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Diet of *Colobus polykomos* on Tiwai Island: Selection of Food in Relation to its Seasonal Abundance and Nutritional Quality

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A group of Colobus polykomos *at Tiwai, Sierra Leone, demonstrated seasonal flexibility in its diet, with seeds, young leaves, and mature leaves each dominating the diet at different times. Comparison of food consumption with phenological data indicates that seeds are eaten whenever available and are preferred to other foods, while young leaves are preferred to mature leaves.* Colobus polykomos *also prefer liane to tree leaves, despite the relatively high quality of mature tree foliage at the Tiwai site. Analysis of protein, fiber, and energy values of foods selected and items available, but not eaten, suggests that preference is related to protein and energy maximization. Leguminous plants, especially Papilionaceae and Mimosaceae, are highlighted as important food sources for* C. polykomos*; seeds and leaves from these families have a high nitrogen content, and the protein content of leguminous seeds often equals or exceeds that found in leaves. It is predicted, therefore, that colobines living in habitats with a high density of legumes will feed heavily on seeds, subject to constraints such as seasonal availability. Where suitable leguminous species are less common, a mixture of fruits, seeds, and young or mature leaves or both is likely to be selected. The results of this and other recent studies of colobines do not support the notion that colobines are specialist folivores.*

KEY WORDS: *Colobus polykomos;* diet; seasonality; food selection; food chemistry; nutritional quality; seed-eating.

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INTRODUCTION

Although colobine monkeys have been described as folivores, leaf-monkeys, and "specialists" (Hill, 1964; Napier, 1970), evidence that they are not obligate leaf-eaters "subject to the constraints of folivory" (Ripley, 1984) is steadily accumulating (McKey, 1978; Davies *et al.*, 1988; Yeager, 1989; Stanford, 1991). A review of published material demonstrates that only species or populations studied in East Africa in the 1970s include <25% of fruit or seeds or both in their annual diets (Table I). Although leaf material is clearly an important dietary component for all colobines, there is also considerable variation in the proportion of young and mature

Table I. Summary of the Major Dietary Components (as Percentage of Total Feeding Records) of Wild Colobine Monkeys

	Dietary components				
Species[a]	Mature leaves	Leaves (unspecified age)	Young leaves/buds	Fruits/seeds	Source of data
P. senex	40		20	28	Hladik, 1977
P. entellus	21		27	45	Hladik, 1977
P. entellus		(54)		37	Oppenheimer, 1978
P. entellus	35		14	25	Newton, 1984
P. obscura	24		32	35	Curtin, 1978
P. obscura	6		33	34	Hardy, 1988
P. johnii	27		26	25	Oates *et al.*, 1980
P. melalophos	8		28	50	Bennett, 1983
P. thomasi		(32)		58	Gurmaya, 1986
P. rubicunda	1		37	49	Davies, 1984
P. rubicunda		(36)		52	Supriatna *et al.*, 1986
P. pileata	42		11	34	Stanford, 1991
N. larvatus		(52)		40	Yeager, 1990
Pr. badius	23		51	6	Struhsaker, 1975
Pr. badius	5		42	36	Gatinot, 1978
Pr. badius	12		36	25	Marsh, 1981
Pr. badius	19		30	29	G. Davies, personal communication
Pr. badius	12		35	42	Starin, 1991
Pr. verus	10		59	25	Oates, 1988
C. guereza	12		58	14	Oates, 1974
C. angolensis		(57)		32	Moreno-Black & Maples, 1977
C. satanas	20		20	53	McKey *et al.*, 1981
C. satanas	3		23	60	Harrison, 1986
C. polykomos	26		30	35	This study

[a] *P., Presbytis; N., Nasalis; Pr., Procolobus; C., Colobus.*

foliage eaten — both within and between species, and it appears that colobines are not as restricted in their feeding habits as was commonly believed.

As a consequence of the earlier focus on leaf-eating, several authors have addressed the question, What determines leaf choice? (Oates *et al.*, 1977, 1980; Waterman *et al.*, 1980; Baranga, 1982). McKey *et al.* (1981) concluded that *Colobus satanas* in Douala-Edéa, Cameroon, ate seeds in response to a lack of suitable foliage and did not focus upon the inherent advantages of seed-eating. A study of the feeding ecology of *Colobus polykomos* conducted at Tiwai Island, Sierra Leone, showed that both seeds and foliage dominated the diet at different times during an annual cycle. This provided an opportunity to reconsider the factors that determine food selection in colobines, particularly the relationship between food availability and nutritional quality.

STUDY SITE, SPECIES, AND METHODS

Study Site

Dasilva (1989) and Oates *et al.* (1990) have described the study site. Tiwai is a riverine island of ≈12 km^2 in southeastern Sierra Leone. Its vegetation is primarily old secondary forest (70–80 years old), with patches of broken canopy, often thick with lianes. Lianes are estimated to account for 22% of forest foliage (Dasilva, 1989). Heterogeneity is increased by the presence of a distinct riverine forest at the island's edge, occasional swamps, and areas of regrowing farmbush. Two study areas, marked by a grid of trails at 50-m intervals, have been designated within the old forest. My results are from a study conducted in the East study area, adjacent to the east branch of the Moa River.

Tiwai's climate is typical of coastal West Africa, being monsoonal, with distinct wet and dry seasons (Fig. 1). This climate is described in more detail by Dasilva (1992). The seasonal changes in temperature, rainfall, and humidity are of considerable importance to vegetative growth and production and, hence, to herbivorous animals.

Study Animals

Five species of black-and-white colobus monkey are recognized (Oates and Trocco, 1983), occupying moist and riverine forests throughout tropical Africa. *Colobus polykomos* occurs in Guinea, Guinea-Bissau, Sierra Leone, Liberia, and Côte d'Ivoire, as far east as the Sassandra River. Mean

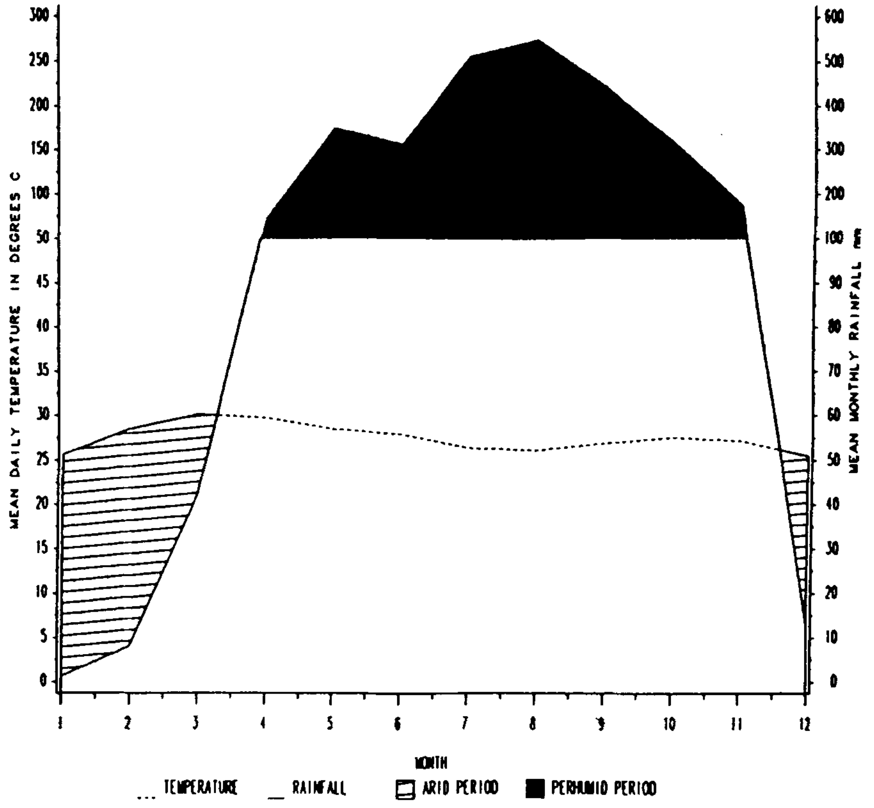


Fig. 1. Climatic diagram for Tiwai Island, based on monthly means for the period August 1982 through February 1986. The rainfall scale above 100 mm is condensed.

