

Feeding Ecology of Guerezas in the Kakamega Forest, Kenya: The Importance of Moraceae Fruit in Their Diet

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Eastern black-and-white colobus (Colobus guereza), or guerezas, have long been considered to be one of the most folivorous primates. I conducted a study of the feeding ecology of two guereza groups (T and O) over an annual cycle in the Kakamega Forest of western Kenya. I found that the annual diets of both groups comprised mostly of leaves (T: 48%, O: 57%) though fruit (T: 44%, O: 33%) also accounted for a substantial portion of the diet. In the six months when fruit was most abundant, fruit consumption constituted an average of 58% of T-group's monthly diet and 42% of O-group's monthly diet. In contrast to most previous studies of colobines, in which seeds were the primary fruit item consumed, almost all of the fruit eaten by guerezas at Kakamega consisted of whole fruits. At least 72% of the whole fruits consumed by T-and O-groups were whole fruits from trees in the Moraceae family, which dominates the tree family biomass at Kakamega. Unlike at sites where guerezas consumed fruit primarily when young leaves were scarce, at Kakamega guerezas ate fruit in accordance with its availability and irrespective of the availability of young leaves. My findings demonstrate that guerezas are more dietarily flexible than was previously known, which may help to explain why the species can survive in such a wide variety of forested habitats across equatorial Africa.

KEY WORDS: *Colobus guereza*; frugivory; folivory; Moraceae; *Prunus africana*.

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INTRODUCTION

Since the 1970s, through long-term field studies of nonhuman primates, researchers have sought to determine how diet varies with spatiotemporal differences in food availability (Oates, 1977a; Milton, 1980; Cords, 1987; Strier, 1991; Silver *et al.*, 1998; Kaplin and Moermond, 2000). One subfamily of primates that has long been of particular interest to researchers investigating primate feeding ecology is the colobine monkeys (Struhsaker, 1975; Hladik, 1977; Oates, 1977a). Colobines are characterized by an enlarged forestomach in which microbial fermentation of food items occurs (Chivers, 1994; Kay and Davies, 1994). This adaptation allows them to exploit food sources that cannot be eaten by primates lacking specialized forestomachs. Early researchers assumed that this dietary specialization arose to allow colobines to feed on otherwise indigestible leaves (Andrews and Aiello, 1984), but recent work suggests that this adaptation may have initially served to cope with the indigestible compounds and toxins in seeds (Chivers, 1994; Waterman and Kool, 1994; Lambert, 1998).

The numerous studies completed on colobine diets show that considerable variation in diet exists among species of colobine monkeys. The most common component in the diet is young leaves for some colobine populations (Struhsaker, 1975; Oates, 1988; Kool, 1989), mature leaves for others (Stanford, 1991; Newton, 1992), seeds for others (McKey *et al.*, 1981; Harrison, 1986), and whole fruit for still others (Starin, 1991). While colobines are consistently more folivorous than most other primates, most researchers now agree that it is overly simplistic to classify most colobines as merely folivorous (Stanford, 1991; Dasilva, 1994; Maisels *et al.*, 1994; Oates, 1994).

Eastern black-and-white colobus (aka guerezas), *Colobus guereza*, are among the most folivorous colobines (Clutton-Brock, 1975; Oates, 1977a; Bocian, 1997). Both Oates (1977a) and Bocian (1997) concluded from long-term studies that guerezas exhibit a dietary preference for young leaves and are specially adapted to exploit foliage. Three of the four other species of black-and-white colobus—*Colobus satanas*, *C. polykomos*, and *C. angolensis*—appear to be more granivorous than guerezas (McKey *et al.*, 1981; Harrison, 1986; Dasilva, 1994; Maisels *et al.*, 1994), and Oates (1977a, 1994) attributed the guereza's greater reliance on leaves to its adaptation to life in gallery and dry forests.

I present results of a long-term study of diet and food choice in guerezas in the Kakamega Forest, Kenya. These results show that guerezas have greater dietary flexibility than was previously believed.

