i>Parkia bicolor</i>	10										10
<i>Blighia welwitschii</i>	9										9
<i>Cynometra leonensis</i>	9										9
<i>Albizia zygia</i>	6					2					8
<i>Santiria trimera</i>	5					1			2		8
<i>Calpocalyx brevibracteatus</i>	4									2	6
<i>Pentaclethra macrophylla</i>								4		1	5
<i>Bridelia grandis</i>	2		2								4
<i>Millettia rhodantha</i>	3										3
<i>Samanea dinklagei</i>	3										3
<i>Soyauxia floribunda</i>	2	1									3
<i>Dialium dinklagei</i>								2			2
<i>Bridelia micrantha</i>	2										2
<i>Drypetes</i> sp.	2										2
Unident. tree sp. B	2										2
Unident. tree sp. D		2									2
<i>Acioa</i> sp.	1										1
<i>Caloncoba echinata</i>					1						1
<i>Macaranga barteri</i>	1										1
<i>Piptadeniastrum africanum</i>					1						1
<i>Zanthoxylum gillettii</i>	1										1
Unident. tree sp. E	1										1
Climbers											
<i>Acacia pennata</i>	23			6							29
<i>Millettia leonensis</i>	2						4	1	2	1	10
<i>Combretum</i> spp. ^b					5		3				8
Climber sp. a							3		3		6
Climber sp. b	3										3
Climber sp. c	3										3
Climber sp. d	3										3
<i>Manniophyton fulvum</i>					2						2
Climber sp. e	1										1
Unident. climbers	51	3		5	2		4			6	71
Species/plant undet.	31	1	1	10					2	42	87
Total	307	10	48	21	38	11	36	39	11	66	587
Percentage of total	58.9	1.9	9.2	4.0	7.3	2.1	6.9	7.5	2.1		

^aYL, young leaves and leaf buds; MLL, mature leaf lamina (blade) or whole leaf; MLP, mature leaf petiole; UL, undetermined age leaf; FL, flowers and floral buds; YF, young fruit (whole fruit or pericarp); YS, immature seeds; MS, mature seeds; UF, undetermined part of fruit; UN, undetermined.

^bAt least two species.

The complete feeding sample was spread unevenly over a total period of 29 months. To examine dietary differences across seasons, samples have been lumped as follows: middle wet season, 1983 (22–24 June, 10–12 July, 21–23 July, 3–5 August); late wet season, 1985 (18–20 and 28–30 October); early dry season, 1984 (8–10 and 14–16 January); and late dry season, 1985 (5–7 February, 7–9 March). These seasonal diets, based on event sampling, are shown in Table IV. Young foliage (leaves and buds) was always the most frequently consumed food item, but it fluctuated greatly in its relative dietary importance, from 85% in the late wet season of 1985 to only 38% in the late dry season of 1984. Seeds were a major dry-season food, with unripe seeds predominating in the early dry season (25% of records) and ripe seeds in the late dry season (26%). The late dry-season sample had the most mature leaf-blade feeding (3%) and the greatest species diversity (14 food tree species definitely identified, versus 9 in the late wet season).

Throughout the year, the young foliage of climbers formed a substantial part of the olive colobus diet. Through the dry season and in the middle of the wet season, such leaves formed 12.5–13.5% of feeding records where the food species and part were identified. In the late wet season, the score rose to 45%, largely as a result of heavy feeding on *Acacia pennata*. Climber foliage seems to be a year-round staple of the olive colobus diet on Tiwai, and its overall importance probably was underestimated as a result of the poor visibility conditions in the liana tangles and canopy gaps in which the monkeys often fed.

Tiwai: Other Evidence

Observations on the Tiwai study group outside the four seasonal periods summarized here did not indicate substantial differences in olive colobus diet at other times of year or between years. In April, May, and early June of 1983 (an early wet-season period when the study group was frequently observed but not yet fully habituated), young foliage comprised 83% of 58 records of feeding on identified plant parts, and *Terminalia* accounted for 20% of 49 records where the food species was determined. During a 3-day sample in June 1984, young foliage formed 71% of 41 records of identified foods, and *Terminalia* accounted for 20% of 41 food-species records.