body weights are just below 10 kg [males, 9.9 kg, females, 8.3 kg (Oates *et al.*, 1990)]. My data are from one habituated group, CT, which contained 9–11 individuals during the study period, including 3 or 4 adult females, 2 or 3 adult males, 1 or 2 subadults and juveniles, and 1–3 infants. Patterns of range use and social behavior in this group are described by Dasilva (1989).

Large Tree Enumeration

All large trees (>40 cm dbh or >20 m high or both) within the study area were identified, mapped, and enumerated by Whitesides, Oates, and other members of the Tiwai research project. Small trees (>5 cm dbh or >5 m high or both) were sampled in 40 2 × 25-m plots within the same area. From this combined sample, the basal area per hectare (ba ha^{-1}) of each species was calculated (Whitesides, 1991).

Collection of Feeding Data

Data used to calculate the annual diet are based on instantaneous sampling of behavior during group scans. I performed scans of 5-min duration at 20-min intervals, from dawn to dusk, for 3 consecutive days, a period referred to as a "follow." I conducted two follows each month. My data presented are from 24 follows (72 days) over 12 months (December 1984 through November 1985). In each scan, I recorded the behavior of each of the first five individuals seen clearly, thus collecting a total of 7789 records. When the behavior was feeding, I noted details of the food item consumed. These records provide a measure of time spent feeding on different items.

Classification of Food Items

Variability in physical structure, chemical composition, and nutritive value of foods selected require a more detailed classification than simply leaves or fruit (Van Roosmalen, 1984; Winkler, 1984). Accordingly, I recorded both species and maturity of plant parts consumed. I took care to distinguish among feeding on leaf petioles, raches, blades, and pinnae, and whether whole or part blades were selected. I also distinguished between consumption of whole fruits and that of seeds and between pulpy fruits and pods. Observations indicated that animals did not distinguish between flowers and large, but still closed, buds; therefore I recorded feeding on them as "flowers/buds."

Phenological and chemical studies suggest considerable differences between trees and lianes. For these reasons, I segregated feeding on them in the analysis of feeding behavior and food selection.

Phenology

I collected phenological data on the day before or after each 3-day group follow. The tree phenological sample consists of 98 large trees (>20 m high and/or >40 cm dbh) within the range of the colobus study group. They are distributed across 12 plots: 8 25 × 50-m quadrats, spaced at 150-m intervals north to south and 100-m intervals east to west; and 4 unequally sized plots along the river edge. The 23 species of sample trees contributed 84% of the large tree biomass in the study area and, therefore, may be considered to represent the forest as a whole.

Because lianes are an important component both of the Tiwai forest, and of the diet of *C. polykomos*, I added several lianes to the phenological sample. Liane phenology presents its own problems (Putz and Windsor, 1987), and the difficulties involved in identifying species and determining whether clumps were ramets or genets precluded a random sample. For this reason, I selected five or six clumps of each of the most common and easily distinguished species of lianes, sufficiently apart to be separated genets, along the route walked for the large tree phenology, together with a mixed clump containing three less common species. I sampled 29 liane clumps and 9 species this way.

In recording tree and liane phenology, I distinguished three categories of vegetative parts: mature leaves, young leaves, and leaf buds. Mature leaves are of the full size, shape, and appearance typical of the species, while young leaves have two or more of the following characteristics: different color, lower turgidity, and smaller size. Leaf buds are bract-covered and quiescent.

Reproductive parts recorded are fruits, flowers, and flower buds. I regarded fruits to be ripe once mature size and color were attained. Most fruits dehisce or fall when fully ripe, which I also used to indicate maturity, particularly when no color change was associated with ripening. Many trees carry unripe slow-maturing fruit for long periods. Accordingly, three classes of unripe fruits are distinguished: class 1 unripe fruits are very small and often a different shape from mature fruits; class 2 fruits are moderate-, but not full-sized; and class 3 fruits are of a mature size, but differ from ripe fruits in color, lack of dehiscence, or pod structure, e.g., pods of *Pentaclethra macrophylla* are thick and woody, while unripe but, on ripening, dry and much thinner).

Both leaf and flower buds are often obscured by foliage and flowers; and flower buds, in particular, are difficult to distinguish from partly open flowers. For this reason I pooled buds with young leaves or flowers.

Estimation of Plant Production

I estimated foliage production as follows: I took the total crown area of each tree capable of bearing foliage as a fixed maximum, such that the combined scores for mature leaves, young leaves, and leaf buds for it could not exceed 5 (scored in 0.5 unit). A score of 5 is therefore equivalent to a crown with 100% of its potential foliage. This method allows comparability both between different vegetative parts and between species.

I applied the same criteria to reproductive part — flowers, ripe and unripe fruits — with a maximum score of 5 (100%) for all three categories. Maxima for flowers and fruits are harder to establish, since in some species they are not borne in all parts of the crown. Differences in fruit size between species may also have profound effects on the volume or weight of fruit produced, and thus these values are less reliable than those for leaves.

To estimate the contribution of each species to forest production, I weighted phenological scores with a measure of that species' ba h^{-1}, using the equation:

$$W_i = \left(\sum \frac{A_i}{n_i}\right) B_i$$

where W_i is the weighted abundance of the part in question for species i, A_i is the phenological score (abundance unit) for that part for each individual of species i, n_i is the number of individuals of species i in the phenological sample, and B_i is the ba h^{-1} of species i.

The relationship between basal area and crown diameter that makes it possible to use basal area per hectare (ba h^{-1}) as a measure of tree biomass (Dawkins, 1956) does not apply to lianes. Hence, their biomass cannot be readily estimated. Therefore, I present results for lianes as either means for each species or the mean of all scores (abundance units).

Phytochemical Analyses

I collected samples of leaves, flowers, and fruits from the most common forest trees and important primate foods either with a mechanical pruner mounted on a long pole or with the aid of local tree-climbers and dried them. I analyzed samples for acid detergent fiber and nitrogen, as an estimator of crude protein, at the Department of Pharmaceutical Chemistry, University of Strathclyde, Glasgow, with staff and students of P. G. Waterman. Oates *et al.* (1980) and Waterman *et al.* (1980) describe the methods that I used. I obtained calorific values via bomb calorimetry samples, performed at the Clinical Nutrition Unit, St. Pancras Hospital, London.