METHODS

Study Site

The Kakamega Forest (0°19' N; 34°52' E; Elev. 1580m) is an island of Guineo-Congolian rain forest in western Kenya (Wass, 1995). The 2-km² study site of Isecheno is part of a forest block that was last estimated to be 86 km² in size (Brooks *et al.*, 1999). Isecheno is subject to some human disturbance and is characterized by heavy undergrowth and a relatively open canopy in some areas. An irregular grid of trails at 50-300-m intervals facilitates primate research (Cords, 1987). Rainfall patterns were monitored at the Kakamega Meteorological Station approximately 20 km from the study site.

Subjects

Guerezas are one of five species of black-and-white colobus inhabiting the forests of tropical Africa (Oates and Trocco, 1983). Their range stretches from Ethiopia to Nigeria and they inhabit a wide range of forest types (Ullrich, 1961; Schenkel and Schenkel-Hulliger, 1967; Leskes and Acheson, 1971; Dunbar and Dunbar, 1974; Oates, 1977a,b; Rose, 1978; Kruger *et al.*, 1998). Guerezas are among the largest of Africa's arboreal monkeys with adult males averaging 11.8 kg and adult females 8.6 kg (Oates *et al.*, 1994).

I collected dietary data over a 12-month period between March 1997 and February 1998 as part of a larger study of guereza behavioral ecology at Isecheno, which I conducted in July 1993, November-December 1995, November 1996-March 1998, and August 1998. Over the course of the study, I observed guerezas for > 3,000 hours. My dietary study included two habituated study groups, T and O, which occupied adjacent ranges with an average of 20.3% overlap (Fashing, 2001). O-group's range bordered the forest edge on one side, while T-group only rarely ventured to the forest edge. O-group was composed of 5-8 individuals between November 1996 and March 1998, including 1 adult male, 3 adult females, 0-1 juveniles, and 1-3 infants. T-group was composed of 10-13 individuals during the same period, including 1-4 adult males, 5 adult females, 3-4 juveniles, and 0-4 infants.

Forest Composition

Under my supervision, Messrs. Benjamin Okalla and Wilberforce Okeka, forest guides with extensive knowledge of the local flora and considerable experience conducting scientific research at Kakamega (Copeland

et al., 1996; Fashing, 1999b), surveyed the large trees of Isecheno. We created a series of vegetation transects which followed 8 existing trails, each of which passed through the home range of at least one of the two study groups. Transect area totalled 1.1 ha in T-group's range and 1.3 ha in O-group's range, and exceeded 5% of the total home range area for both groups.

We identified to species all trees ≥ 20 cm girth at breast height (GBH) ≤ 5 m from the center of the transect, assigned them to a particular 25×10 -m quadrat, and enumerated them. I converted GBH to diameter at breast height (DBH), and calculated basal area (BA) for each tree from the DBH value using the formula:

$$BA = [.5 \times DBH]^2 \times \pi.$$

I used BA per hectare to estimate each tree species' biomass within the home range of each group per Kool (1989).

Forest Phenology

To produce a quantitative measure of food availability, I monitored the phenological patterns of 109 trees in T-group's range and 101 trees in O-group's range on a monthly basis. Range here refers to those areas entered by the study groups during preliminary observations from November 1996–February 1997. I chose 13 tree species for phenological monitoring because (1) they were also monitored by Oates (1977a) at Kibale [*Celtis africana*, *Celtis gomphophylla* (syn. *C. durandii*), *Ficus exasperata*, *Funtumia africana* (syn. *F. latifolia*), *Markhamia lutea* (syn. *M. platycalyx*), and *Trilepisium madagascariense* (syn. *Bosqueia phoberos*)], (2) they were common at Kakamega (*Croton megalocarpus*), or (3) they contributed to the diet of guerezas at Kakamega during preliminary observations [*Albizia gummifera*, *Antiaris toxicaria*, *Morus mesozygia* (syn. *M. lactea*), *Prunus africana*, *Teclea nobilis*, and *Zanthoxylum gillettii* (syn. *Fagara macrophylla*)].