The tree-species composition of the forest in the west study area on Tiwai was different from that of the east of the island. *Terminalia* and *Sapium*, the chief foods of the eastern study group, were very rare trees in the west area and were not seen to be eaten by olive colobus. Ten of the 11 feeding observations on the small olive colobus group in the west area during February 1983 were of the young foliage of two deciduous trees, *Chlorophora regia* and *Zanthoxylum gillettii*; *Chlorophora* was absent in the eastern study group's range, and *Zanthoxylum* comprised a smaller part of the forest cano-

Table IV. Seasonal Diets of *Procolobus verus* on Tiwai Island^a

Food plant species	Food part													Total	
	YL	MLL	MLP	UL	FL	YF	YS	MS	UF	UN	N	%			
	Mid wet season (July-August 1983)														
<i>Terminalia ivorensis</i>	45										6	51	30.7		
<i>Sapium aubrevillei</i>	7	1	19									27	16.3		
<i>Xylopia quintasii</i>	2	1	13								2	18	10.8		
11 other tree spp. (each <10%)	31			8	3						3	45	27.1		
Climbers	20					3					2	25	15.1		
Undetermined	4		1	4							16	25			
Total (N)	109	2	33	4	8	3	3				29	191			
Percentage	67.3	1.2	20.4	2.5	4.9	1.9	1.9								
	Late wet season (October 1985)														
<i>Myrianthus libericus</i>	12				1						1	14	18.4		
<i>Terminalia ivorensis</i>	8											8	10.5		
7 other tree spp. (each <10%)	9				1	1			2	3	16	21.1			
<i>Acacia pennata</i>	17			2							1	19	25.0		
Other climbers	14	1		1	2						7	18			
Undetermined	10			1							12	12			
Total (N)	70	1	1	4	4	1			2	12	94				
Percentage	85.4	1.2		4.9	4.9	1.2			2.4						

	Early dry season (January 1984)				Late dry season (February-March 1985)			
<i>Sapium aubrevillei</i>	26	3						
<i>Eugenia</i> sp.			10					
<i>Plagiosiphon emarginatus</i>			1	8				
8 other tree spp. (each <10%)	4	1	4	2	6	1		
Climbers	12	1	4	7	2	2	28	21.1
Undetermined	4		4		1	9	18	
Total (N)	46	2	7	8	3	25	6	12
Percentage	45.5	2.0	6.9	7.9	3.0	24.8	5.9	4.0
<i>Funtumia africana</i>					2	1	22	1
<i>Lovoa trichilioides</i>				17				26
<i>Pterocarpus santalinoides</i>	13							17
11 other tree spp. (each <10%)	15	2	8	2	3	10		13
Climbers	15	1	1	7	1		1	40
Undetermined	5	1	1				9	26
Total (N)	48	4	8	2	4	4	33	16
Percentage	37.5	3.1	6.3	1.6	18.8	3.1	25.8	10
Across-season average	58.9	1.9	8.4	4.2	7.2	2.3	7.5	138

*Numbers are frequency scores from event sampling of PF study group. Food part abbreviations as in Table III; percentages exclude undetermined species and parts. Only species comprising at least 10% of the diet in a particular season are individually named.

py in the east than in the west (0.6 vs 0.2% of basal area/ha). The eleventh observation was of feeding on the seeds of the common leguminous liana, *Millettia leonensis*, a species whose seeds were also eaten by the eastern group.

Pujehun

In August 1979 and January 1980, 13 records of feeding by olive colobus were made along the Makibi stream. In 11 of these cases the plant part (but not the species) was identified. Nine of the 11 records were of young foliage, one was of leaf petioles, and one was of small green fruits.