RESULTS

Seasonality in Plant Production

The proportion of mature leaves of trees and lianes in the forest was relatively constant over the year, despite the deciduous nature of some species. Young leaf production was variable, with two main peaks of production: in the late dry and early-to-mid wet seasons. Outside these periods, a low level of production continued throughout the year. These two peaks reflect different production cycles of the species that dominate forest biomass. *Pentaclethra macrophylla* (Mimosaceae) is the dominant species in the study area, comprising 24% of the large tree biomass; *Pentaclethra* produced a new crop of leaves before the onset of the rains, while other common tree species produced the bulk of their new leaves during and after the early rains (Fig. 2). I observed similar differences in timing for lianes. While most species produced new leaves after the first rains, the most common liane in the forest, *Milletia leonensis* (Papilionaceae), produced its new crop before the rains (Fig. 5).

Most tree species flowered before new leaf production. Timing of liane flowering differed from that of trees, with peaks both before and after tree flowering. Despite the sharp peak of flower production, there was only a short period (March–April) with almost no fruit in the forest. This is a result of the slow maturation of many fruits. I saw tree fruits in the greatest quantities from May, and they developed during the wet season. Maximum availability of class 3 young fruit, i.e., ones of full size but unripe, therefore occurred in the late wet through early dry seasons and was followed by two peaks of mature fruit availability, again reflecting the different production patterns of dominant species. Fruit of *P. macrophylla* matured in the early dry season, while fruit of another abundant tree, *Funtumia africana* (Apocynaceae), matured later. Liane fruit production was again out of phase, generally occurring after that of trees. Most unripe liane fruit 3 was available after tree fruit had matured and fallen. I noted only one sharp peak of mature liane fruit production — almost all from *Landolphia hirsuta* (Apocynaceae), one of the most common liane species on Tiwai. It produces bright orange, fleshy fruits containing a tangy sweet pulp surrounding large seeds. The quantity of liane fruit was strikingly lower than that of trees.

Annual Diet of *C. polykomos*

The annual diet of the study group of *C. polykomos*, based on 2196 scan-sample records of feeding, comprised three main components: fruit and seeds (34.6%), young leaves (29.7%), and mature leaves (26.4%) (Fig. 3). Their other foods included pith, bark, and whole twigs, sometimes eaten indiscriminately with leaf raches. I observed no instance of feeding upon insects or other animal matter.

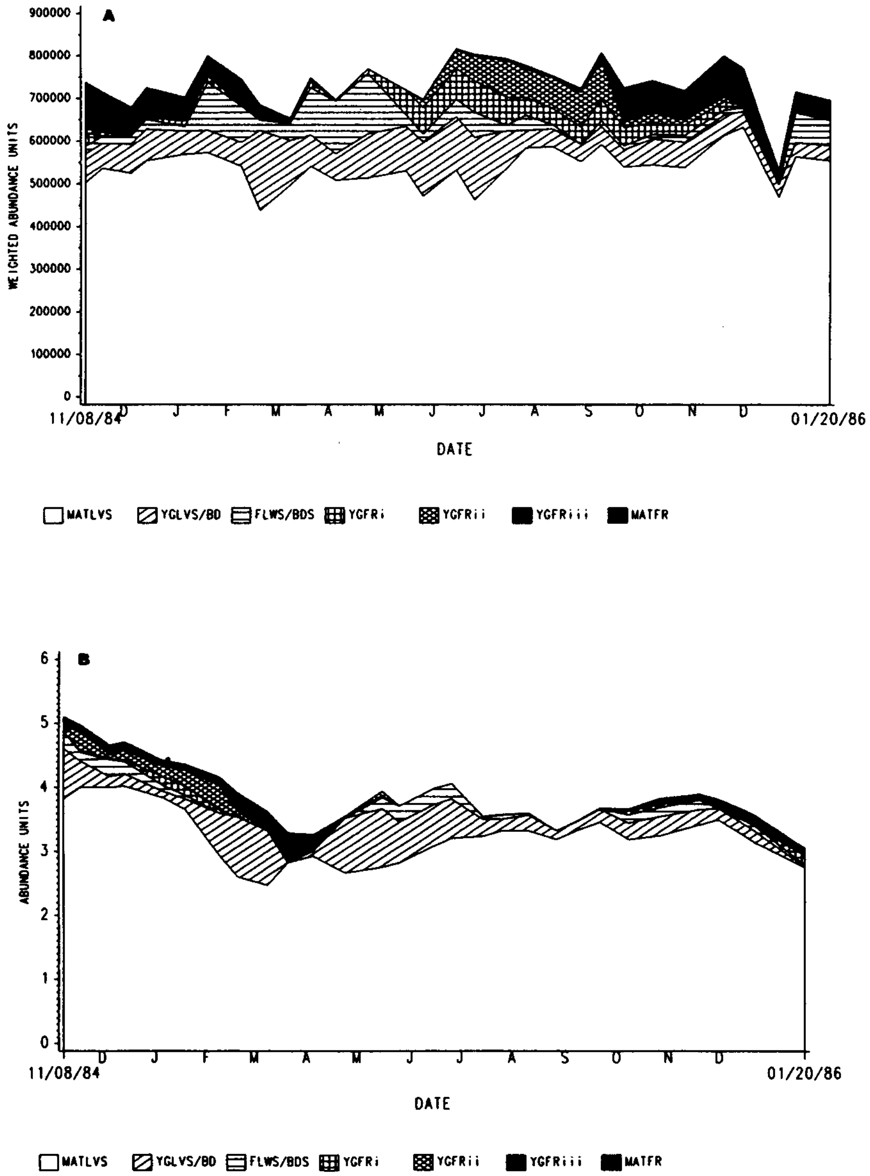


Fig. 2. Estimated production of different plant parts from phenological sampling in Tiwai study area. (A) Trees; (B) lianes. Calculation of weighted abundance units is described in the text. MATLVS, mature leaves; YGLVS/BD, young leaves/buds; FLWS/BDS, flowers/buds; YGFRi, young fruits, class 1; YGFRii, young fruits, class 2; YGFRiii, young fruits, class 3; MATFR, mature fruits.

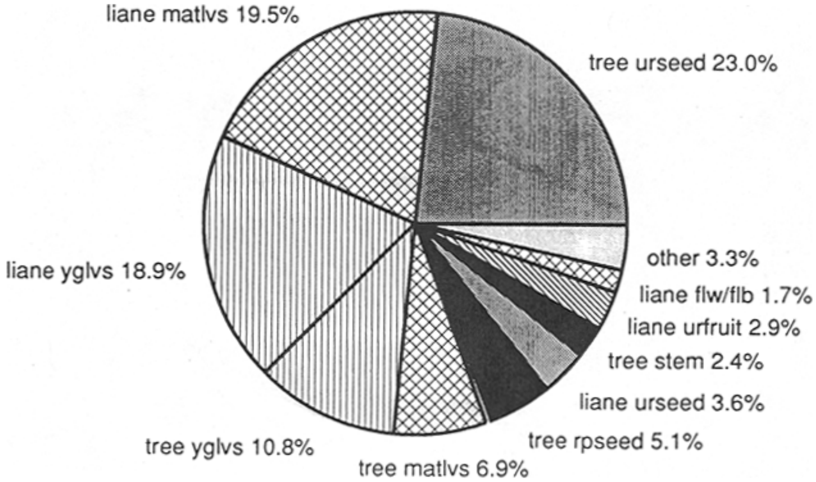


Fig. 3. Annual diet of *Colobus polykomos* at Tiwai, based on identified food items from scan sampling December 1984–November 1985. Matlvs, mature leaves, yglvs, young leaves; rpseed, ripe seed; urseed, unripe seed; urfruit, unripefruit; flw/flb, flower and/or flower bud.