I conducted the phenological assessment of the trees in a group's range 1–4 days after I completed monthly dietary data collection for the group. I determined the relative abundance of leaf buds, young leaves, mature leaves, flowers, whole fruits, and seeds on each tree using Leitz 8×40 binoculars. Fruits composed of pulp and small seeds, e.g., *Ficus exasperata*; *Teclea nobilis*, or those with large seeds surrounded by pulp from which guerezas generally consumed the pulp, e.g., *Antiaris toxicaria*; *Trilepisium madagascariense*, were considered to be whole fruits. I pooled unripe and ripe whole fruits as it was often difficult to distinguish confidently between the two whole fruit categories in the upper canopy. I divided whole fruits for certain species, such as *Antiaris toxicaria* and *Trilepisium madagascariense*, into small (inedible) and

large (edible) categories because the size of fruits in these species appeared to have an influence on whether guerezas chose to eat them. I categorized fruits composed primarily of seeds, and for which seeds were the fruit item eaten, as seeds for the purposes of phenological monitoring: *Albizia gummifera* and *Zanthoxylum gillettii*. I pooled flower buds and flowers as flowers because it was often difficult to distinguish between them.

I scored plant parts at intervals of 0.5 on a scale of 0.0 to 4.0 with 4.0 representing the score for a tree with the plant part at its greatest possible abundance, i.e. when the canopy was maximally laden with that part. I also assigned scores of very few and few to plant parts and gave them numeric values of 0.05 and 0.10.

I computed a food item availability index (FAI) based on the monthly phenology scores and tree species biomass values for each study group (Dasilva, 1994:661) using the following formula:

$$\text{FAI} = \text{average availability score} \times \text{basal area for species } i$$

For 9 tree species, *Antiaris toxicaria*, *Celtis africana*, *Croton megalocarpus*, *Ficus exasperata*, *Funtumia africana*, *Morus mesozygia*, *Prunus africana*, *Trilepisium madagascariense*, and *Zanthoxylum gillettii*, only individuals ≥ 125 cm GBH (40 cm DBH) are included in the tree species biomass estimates for fruit availability because they appeared not to fruit until they were ≥ 125 cm GBH. I assumed that the density of fruits per m^3 is the same for all fruit tree species. Although this assumption may be simplistic, it probably does not greatly affect abundance indices because many of the major fruiting trees that were phenologically monitored, e.g., *Antiaris toxicaria*, *Ficus exasperata*, *Morus mesozygia*, *Trilepisium madagascariense*, appeared to have similar volumes of fruit when their canopies were laden.

Diet

I collected feeding data on 5 consecutive study days each month for both groups from March 1997-February 1998. 5-day samples for T-group began between the 1st and the 4th of each month, while 5-day samples for O-group began between the 14th and the 18th of each month. During 5-day samples, I conducted activity scan samples of 5-min duration every 15 min from dawn-to-dusk. I collected data on up to the first 6 adults or juveniles and all infants ≥ 2 months old seen at the time of each scan. I set the cut-off at 6 adults and juveniles when it became clear that 6 was the maximum number of large individuals that I could scan before it was difficult to avoid counting the same individuals twice during the scan. In practice, however, limited visibility in the forest ensured that this cut-off was rarely reached.

I recorded the following activities during scan sampling: rest, move, feed, or social (Fashing, 1999a). The activity recorded for each individual was the first activity that lasted ≥ 3 sec once the individual was sighted. This requirement that activities persist for 3 secs eliminated eye-catching, but ephemeral activities from being overrepresented in the data set.

If a monkey was feeding at the time of a scan, I recorded the plant species and food item upon which it was feeding. Feeding is any occasion during which a monkey plucked food items, pulled food items towards its mouth, masticated, or swallowed. I designated food items as leaf buds, young leaves, mature leaves, unclassified leaves (leaves of undetermined age), whole fruit, seeds, flowers, bark, or unidentified.

I measured monthly dietary overlap between groups in terms of species-specific food items by calculating the percent overlap in the consumption of each dietary item for each plant species between T- and O-groups for each pair of monthly 5-day samples. I calculated yearly dietary overlap in terms of species-specific food items by taking the mean of the 12 monthly values for dietary overlap between the two groups.

I measured dietary diversity and evenness via the Shannon-Weaver index, H' , and the evenness index, J . The formula for dietary diversity is:

$$H' = - \sum_{i=1}^s p_i \log p_i$$

in which s is the number of species, and p_i is the proportion of the total number of individuals represented by the i th species. The formula for dietary evenness is:

$$J = H'/H' \text{ maximum}$$

J provides a measure of how evenly the different food tree species were represented in the diets of the study groups each month. Potential scores range from 0 (most even) to 1 (least even).