Food Selection in Relation to Abundance

Olive colobus were highly selective feeders at Tiwai. Although mature foliage was always abundantly available, the monkeys largely ignored it, except when eating the petioles (and sometimes adjacent leaf bases) of mature leaves from a small number of relatively uncommon tree species. Even when eating young foliage, the monkeys avoided many common species. Of the 20 tree species making up 75% of the estimated biomass within their range (Table I), the study group ate foliage from only 6, and this feeding comprised only 19% of all tree-foliage feeding records. I did not observe olive colobus feeding on foliage from any of the top five species, which together made up 47% of the estimated tree biomass. Most foliage eaten came from a small number of relatively rare middle-canopy trees (most of them deciduous species) and from climbers and understory trees.

Table V compares the frequency of all foliage feeding accounted for by each of the top 10 tree-foliage food sources in the systematic sample with

Table V. Selection of Foliage of the 10 Tree Species Most Frequently Consumed by the *Procolobus* versus Study Group on Tiwai Island^a

Tree species	A = % of all tree-foliage feeding records	B = percentage of total tree biomass (basal area/ha) in study area	A/B
<i>Sapium aubrevillei</i>	24.3	0.2	121.5
<i>Terminalia ivorensis</i>	24.3	0.3	81
<i>Xylopia quintasii</i>	7.8	0.04	195
<i>Myrianthus libericus</i>	5.8	2.4	2.4
<i>Pterocarpus santalinoides</i>	5.3	<0.1	>50
<i>Parkia bicolor</i>	4.1	1.2	3.4
<i>Vitex micrantha</i>	4.1	3.2	1.3
<i>Blighia welwitschii</i>	3.7	1.2	18.5
<i>Cynometra leonensis</i>	3.7	1.2	3.1
<i>Albizia zygia</i>	2.5	0.8	3.1

^a"Foliage" includes young leaves, leaf buds, mature leaf blades, and mature leaf petioles.

Table VI. Selection of Tree Fruits and Seeds by the *Procolobus verus* Study Group on Tiwai Island

Tree species	A = % of all tree-fruit feeding records	B = percentage of total tree biomass (basal area/ha) in study area	A/B
<i>Funtumia africana</i>	34.7	8.3	4.2
<i>Plagiosiphon emarginatus</i>	17.3	4.1	4.2
<i>Eugenia</i> sp.	13.3	<0.1	>100
<i>Dialium guineense</i>	13.3	4.8	2.8
<i>Pentaclethra macrophylla</i>	5.3	15.0	0.4
<i>Vitex micrantha</i>	4.0	3.2	1.3
<i>Santiria trimera</i>	4.0	0.8	5.0
<i>Albizia zygia</i>	2.7	0.8	3.4
<i>Sapium aubrevillei</i>	2.7	0.2	13.5
<i>Dialium dinklagei</i>	2.7	0.9	3.0

the abundance of these tree species in the forest. Of the top 10 sources of tree foliage, only *Vitex micrantha* (an understory tree) was consumed at a relative frequency similar to its relative abundance. All the other major sources of tree foliage were consumed much more frequently than would be predicted on the basis of their abundance; for *Xylopia quintasii*, *Sapium aubrevillei*, *Terminalia ivorensis*, and *Pterocarpus santalinoides*, the ratio of percentage foliage feeding to percentage basal area per hectare exceeded 50.

The systematic feeding sample includes fruits and seeds from only 10 tree species. Table VI compares their consumption with the relative abundance of these trees in the forest. A few common species (notably *Funtumia africana*) featured more heavily here than they did in the foliage part of the diet. Conversely, feeding on the fruits of some very common emergent and upper-canopy trees (e.g., *Piptadeniastrum africanum*, *Uapaca guineensis*, and *Parinari excelsa*) was never seen. Flowers, an infrequently available potential food, were eaten from an even smaller range of trees; in part, this is probably due to the patchy nature of the sample.