Most leaves eaten —63.7% of young leaves and 73.8% of mature leaves—were from lianes, which indicates a marked preference for liane leaves. While ≥97% of eaten mature liane leaves were whole blades, 54% of tree mature leaf records are for leaf tips, petioles, and raches, suggesting further selectivity in feeding on them. When they selected young leaves, they usually ate whole blades. At least nine liane species provided *C. polykomos* with young leaves, with 16% of all young liane food leaves being from *Millettia leonensis. Millettia* species provided almost 20% of all young leaves consumed. Lianes of the genus *Strychnos* (Loganiaceae) were also important sources of young leaves, two species supplying 17% of all immature liane leaves (11% of young leaves), despite being relatively uncommon.

Flowers and flower buds constituted only 2.6% of feeding records and featured in the diet in only 6 months; 64% of all flowers consumed were taken from lianes. *Millettia leonensis* and *M. rhodantha* accounted for 54.6% of all flower/flower-bud feeding records. Flowers were not taken from common tree species.

Unripe seeds class 3 of *Pentaclethra macrophylla* were the most commonly recorded food item and accounted for 37% of all time spent consuming seeds and fruits; a further 8% of fruit and seed records involved ripe seeds of the same species. The second most important seed source is *Samanea dinklagei.* This tree, which is also in the Mimosaceae, comprised only 1.9% of large tree biomass, but its unripe seeds (class 3) accounted for 6.5% of all feeding records and 16% of fruit/seed records. Overall, 68% of seed/fruit feeding records are from leguminous trees, which accounted for 45% of large tree biomass in the East study area.

Most records of feeding on liane seeds/fruits (6.5% of annual diet) are of unripe fruit (classes 2 and 3) of two species of *Strychnos* (UL11 and UL19). Together, these accounted for 54.6% of liane seed/fruit records and 5.5 and 4.8%, respectively, of all seeds/fruits. All records for UL11 are seeds, but UL19 fruits, which are smaller, were most often eaten whole.

Seasonality of Food Selection

Although the monkeys ate the three main food classes — seeds, young leaves, and mature leaves — in roughly equal proportions over 12 months, there is considerable seasonal variation in consumption (Fig. 4). Each class of food dominated the diet for part of the year. For instance, seeds and/or fruit varied from a maximum of 75% in the second December group follow to 0% in both June follows and the second August follow. Almost all records of feeding on fruit and seeds fell within the dry and transitional seasons, with minimal intake in early and mid wet seasons.

They consumed immature liane leaves more than any other item during the dry–wet transition and early wet seasons (April to June), contributing between 4.7 and 55.1% of records each month. Lowest values were recorded in August (mid wet season), when they comprised only 2.2% of feeding observations. Although young leaves from trees were never the major item in any month, percentage consumption per month ranged between 3.2 and 24.4%, the highest values being in February and June.

Mature liane leaves were the most important food item during the mid wet season, comprising 72.3% of all feeding records in August. During the wet–dry transition, however, only 4.9% of records are for mature liane-leaf consumption.

Selection of Food Classes

Correlations between proportions of items in the annual diet and measures of plant part production may be used to indicate preference (Newton, 1984; Yeager, 1989; Stanford, 1991). I calculated Spearman rank correlation coefficients for the consumption of major food classes in relation to their weighted phenological abundance or abundance units for trees and lianes, respectively. The strongest positive correlations between consumption and abundance ($p < 0.001$) are for tree-fruit consumption and

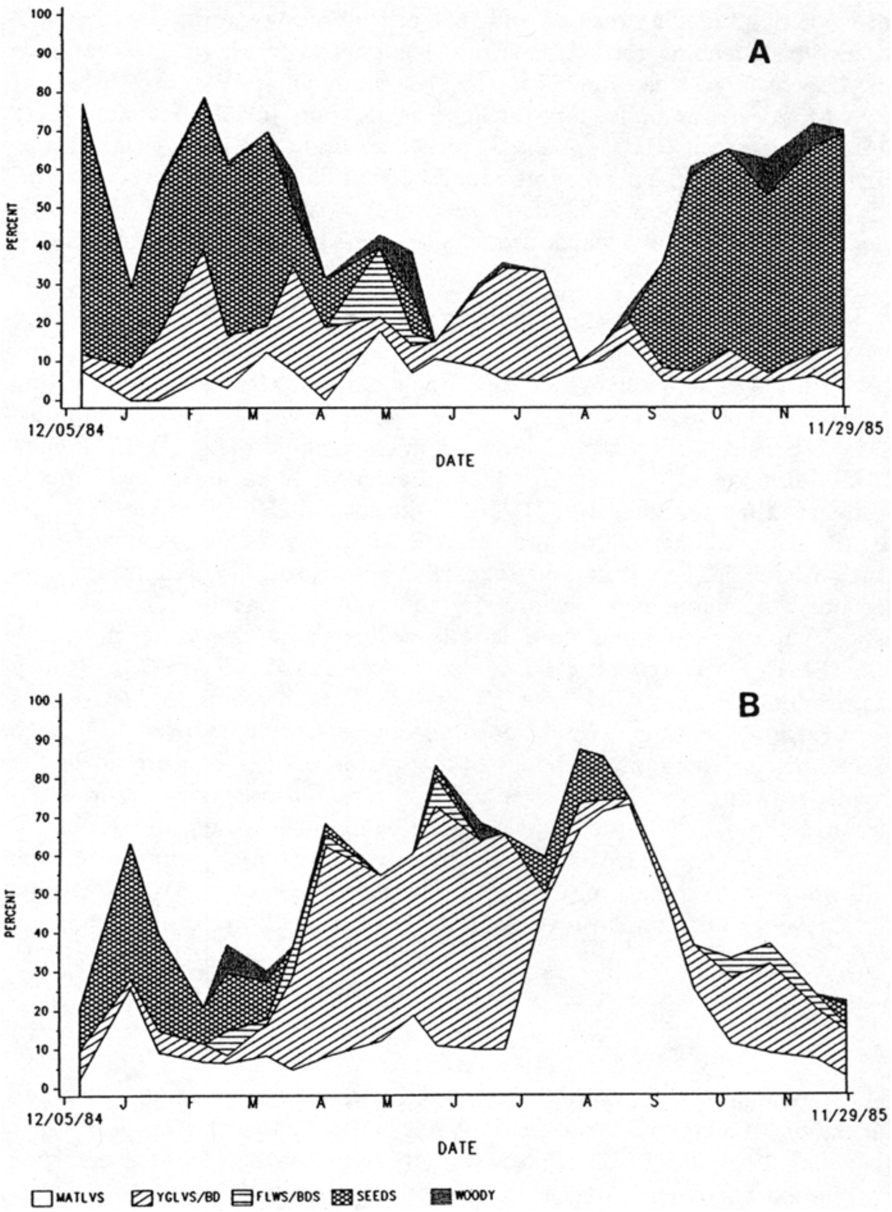


Fig. 4. Relative frequencies (per follow) of identified food items in the diet of *C. polykomos.* (A) Items eaten from trees; (B) items eaten from lianes. MATLVS, mature leaves; YGLVS/BD, young leaves/buds; FLWS/BDS, flowers/buds.

availability: mature tree-fruit consumption and mature tree-fruit/seed abundance ($r_s = 0.750$), young tree-fruit 3 consumption and young tree-fruit/seed abundance ($r_s = 0.743$), and mature tree-fruit consumption and young tree-fruit/seed abundance ($r_s = 0.614$). There is also a highly significant negative correlation between liane fruit abundance and mature leaf feeding ($r_s = -0.696, p < 0.001$). These correlations suggest that fruits or their seeds or both are preferred food items and that mature leaves are consumed only when preferred items are not available.