I calculated selection ratios for food species in the diets of the two colobus groups as a means of measuring dietary selectivity. A food species that is selected is eaten more frequently than expected based on its proportional representation in the forest. I used two formulae to calculate selection ratios, one based on the stem densities of different tree species and the other based on the basal area (BA) of different tree species:

1. Selection ratio = $\frac{\% \text{ of annual feeding time spent feeding on species } i}{\% \text{ of total stem density contributed by species } i}$
2. Selection ratio = $\frac{\% \text{ of annual feeding time spent feeding on species } i}{\% \text{ of total BA contributed by species } i}$

In addition, I examined the manner in which diet varied with temporal changes in food availability. To investigate this topic, I calculated Spearman rank-order correlation coefficients (r_s) between food item consumption and food item availability.

RESULTS

Rainfall

A total of 1859 mm of rain fell at the Kakamega Meteorological Station in Kakamega town between March 1997 and February 1998. As in many tropical rain forests, there was considerable month-to-month variation in rainfall at Kakamega during the study period (Figure 1). Rainfall patterns for the year of study were atypical in that the dry season that normally occurs between December and February did not occur because of an El Niño event.

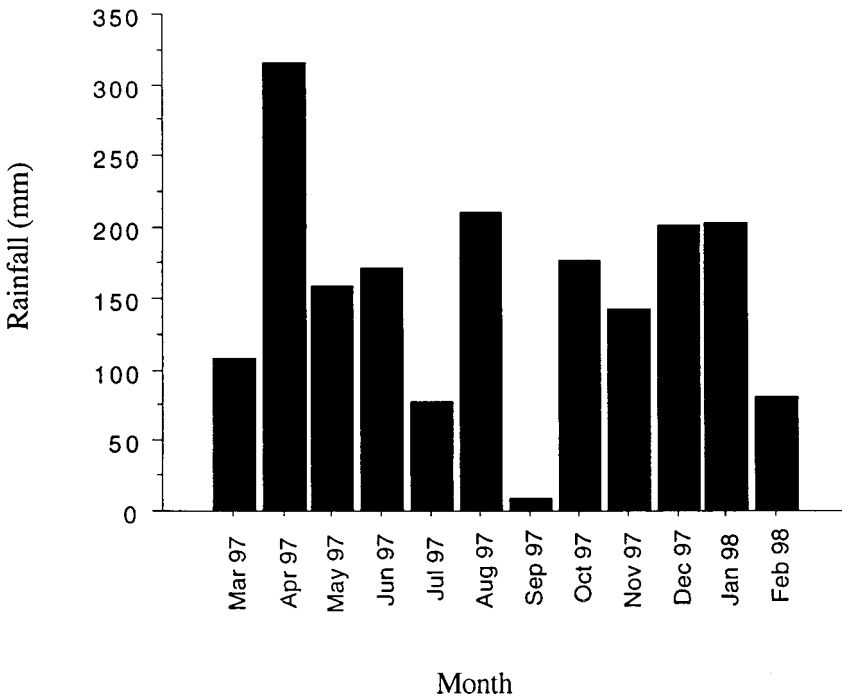


Fig. 1. Rainfall pattern in Kakamega town over the 12 months for which dietary data are presented.

Forest Composition

A total of 65 tree species in 33 families were within the vegetation transects. T-group had 57 tree species in 30 families in its 1.1 ha of transects, while O-group had 54 tree species in 29 families in its 1.3 ha of transects. T-group's range featured a much greater stem density (617.2 stems/ha) than that of O-group's range (407.7 stems/ha), probably due to the greater level of human disturbance and harvesting of small trees in O-group's range. The stem density for large trees (≥ 125 cm GBH) was actually slightly higher for O-group (84.6 stems/ha) than for T-group (80.9 stems/ha).