Food Selection in Relation to Chemistry

Table VII compares the fiber, tannin, and protein contents of (a) the five most frequently recorded food items in the olive colobus diet with (b) the mature leaf blades of the five tree species contributing most to the biomass of the canopy (Table I), none of which was eaten by olive colobus. Fiber levels are much higher in all the uneaten mature leaves than in any of the food items ($U = 0$, $p = .004$). Although the tannin content of *Acacia pennata* young leaves is higher than that of several of the uneaten items, as a group preferred food items have significantly lower tannin levels than uneaten items ($U = 2$, $p = .016$). The average protein content of food items

Table VII. Comparison of the Chemistry of the Top Five Items in the Feeding Sample from the PF Group with That of the Leaf Blades of the Five Tree Species Contributing Most of the Forest Canopy Biomass

Plant species	Plant part ^a	Sample <i>N</i>	% fiber ^b	% tannin ^c	% protein ^d
Top 5 items (from Table III)					
<i>Terminalia ivorensis</i>	YL	3	24.6	1.5	13.4
<i>Sapium aubrevillei</i>	YL	1	15.4	0	16.2
<i>Sapium aubrevillei</i>	MLP	1	23.0	0.8	9.4
<i>Acacia pennata</i>	YL	1	20.9	14.1	27.9
<i>Funtumia africana</i>	MS	1	13.4	0.5	20.6
X			19.5	3.4	17.5
Mature leaf blades (Table I)					
<i>Pentaclethra macrophylla</i>	MLL	2	51.6	9.1	17.2
<i>Uapaca guineensis</i>	MLL	1	43.7	16.4	8.7
<i>Funtumia africana</i>	MLL	2	29.5	26.5	15.2
<i>Piptadeniastrum africanum</i>	MLL	2	44.5	10.7	19.4
<i>Digilium guineese</i>	MLL	2	44.2	29.8	11.0
X			42.7	18.5	14.3

^aPlant part abbreviations as in Table II, footnote *a*.

^bAcid detergent fiber, as percentage dry weight.

^cCondensed tannin, as percentage dry weight, on quebracho tannin standard.

^dCrude protein, as percentage dry weight, based on nitrogen \times 6.25.

is higher than that of uneaten mature foliage items, but some uneaten foliage has a higher protein content than some preferred foods, and the difference between the two groups of samples is not significant ($U = 9$, $p = .274$). Fiber and tannin have been implicated as major digestion inhibitors in colobine monkeys (McKey *et al.*, 1981; Waterman, 1984), but tannin content is less often strongly correlated with food choice than is fiber (Davies *et al.*, 1988). The average protein value for both eaten and uneaten items at Tiwai exceeds the average values found at all other sites where the chemistry of colobine food choice has been studied, with the exception of Uganda's Kibale Forest (Waterman *et al.*, 1988).

When olive colobus do eat mature leaves they most commonly select the petiole and drop the blade; this is a common colobine trait and probably relates to the higher digestibility of petioles compared with blades (Waterman, 1984). Limited data from this study support this proposition: the blades of one sample of *Sapium aubrevillei* mature leaves contained 30.0% acid-detergent fiber and 3.0% condensed tannin, while the petioles of the same leaves contained 23% fiber and only 0.8% tannin; young leaf blades contained even less fiber, no tannin, and more protein (Table VII).

SUMMARY AND DISCUSSION

The characteristics of the olive colobus diet in Sierra Leone seem to result from the interaction of two main factors: the selection of food quality