Selection of Specific Items

The phenological records represent overall forest production, including species that are not consumed. It is possible that selection of specific young and mature leaves is hidden by these general correlations or that seed selection is overemphasized. Therefore, for the 12 dietary items for which phenological records are available (together representing 36.5% of the annual diet), I plotted abundance against dietary records (Fig. 5) and ran Spearman correlations.

Seeds of *P. macrophylla* (both unripe class 3 and ripe) show very strong correlations between consumption and availability ($r_s = 0.878$ and $0.883, p \leq 0.001$); this is also true for young leaves of *Alstonia boonei* (Apocynaceae) ($r_s = 0.747, p \leq 0.001$). Correlation of consumption of mature seeds of *Pycnanthus angolensis* (Myristicaceae) with abundance is less strong, but still significant ($r_s = 0.367, p \leq = 0.039$). Consumption of *P. angolensis* mature leaves is not correlated significantly with production but is inversely related to availability of seeds of *P. angolensis* and young leaves of *A. boonei* ($r_s = -0.380, p \leq 0.05$; $r_s = -0.583, p \leq 0.01$; respectively). This indicates that these leaves are fed upon only when preferred items are not available. Furthermore, plots of seed and mature leaf production by *P. angolensis* against consumption (Fig. 5) do not show the very close correspondence between abundance and diet seen for seeds of *P. macrophylla* and young leaves of *A. boonei*.

Correlations between production and consumption of flowers and flower buds of *M. leonensis* ($r_s = 0.878, p \leq 0.001$) and of seeds and young leaves of *Strychnos* sp. UL11 are very strong ($r_s = 0.862$ and $r_s = 0.667$, respectively; $p \leq 0.001$). The percentage of young leaves taken from *M. leonensis* is less strongly correlated with abundance but still significant ($r_s = 0.351, p \leq 0.05$). Plots of production against consumption suggest that this item is heavily selected before it is widely available, at which time attention switches to young leaves from other, less common and widespread liane species such as *Strychnos* sp. UL11. Young leaf feeding upon *Strychnos*

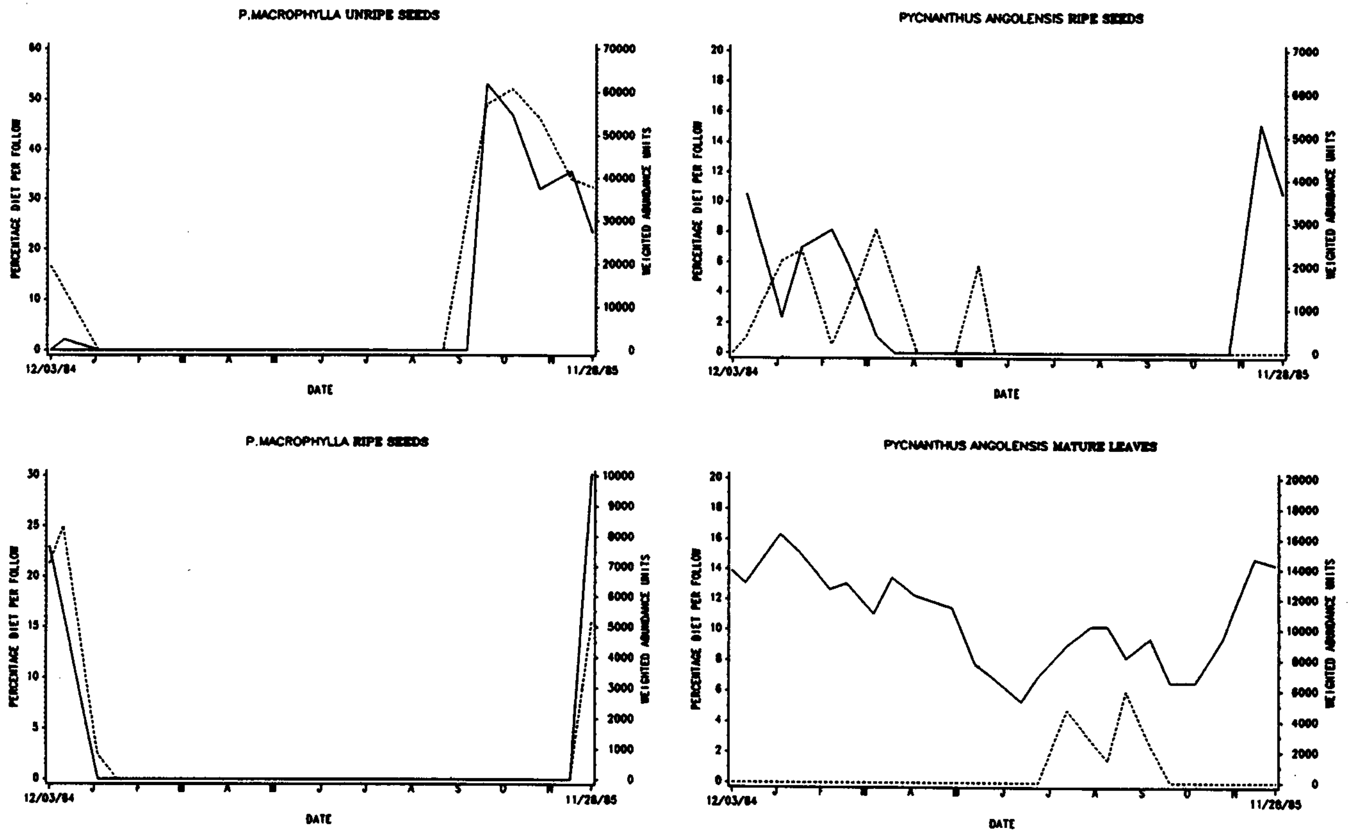
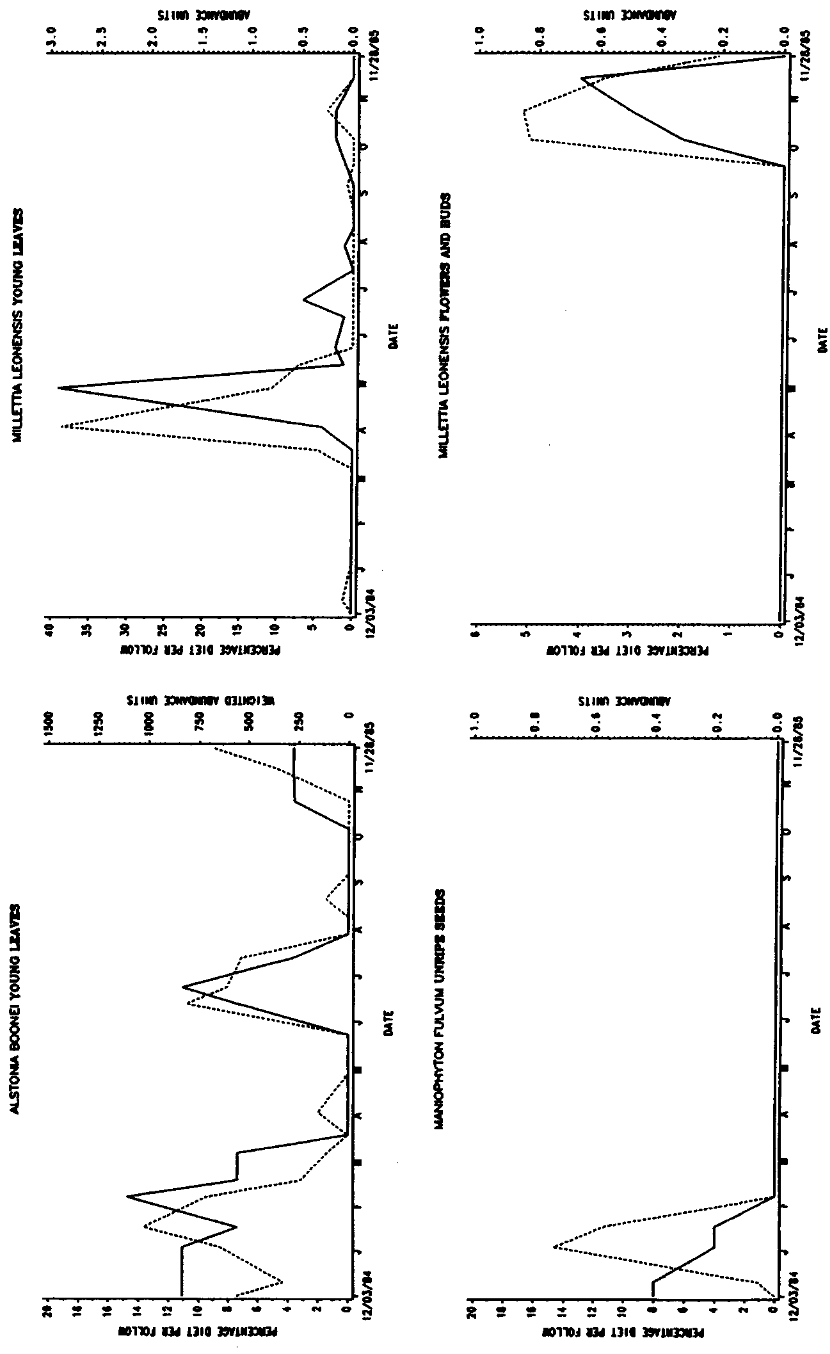