There was considerable overlap between the two groups in the species that ranked among the top 20 tree species in their home ranges. Twelve species were among the 20 most common tree (≥ 20 cm GBH) species in the ranges of both groups, and overall overlap in species stem density between the ranges of the two groups was 66.3%. Fourteen species were among the 20 highest-ranking trees in terms of biomass in the ranges of both groups (Table I) and overall overlap in species biomass between the ranges of the two groups was 70.3%. The Moraceae, which includes all the fig species, was the top tree family in terms of both stem density and biomass in the ranges of both study groups. Trees of Moraceae made up 19.0% of the stems and 52.5% of the biomass in T-group's range and 21.7% of the stems and 44.9% of the biomass in O-group's range. No other tree family was nearly as well-represented in the forest. In fact, based on the values presented here, it could be argued that the Moraceae dominate the large tree biomass of the Isecheno study area.

Forest Phenology

Mature leaves were the most abundant item (in terms of food availability index units/ha) in the ranges of both study groups and were available in large quantities throughout the year. Two items important in the diets of both study groups, fruit and young leaves, varied considerably in FAI units/ha from month to month.

Figure 2 shows the monthly patterns of fruit availability within the ranges of the two study groups. T-group had more fruit available per hectare than O-group during 11 of 12 months. This difference in fruit availability between the home ranges of the two groups is significant (Wilcoxon S.R.; $n = 12$; $p = .008$). Conversely, over the course of the year, there is no significant difference between the two groups in the amount of young leaves available to them per hectare (Figure 3; Wilcoxon S.R.; $n = 12$; $p = .433$).

Table 1. The 20 highest-ranking trees in terms of biomass (basal area per ha) along transects in the home ranges of groups T and O

T-Group				O-Group					
Rank	Species	Family	Basal area/ha (cm ² /ha)	% total biomass	Rank	Species	Family	Basal area/ha (cm ² /ha)	% total biomass
1	<i>Ficus exasperata</i>	Moraceae	86734	18.0	1	<i>Ficus thonningii</i>	Moraceae	62854	12.2
2	<i>Ficus thonningii</i>	Moraceae	73719	15.3	2	<i>Ficus exasperata</i>	Moraceae	56941	11.1
3	<i>T. madagascariense</i> [†]	Moraceae	48039	10.0	3	<i>T. madagascariense</i> [†]	Moraceae	54466	10.6
4	<i>Antiaris toxicaria</i>	Moraceae	40355	8.4	4	<i>Albizia gummifera</i>	Mimosaceae	37416	7.3
5	<i>Croton megalocarpus</i>	Euphorbiaceae	37775	7.9	5	<i>Croton megalocarpus</i>	Euphorbiaceae	27948	5.4
6	<i>Celtis africana</i>	Ulmaceae	25711	5.3	6	<i>Celtis africana</i>	Ulmaceae	27356	5.3
7	<i>Funtumia africana</i>	Apocynaceae	24841	5.2	7	Urid <i>Ficus</i> species	Moraceae	25876	5.0
8	<i>Albizia gummifera</i>	Mimosaceae	18498	3.8	8	<i>Funtumia africana</i>	Apocynaceae	25490	5.0
9	<i>Prunus africana</i>	Rosaceae	16126	3.4	9	<i>Bischoffia javanica</i> [*]	Euphorbiaceae	24983	4.9
10	<i>H. madagascariensis</i> ^z	Guttiferae	10673	2.2	10	<i>Antiaris toxicaria</i>	Moraceae	20843	4.1
11	<i>Polyscias fulva</i>	Araliaceae	10629	2.2	11	<i>Toona ciliata</i>	Meliaceae	19776	3.8
12	<i>Maesopsis eminii</i>	Rhamnaceae	10149	2.1	12	<i>Olea capensis</i>	Oleaceae	19024	3.7
13	<i>Strombosia scheffleri</i>	Olacaceae	8405	1.7	13	<i>Aningeria altissima</i>	Sapotaceae	11396	2.2
14	<i>Blighia unijugata</i>	Sapindaceae	6542	1.4	14	<i>Bridelia micrantha</i>	Euphorbiaceae	11260	2.2
15	<i>Croton sylvaticus</i>	Euphorbiaceae	6477	1.3	15	<i>Cordia africana</i>	Boraginaceae	8165	1.6
16	<i>Diospyros abyssinica</i>	Ebenaceae	5114	1.1	16	<i>Croton sylvaticus</i>	Euphorbiaceae	8000	1.6
17	<i>B. oblancoelatum</i> [*]	Sapotaceae	4515	0.9	17	<i>Blighia unijugata</i>	Sapindaceae	7012	1.4
18	<i>Markhamia lutea</i>	Bignoniaceae	4432	0.9	18	<i>Strombosia scheffleri</i>	Olacaceae	6926	1.3
19	<i>Morus mesozygia</i>	Moraceae	3186	0.7	19	<i>Prunus africana</i>	Rosaceae	5962	1.2
20	<i>Bridelia micrantha</i>	Euphorbiaceae	3164	0.7	20	<i>Markhamia lutea</i>	Bignoniaceae	5438	1.1