and the selection of particular feeding sites. The diet is dominated by the young foliage of climbing plants and that of trees that either are deciduous or produce large crops of new leaves over limited periods of time. Seeds are also important in the diet, but on a seasonal basis. Variation in seed eating is apparently a response to two factors: the increased availability of seeds in the dry season and a decrease in the abundance of young leaves as the dry season progresses. Young leaves and seeds are both high-quality food items, in the sense that both their nutrient content and their digestibility are usually relatively high (Waterman, 1984). Limited data from Tiwai show preferred food items to have much lower fiber levels and generally lower tannin levels than the most abundantly available tree foliage in the forest. The selection of such highly digestible foods by the olive colobus is predicted by its small body size. A physiological correlate of the olive colobus strategy is a high rate of microbial fermentation in the forestomach [found by Drawert *et al.* (1962) to be 230 mmol of VFA/liter]. The diet found at Tiwai also accords with inferences made from the anatomy of the dentition, which has features suggesting both a highly folivorous diet and adaptations to fruit processing (Hylander, 1975; Kay, 1981); young foliage dominates the diet for most of the year, but seeds and other reproductive parts are seasonally important.

The olive colobus studied at Tiwai include less mature foliage in their diet than most other carefully studied populations of African colobines. Only in the early dry season did mature foliage exceed 10% of feeding records for the Tiwai olive colobus, and most of this feeding was on leaf petioles rather than on blades or whole leaves. The highest frequency of mature leaf blades feeding (3% of the diet) was in the late dry season, when preferred foods were apparently least available. Similar low levels of mature foliage consumption have been reported in the small Asian colobines *Presbytis melalophos* and *P. rubicunda*, each of which has been found to consume large quantities of seeds on a seasonal basis (Bennett, 1983; Davies, 1984). In Africa, however, only the population of *Colobus satanas* at Lopé, Gabon, has been found to have dietary levels of mature foliage as low as those of olive colobus at Tiwai. Harrison and Hladik (1986) report that mature leaves exceeded 10% of the Lopé *C. satanas* diet only at the end of the local dry season in September. Elsewhere, mature leaves form at least 30% of colobus diet in some months—e.g., *Colobus guereza* in Uganda (Oates, 1977), *C. satanas* in Cameroon (Mckey *et al.*, 1981), and *Procolobus badius* in East Africa (Struhsaker, 1975; Marsh, 1981). These other African species are considerably larger than *P. verus*: *C. guereza* and *P. badius* adult females typically weight about 8 kg, versus 4 kg for *P. verus* (data collated by the author and W. L. Jungers from wild-shot museum specimens). In all colobine populations, a high frequency of mature foliage consumption seems to be largely a response to scarcities of higher-quality food items.

In terms of feeding sites, olive colobus at Tiwai were found to avoid feeding in the crowns of tall trees and instead fed most frequently in the thicker middle canopy, in liana tangles, and in dense low growth in canopy gaps. During scan sampling of the behavior of the Tiwai study group, the observed animal was below 15 m in 53% of 310 cases in which the recorded activity was feeding, while only 34% of 816 cases of other activities occurred below this height; this is a highly significant difference ($G = 33.38, p < .001$). Due to the difficulty of observing the animals in low, thick growth, these figures probably underestimate the importance of feeding in such sites. Booth (1956) describes the olive colobus as a "thicket-haunter" in Ghanaian forests, and Galat and Galat-Luong (1985) report that it uses the lower levels of the forest canopy more than the red and black-and-white colobus in the Tai Forest of Côte d'Ivoire.

If, as the evidence presented here suggests, the small body size of the olive colobus constrains it to be highly selective in its choice of food, what is limiting its body size? Forestomach fermentation is not an efficient digestive strategy for a very small (or very large) herbivore (Janis, 1976; Parra, 1978; Demment and van Soest, 1985). Presumably the olive colobus could exploit a wider range of foods if it were larger, and this could allow increases in reproductive rate, population density, and/or area inhabited. What, then, has prevented the evolution of a larger body size in the olive colobus? One possibility is that the species has evolved in competition with its close (and much larger) relative the red colobus (*Procolobus badius*), with which it is broadly sympatric in West Africa; such competition could have favored and maintained character displacement (size differentiation) and consequent niche separation in the two species. Alternatively (or additionally), perhaps an ancestral olive colobus population was restricted to an environment in which large body size was a positive disadvantage (e.g., a forest in which large supports were rare).