Fig. 5. Availability of food items of *C. polykomos* measured by phenological sampling (solid lines), compared with their consumption as measured by scan sampling of group CT (dashed lines).



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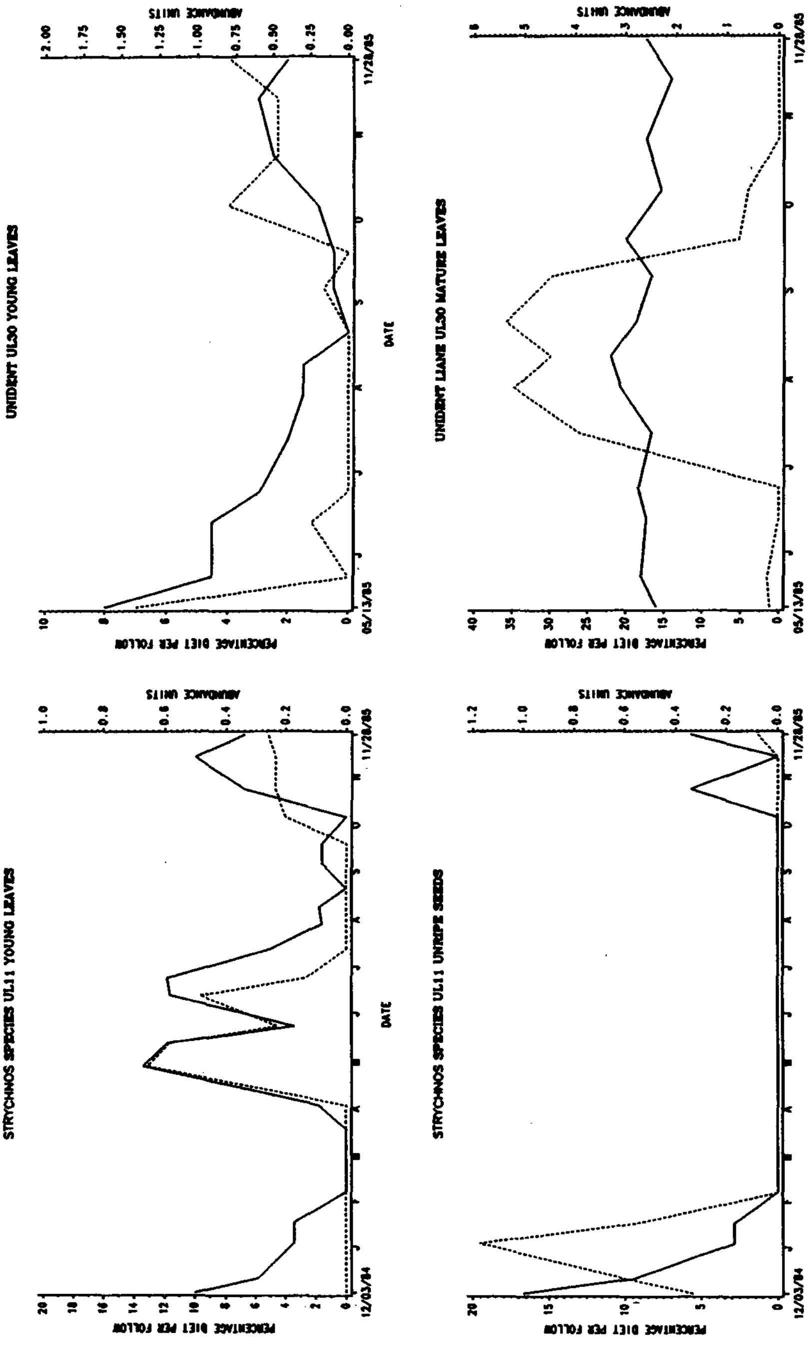

Fig 5. Continued

closely follows production in the early rains but not in the late wet season and the dry season — when seeds are available.

Correlations between consumption and availability for mature and young leaves of unidentified liane UL30 are not significant, though abundance and consumption of mature leaves are nearly so. This further indicates that mature leaf consumption occurred only when preferred items were not available.