[†] *Trilepisium madagascariense*.

^z *Harungana madagascariensis*.

^{*} The estimate of basal area per hectare for *Bischoffia javanica* is greatly inflated for O-group's range because the species was planted solely along the edges of trails which are where all vegetation surveys were carried out.

^{*} *Bequaertiodendron oblancoelatum*.

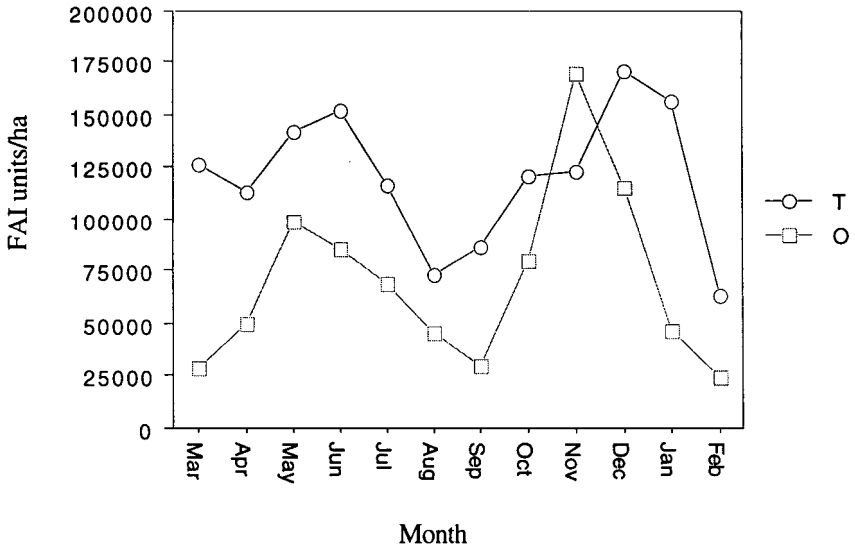


Fig. 2. Monthly variation in whole fruit availability in FAI units/ha for 13 shared phenology tree species in the ranges of groups T and O from March 1997-February 1998. Wilcoxon Signed Ranks Test, $p = .008$.

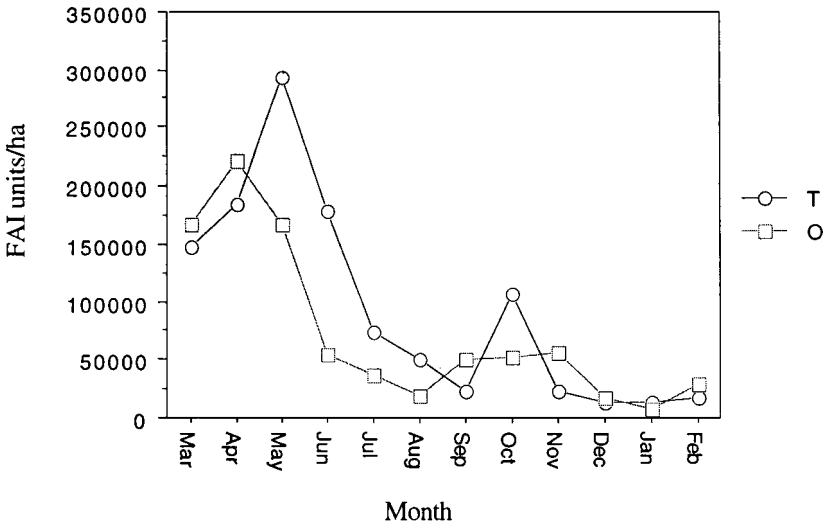


Fig. 3. Monthly variation in young leaf availability in FAI units/ha for 13 shared phenology tree species in the ranges of groups T and O from March 1997-February 1998. Wilcoxon Signed Ranks Test $p = .433$; not significant.