Whatever the original causes of small body size in the olive colobus, its adaptive strategy today seems to limit the species to particular habitats. Almost all olive colobus populations occur south of latitude 8°N (Oates, 1981). Booth (1957) ascribes this to the species' unwillingness to travel on the ground in northerly forests where trees are not always densely packed; but such a distribution could also be related to the greater length of the dry season away from the coast, which is likely to extend seasonal food shortages. Within its geographical range, the olive colobus is most abundant in those parts of the high forest zone where "tall timber is relatively scarce, and where light can penetrate, thus permitting the growth of dense, tangled vegetation near ground level" (Booth, 1956, p. 424). Such conditions occur at sites of natural tree-falls within the forest, in areas where there has been cultivation or tree-cutting by humans, and in swamps and along river banks.

In Sierra Leone, the olive colobus is most frequently seen in riverine and secondary forests and is only rarely encountered in undisturbed high forest. This habitat preference, together with its diet and small body size (three factors that are probably closely linked), has other behavioral consequences for the olive colobus monkey, which will be pursued in subsequent papers.

ACKNOWLEDGMENTS

This study forms part of a project funded by grants from the U.S. National Science Foundation (BNS 8120206 and 8505702), the Research Foundation of the City University of New York, and the New York Zoological Society.

In Sierra Leone, local support was provided by the Department of Biological Sciences, Njala University College; I am grateful to the heads of this department, Drs. A. Sesay and P. T. White, for all their help. In the field, much assistance was given by the people of Barri and Koya Chiefdoms. Special thanks are due to field-research colleagues who helped to collect data and shared ideas, in particular G. H. Whitesides, R. P. Kluberanz, Dr. S. Green, G. L. Dasilva, and Dr. A. G. Davies. Nigel and Rachel Wakeham were unfailingly generous hosts during visits to Freetown.

For the chemical analysis of plant samples, thanks are due to G. McGee and G. L. Dasilva, as well as to Professor P. G. Waterman (Department of Pharmacy, University of Strathclyde, Scotland), in whose laboratory the analyses were performed. Finally, G. H. Whitesides and two reviewers provided helpful comments on a draft of the manuscript.

APPENDIX

Table AI

Family	Species	Growth form and phenology ^a	Parts eaten		
			Leaves	Flowers	Fruits/ seeds
Annonaceae	<i>Xylopia quintasii</i>	E	x		
Apocynaceae	<i>Funtumia africana</i>	E			x
Burseraceae	<i>Santiria trimera</i>	E	x		x
Caesalpinaceae	<i>Cynometra leonensis</i>	D	x		
Caesalpinaceae	<i>Detarium senegalense</i>	D	x ^b		
Caesalpinaceae	<i>Dialium dinklagei</i>	D			x
Caesalpinaceae	<i>Dialium guineense</i>	E			x
Caesalpinaceae	<i>Plagiosiphon emarginatus</i>	E	x	x	x
Combretaceae	<i>Combretum</i> spp.	C		x	x

Table AI. (Continued)