Ripeness of Fruits and Seeds Selected

Although the majority of consumed seeds was unripe, my impression is that *C. polykomos* was not "avoiding" ripe seeds but began feeding on seeds when they attained full size (and presumably of maximum nutritive value). For all but the most common species — *P. macrophylla* — this resulted in the virtual elimination of these seeds before maturity was achieved. The same may be true of liane fruits of *Strychnos* spp., which were not seen to reach maturity. However, fruits that become fleshy upon ripening were eaten only when unripe — liane (UL31) fruits were taken whole by *C. polykomos* when unripe but not when bright orange with soft flesh surrounding the seed. Similarly, *Hannoa klaineana* (Simaroubaceae) was not eaten once fruits became dark purple and their pulp softened. Both these fruits, when ripe, were consumed by *Cercopithecus* spp.

Phytochemical Aspects of Food Selection

Mature tree leaves eaten by *C. polykomos* had, on average, lower protein and lower fiber levels than leaves that were not consumed (Table IIA), but these differences are not significant (Mann–Whitney *U*). I included few mature liane leaves in phytochemical tests, but two unidentified species (coded UL30 and UL31) had high levels of protein and average to low fiber levels. Both contained more protein than mature tree leaves do (Table IIB). The presence of inhibitory chemicals may be more important in the selection of mature leaves from trees than the levels of protein and fiber; for instance, phenols seem to be more consistently avoided by *C. polykomos* than by the other Tiwai colobines (G. L. Dasilva, unpublished data).

A comparison of the protein and fiber values in eaten and avoided young tree leaves shows that those selected have, on average, less fiber, though protein values for both groups are similar (Table IIC). The number of species tested is small, variability between values is high, and the difference in fiber content is not statistically significant (Mann–Whitney *U*). Some young leaves may have been selected for nutrients other than protein

Table II. Nutrient Composition of Foods Consumed by *C. polykomos* Group CT, Compared with Available items that Were Not Eaten[a]

	Protein	Fiber	Protein/ Fiber	Energy
(A) Mature tree leaves				
Species eaten				
Alstonia boonei	10.6	36.4	0.29	23.4
Cleistopholis patens	12.6	38.2	0.33	19.1
Cynometra leonensis (mlr)	13.5	53.1	0.25	19.6
Pycnanthus angolensis	11.7	35.7	0.33	—
Vitex micrantha	13.5	39.8	0.34	—
Mean	12.4	40.6	0.30	20.7
Species not eaten				
Funtumia africana (mlp)	10.4	31.1	0.33	18.67
Hymenocardia lyrata	14.2	35.5	0.40	19.88
Millettia rhodantha	17.4	56.3	0.31	—
Parinari excelsa	10.1	64.0	0.16	—
Pentaclethra macrophylla	17.2	51.6	0.33	—
Piptadeniastrum africanum	19.4	44.5	0.44	—
Terminalia ivorense	34.1	35.1	0.99	19.78
Mean	17.5	45.4	0.42	19.44
(B) Mature liane leaves				
Species eaten				
UL30	18.6	32.6	0.57	20.8
UL31	24.5	46.3	0.53	21.8
Mean	21.6	39.5	0.55	21.3
Species not eaten				
Landolphia hirsuta (mlp)	6.4	30.2	0.21	15.65
Strychnos UL19	13.3	39.5	0.33	22.89
Mean	9.9	34.5	0.27	19.27
(C) Young tree leaves				
Species eaten				
Alstonia boonei	8.7	45.6	0.19	22.6
Albizia ferruginea	23.4	26.7	0.88	20.5
Millettia rhodantha	33.4	15.7	2.13	—
Mean	21.8	29.3	1.07	21.6
Species not eaten				
Afrosersalisia africana	20.2	34.7	0.58	—
Cynometra leonensis	28.9	55.5	0.52	20.47
Hymenocardia lyrata	13.4	26.2	0.51	18.40
Parinari excelsa	11.8	65.6	0.18	17.79
Piptadeniastrum africanum	20.5	48.4	0.42	22.61
Samanea dinklagei	19.3	41.6	0.46	19.89
Mean	19.0	45.3	0.45	19.83

Table II. Continued

	Protein	Fiber	Protein/ Fiber	Energy
(D) Young liane leaves				
Species eaten				
Millettia leonensis	27.1	29.0	0.93	24.5
Strychnos UL11	19.9	19.4	1.03	22.7
Strychnos UL19	21.0	25.0	0.84	22.8
UL30	—	42.0	—	19.2
Mean	22.7	28.9	0.93	24.1
(E) Unripe seeds/fruit				
Species eaten				
Erythrophleum ivorense	24.2	13.0	1.86	20.4
Hannoa klaineana	24.3	14.4	1.69	29.7
Pentaclethra macrophylla	39.1	19.2	2.04	24.2
Samanea dinklagei	19.4	66.4	0.29	—
Strychnos UL11	13.8	12.0	1.15	17.9
Strychnos UL19	13.7	24.3	0.56	—
UL31	21.5	35.8	0.60	24.9
Mean	22.3	26.4	1.17	23.4
Species not eaten				
Funtumia africana	18.0	8.2	2.20	24.6
Holarrhena floribunda	15.6	19.8	0.79	19.7
Plagiosiphon emarginatus	10.3	35.3	0.29	16.3
Pentaclethra macrophylla (unripe fruit stage i)	10.6	25.4	0.42	19.5
Mean	13.6	22.2	0.93	20.0
(F) Ripe seeds/fruit				
Species eaten				
Pycnanthus angolensis (seed)	9.4	27.4	0.34	29.1
Species not eaten				
Hannoa klaineana (pulp)	11.7	29.2	0.40	16.5
Pycnanthus angolensis (aril)	4.4	34.4	0.13	36.5
UL31 (seed + pulp)	21.1	31.5	0.67	24.1
Mammea africana (pulp)	4.4	29.8	0.14	—
Uapaca guineensis (pulp)	3.5	63.6	0.06	—
Nauclea diderrichi (pulp)	5.5	64.4	0.09	—
Mean	8.4	42.2	0.23	25.7

[a] Protein (6.25 N) and fiber (ADF) values are given as percentage of dry weight; energy is kJ g^{-1} of dry weight.

and energy. For example, the protein and fiber contents of young leaves of *A. boonei* indicate poor nutritional value, yet these leaves were a favored item, though they never constituted a large percentage of the diet in any one month or follow.

Immature liane leaves eaten by *C. polykomos* also have low levels of fiber, and the mean protein content of these leaves is quite high (Table IID); the protein level of young leaves of *M. rhodantha* is exceptionally high, at 33.4%.

Phytochemical analyses of seeds (Table IIE and F) indicate that most seeds selected by *C. polykomos* have a high protein content, especially *P. macrophylla* unripe seeds, and often relatively low levels of fiber that are comparable to the levels found in some young leaves.

DISCUSSION

The study group *C. polykomos* consumed foliage more often than fruit and seeds. Not all this foliage is the same, however. Young leaves usually have higher levels of protein and lower fiber content than mature leaves do, and the availability of young leaves, both spatially and temporally, is considerably different from that of mature leaves. Hence, young and mature leaves should be regarded as different food items, and not be lumped as leaves. Seasonal differences in the use of mature and young leaves by *C. polykomos* reinforce this view.

Similarly, differences in the nutritional value of fruit pulp and dry seeds (Table II) (Gaulin, 1979; Sourd and Gautier-Hion, 1986) make the distinction between seeds and whole fruits an important one. Most whole fruits consumed by *C. polykomos* are small berries with little pulp, and it is likely that they were selected for their seeds. Larger fruits from which pulp was consumed seem also to be selected for their seeds — with small amounts of flesh eaten only in the process of seed extraction. They did not eat the pulp of ripe fruit, which is often the principle component of simple-stomached primates' diets (Terborgh, 1983; Gautier-Hion, 1984).

Indicators of Preference for Seeds and Fruits

Spearman correlations show seeds or fruits or both to be generally preferred over other foods; the observed fluctuation in seed/fruit-eating is caused by a marked seasonality of production, which is typical of the dry fruits selected by *C. polykomos* (Frankie *et al.*, 1974; Alexandre, 1980). Although the consumption of liane fruits and seeds is roughly proportional to the amount of liane foliage in the forest, correlations suggest that these items are perhaps preferred to seeds from trees. This might be a genuine preference, with only lower fruit production in lianes preventing higher levels of consumption, but it could equally reflect temporal differences in production and the greater rarity of lianes, which will tend to increase the importance of their fruits in correlations.

The Importance of Legumes

Leguminous trees are important food sources for colobines in southeast Asia (Davies *et al.*, 1988) and are major contributors to the diet of *C. polykomos*. This appears to be a response to high levels of nitrogen in both seeds and leaves. Although the 14.3% of all leaves that are from legumes does not suggest strong preference for these families, which together contribute 45% of large tree biomass in the study area, most legume foliage was taken from species of the family Papilionaceae, which is not particularly common on Tiwai. One species of papilionaceous tree—*Millettia rhodantha*—constitutes 0.47% of large tree biomass, and one liane—*M. leonensis*—contributes perhaps 5–7% of forest foliage. Of the three leguminous families, Mimosaceae both is the most dominant on Tiwai and contributes 23% of feeding time by *C. polykomos.* Mimosaceae also appear to constitute a significant proportion of the diet of *C. satanas* in Lopé (Harrison and Hladik, 1986), while the relative paucity of leguminous species at Douala-Edéa—particularly of Mimosaceae and Papilionaceae—may explain the close relationship between the protein content of seeds and their contribution to the diet of *C. satanas* at this site (McKey *et al.*, 1981).

At another African site where leguminous trees dominate the forest (Salonga National Park, Zaire), Maisels *et al.* (1994) also found that leaves and seeds from legumes make up a large part of the diet of both black-and-white and red colobus.

Stanford (1991) shows significant correlations between both fruit and young leaf availability and consumption by *Presbytis pileata* in Bangladesh. Fruits and seeds selected, however, are *Ficus* and other nonleguminous species; protein levels in these foods are likely to be low, and leaves may continue to be the main protein source in periods of high fruit availability and consumption. Legumes do not appear to be common at Stanford's site, but the time spent feeding on legumes by his main study group, at 11.4% of the total, was greater than their contribution to crown cover. Hence these species appear to be selected for.

Seasonality of the Study Group Diet

Where forest production is seasonal, significant effects on primate diets are common (Chapman, 1987; Stanford, 1991) and hardly surprising. In seasons in which fruit is absent, or when availability of young foliage is low, or when both conditions prevail, there is an inevitable reduction in the contribution that these items can make to the diet. The study group's diet over a 12-month span indicates the flexibility of *C. polykomos*, which switched quite dramatically among the three classes that dominated their diet in different periods: unripe tree seeds, young liane leaves, and mature liane leaves. Liane seeds and young tree leaves also made an important contribution.

Stanford (1991) proposed that seeds are selected as an alternative to leaves when the latter are hard to digest, but selection of seeds and fruits by *C. polykomos* is clearly not a means to compensate for poor-quality foliage. The high proportion of seeds consumed by *C: polykomos*, relative to their abundance, strongly suggests a preference for them, particularly compared to mature leaves, which are available throughout the year and in a much greater quantity. *C. polykomos* are highly selective when feeding on mature leaves, concentrating primarily on lianes, which seem to be more digestible than tree leaves. It is also striking that young leaves predominate in the diet when the abundance of unripe (class 3) or mature seeds and fruit is low; similarly, mature leaves are a major item only when young leaves are at low levels. This pattern of diet suggests considerable selectivity, in that high-quality seasonally available items are consumed when possible, rather than depending upon ever-present lower-quality food sources, such as mature leaves.

Interestingly, on Tiwai, it is the main wet season that is the period of low fruit and young leaf availability, rather than the dry season. This reflects the location of the site — 7°N — and the nature of the vegetation. During the wet season, in the absence of good sources of protein or energy, *C. polykomos* relies on mature leaves, which do not require much expenditure of energy to find and to harvest. Mature liane leaves, which appear to be less heavily protected by secondary chemicals than mature tree leaves, serve as an ideal "fall-back" food, although there is some evidence that the monkeys are not able to meet all their energy needs during this period (Dasilva, 1992).

Nutritional Value of Seeds

Seeds provide a rich source of easily digested carbohydrate or lipid (Waterman, 1984) and also tend to be less fibrous than ripe fruits and leaves are. Furthermore, the very low water content of seeds, compared to fruits and leaves, makes them a richer source of energy, in terms of fresh weight than either of the latter (Dasilva, 1992). Unlike fleshy fruits, seeds also may contain considerable quantities of protein. Levels of protein in seeds eaten by Tiwai colobines are markedly higher than those of fruits eaten by African cercopithecines (Sourd and Gautier-Hion, 1986). They are also similar to levels of protein in leaves, which are usually considered to be the main protein source of primates that do not consume large quantities of insects.

In suggesting that seed-eating in colobines may be a means to avoid interspecific feeding competition, Stanford (1991) assumes that there are fewer competitors for seeds than for ripe, fleshy fruits. However, this is an insufficient explanation for the colobine preference for seeds over mature leaves when the latter are highly digestible and widely available both spatially and temporally, as at Tiwai. Furthermore, competition with other leaf-eating animals appears to be negligible, and it is to be expected that trees will invest more in mechanical and chemical protection of seeds than of leaves. For colobines to take on the task of breaking into seed pods and cases, and of detoxifying protective chemicals, there should be an additional advantage to that of avoiding competition. For the Tiwai *C. polykomos*, this advantage is that by feeding upon seeds and fruit, they are able to maximize both energy and protein intake. Seasonal availability is clearly important. For example, it must be assumed that *C. polykomos* would eat more seeds if they were available for a longer period.

Seed-eating in colobines is linked to the high levels of lipids and carbohydrates in seeds, and it provides more than enough energy to meet the daily needs of my study group (Dasilva, 1992). In some cases, however, seeds may not fulfil protein requirements. This leads to the prediction that, where the protein content of seeds is high, as in certain leguminous species, seeds will be preferred, even to young leaves, since both energy and protein needs can be met. However, in habitats in which the protein content of seeds is lower than that of leaves, a combination of fruits, seeds, and young foliage should be selected to maintain protein and energy intakes. Achieving such "optimal" diets, however, will be constrained by factors such as body size and, particularly, habitat seasonality, which can limit the availability of preferred foods. During lean seasons, leaf quality and the ability of an animal to digest mature foliage will become important. Far from restricting them to a specialist diet, it seems that the forestomach fermentation system of colobines allows them to exploit a wide variety of foods, many of which cannot be eaten by sympatric cercopithecines.

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