Family	Species	Growth form and phenology ^a	Parts eaten		
			Leaves	Flowers	Fruits/ seeds
Combretaceae	<i>Terminalia ivorensis</i>	D	x	x	
Euphorbiaceae	<i>Bridelia grandis</i>	E	x		
Euphorbiaceae	<i>Bridelia micrantha</i>	D?	x		
Euphorbiaceae	<i>Drypetes</i> sp.	E	x		
Euphorbiaceae	<i>Macaranga barteri</i>	D?	x		
Euphorbiaceae	<i>Manniophyton fulvum</i>	C		x	
Euphorbiaceae	<i>Sapium aubrevillei</i>	E	x		x
Flacourtiaceae	<i>Caloncoba echinata</i>	E		x	
Medusandraceae	<i>Soyauxia floribunda</i>	E	x		
Meliaceae	<i>Lovoa trichilioides</i>	D		x	
Mimosaceae	<i>Acacia pennata</i>	C	x		
Mimosaceae	<i>Albizia zygia</i>	D	x		x
Mimosaceae	<i>Calpocalyx brevibracteatus</i>	D?	x		
Mimosaceae	<i>Parkia bicolor</i>	D	x		
Mimosaceae	<i>Pentaclethra macrophylla</i>	E			x
Mimosaceae	<i>Piptadeniastrum africanum</i>	D		x	
Mimosaceae	<i>Samanea dinklagei</i>	D	x		
Moraceae	<i>Chlorophora regia</i>	D	x		
Moraceae	<i>Myrianthus libericus</i>	E	x	x	
Myrtaceae	<i>Eugenia</i> sp.	E		x	x
Papilionaceae	<i>Baphia nitida</i>	E	x		
Papilionaceae	<i>Millettia leonensis</i>	C	x		x
Papilionaceae	<i>Millettia rhodantha</i>	D	x	x ^b	
Papilionaceae	<i>Pterocarpus santalinoides</i>	D	x	x	
Passifloraceae	<i>Smeathmannia pubescens</i>	E	x		
Rosaceae	<i>Acioa</i> sp.	E	x		
Rosaceae	<i>Parinari excelsa</i>	E	x ^b		
Rutaceae	<i>Zanthoxylum gillettii</i>	D	x		
Sapindaceae	<i>Blighia welwitschii</i>	E	x		
Verbenaceae	<i>Vitex micantha</i>	E	x		x

^aD, deciduous tree; E, evergreen tree; C, climber.

^bObserved by G. H. Whitesides (personal communication).

^cAt least two species.

REFERENCES

- Bennett, E. L. (1983). *The Banded Langur: Ecology of a Colobine in West Malaysian Rain-forest*, Ph.D. dissertation, University of Cambridge, Cambridge.
- Booth, A. H. (1956). The distribution of primates in the Gold Coast, *J. W. Afr. Sci. Assoc.* 2: 122-133.
- Booth, A. H. (1957). Observations on the natural history of the olive colobus monkey, *Procolobus verus* (van Beneden). *Proc. zool. Soc. Lond.* 129: 421-430.
- Clutton-Brock, T. H. (1977). Methodology and measurement. In Clutton-Brock, T. H. (ed.), *Primate Ecology*, Academic Press, London, pp. 585-590.
- Davies, A. G. (1984). *An Ecological Study of the Red Leaf Monkey (Presbytis rubicunda) in the Dipterocarp Forest of Northern Borneo*, Ph.D. dissertation, University of Cambridge, Cambridge.

- Davies, A. G., and Baillie, J. C. (1988). Soil-eating by red leaf monkeys (*Presbytis rubicunda*) in Sabah, Northern Borneo. *Biotropica* 20: 252-258.
- Davies, A. G., Bennett, E. L., and Waterman, P. G. (1988). Food selection by two South-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biol. J. Linn. Soc.* 34: 33-56.
- Demment, M. W., and Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125: 641-672.
- Drawert, F., Kuhn, H.-J., and Rapp, A. (1962). Reaktions-Gaschromatographie. III. Gaschromatographische Bestimmung der niederflüchtigen Fettsäuren im Magen von Schlankaffen (Colobinae). *Hoppe-Seyler Z. Physiol. Chem.* 329: 84-89.
- Fleagle, J. G. (1977). Locomotor behavior and skeletal anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Yb. phys. Anthropol.* 20: 440-453.
- Galat, G., and Galat-Luong, A. (1985). La commonauté de primates diurnes de la forêt de Tai, Côte d'Ivoire. *Rev. Ecol. (Terre Vie)* 40: 3-32.
- Gaulin, S. J. C. (1979). A Jarman/Bell model of primate feeding niches. *Hum. Ecol.* 7: 1-20.
- Greig-Smith, P. (1983). *Quantitative Plant Ecology*, 3rd ed., University of California Press, Berkeley.
- Gwynne-Jones, D. R. G., Mitchell, P. K., Harvey, M. E., and Swindell, K. (1978). *A New Geography of Sierra Leone*, Longman, London.
- Harrison, M. J. S. (1986). Feeding ecology of black colobus, *Colobus satanas*, in Gabon. In Else, J. G., and Lee, P. C. (eds.), *Primate Ecology and Conservation*, Cambridge University Press, Cambridge, pp. 31-37.
- Harrison, M. J. S., and Hladik, C. M. (1986). Un primate granivore: Le colobe noir dans le forêt du Gabon; potentialité d'évolution du comportement alimentaire. *Rev. Ecol. (Terre Vie)* 41: 281-298.
- Hungate, R. E., Phillips, G. D., McGregor, A., Hungate, D. P., and Buechner, H. K. (1959). Microbial fermentation in certain mammals. *Science* 130: 1192-1194.
- Hylander, W. L. (1975). Incisor size and diet in anthropoids with special reference to Cercopithecidae. *Science* 189: 1095-1098.
- Janis, C. (1976). The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution* 30: 757-774.
- Kay, R. F. (1981). The nut-crackers—a new theory of the adaptations of the Ramapithecinae. *Am. J. phys. Anthropol.* 55: 141-151.
- Kuhn, H.-J. (1964). Zur Kenntnis von Bau und Funktion des Magens der Schlankaffen (Colobinae). *Folia primatol.* 2: 193-221.
- Marsh, C. W. (1981). Diet choice among red colobus (*Colobus badius rufomitratus*) on the Tana River, Kenya. *Folia primatol.* 35: 147-178.
- McKey, D. B. (1978). Soils, vegetation, and seed-eating by black colobus monkeys. In Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores*, Smithsonian Institution Press, Washington, D.C., 423-437.
- McKey, D. B., Gartlan, J. S., Waterman, P. G., and Choo, G. M. (1981). Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biol. J. Linn. Soc.* 16: 115-146.
- Oates, J. F. (1977). The guereza and its food. In Clutton-Brock, T. H. (ed.), *Primate Ecology*, Academic Press, London, pp. 276-321.
- Oates, J. F. (1981). Mapping the distribution of West African rain-forest monkeys: Issues, methods, and preliminary results. *Ann. N.Y. Acad. Sci.* 376: 53-64.
- Oates, J. F., Waterman, P. G., and Choo, G. M. (1980). Food selection by the South Indian leaf-monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* (Berlin) 45: 45-56.
- Parra, R. (1978). Comparison of foregut and hindgut fermentation in herbivores. In Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores*, Smithsonian Institution Press, Washington, D. C., pp. 205-229.
- Richard, A. F. (1985). *Primates in Nature*, W. H. Freeman, New York.
- Savill, P. S., and Fox, J. E. D. (1967). *Trees of Sierra Leone*, Forestry Division, Freetown.
- Waterman, P. G. (1984). Food acquisition and processing as a function of plant chemistry. In Chivers, D. J., Wood, B. A., and Bilsborough, A. (eds.), *Food Acquisition and Processing in Primates*, Plenum, New York, pp. 177-211.

- Waterman, P. G., Choo, G. M., Vedder, A. L., and Watts, D. (1983). Digestibility, digestion-inhibitors and nutrients of herbaceous foliage and green stems from an African montane flora and comparison with other tropical flora. *Oecologia* (Berlin) 60: 244-249.
- Waterman, P. G., Ross, J. A. M., Bennett, E. L., and Davies, A. G. (1988). A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forests and the influence of leaf chemistry on populations of colobine monkeys in the Old World. *Biol. J. Linn. Soc.* 34: 1-32.
- Whitesides, G. H., Oates, J. F., Green, S. M., and Kluberanz, R. P. (1988). Estimating primate densities from transects in a West African rain forest: A comparison of techniques. *J. Anim. Ecol.* 57: 345-367.
- Whitmore, T. C. (1975). *Tropical Rain Forests of the Far East*, Oxford University Press, Oxford.