Table II. Percent plant part composition in the annual diets of groups T and O

Plant part	T Group (n = 2211)	O Group (n = 2043)
Leaf buds	2.5	4.1
Young leaves	21.7	19.1
Mature leaves	4.6	8.6
Unclassified leaves	19.3	25.6
Total leaves	48.1	57.4
Seeds	1.4	1.0
Whole fruits	42.6	32.1
Total fruits + seeds	44.0	33.1
Flowers	0.7	0.2
Bark	1.4	3.5
Unclassified items	5.7	5.7
	100.0	100.0

Diet

More than 89% of the overall diet in both study groups consisted of leaves and whole fruit (Table II). Both groups also spent a relatively small percentage of time feeding on bark, seeds, and flowers. Soil was occasionally consumed by O-group, though no record of soil-feeding appears in the activity scan samples. Drinking was also a rare behavior and occurred only at water-filled treeholes. I never saw faunivory though it is likely that the monkeys ingested insects, such as parasitic wasp larvae in figs, along with the whole fruit from some fruit trees.

Bark accounted for a relatively small proportion of the overall diet, but groups periodically made long journeys to feed on bark from two eucalyptus trees (*Eucalyptus* sp.), that had been planted on the edge of the forest (Fashing, 2001). O-group also consumed the bark of several bottlebrush trees (*Callistemon* sp.), that had been planted in their range.

Based on data in Table II, both groups appeared to spend a greater proportion of time feeding on young leaves than on mature leaves. However, a large percentage of the leaves consumed by members of both groups could not be identified as young or mature with absolute certainty. These leaves were labelled as unclassified leaves, many of which were from *Prunus africana*. Most of the unclassified leaves from *Prunus africana* were probably mature, but poor visibility into many trees of *P. africana* precluded confirmation of this impression.

The diets of the two study groups differed primarily in the relative proportion of time each group spent feeding on leaves and whole fruit. During the 12-mo period, T-group spent 10.5% more time feeding on whole fruit and 9.3% less time feeding on leaves than O-group did.

Table III. Percent monthly plant part consumption in groups T and O

Month	Leaf	Young	Mature	Unclass	Total	Fruit	Seeds	Total			
	Buds	Leaves	Leaves	Leaves	Leaves			Fruit	Flowers	Bark	Uid
	T-Group										
3/97	0	19	10	11	40	48	0	48	0	2	11
4/97	8	35	2	5	51	45	0	45	0	0	4
5/97	0	24	11	18	52	47	0	47	0	0	2
6/97	0	37	1	14	53	45	0	45	0	1	2
7/97	0	29	1	23	53	36	0	36	7	0	4
8/97	0	17	12	41	69	26	0	26	0	0	5
9/97	0	7	8	36	50	38	0	38	0	0	11
10/97	0	20	1	20	41	28	0	28	1	15	14
11/97	0	9	1	7	17	81	0	81	0	1	1
12/97	0	25	1	2	27	68	1	69	0	0	4
1/98	0	25	4	11	40	51	6	57	0	0	3
2/98	18	16	2	23	59	23	12	35	0	0	6
	O-Group										
3/97	10	15	22	12	59	33	1	34	0	1	6
4/97	0	36	3	15	55	36	0	36	0	1	8
5/97	0	15	4	26	45	48	0	48	0	4	3
6/97	0	23	1	23	46	43	0	43	0	4	8
7/97	0	17	7	57	80	14	1	16	0	1	4
8/97	0	10	29	35	73	17	5	21	0	0	6
9/97	11	9	16	23	58	26	2	28	2	5	7
10/97	0	39	5	24	68	26	1	26	0	0	5
11/97	0	10	1	12	23	67	0	67	0	10	1
12/97	0	24	0	14	37	51	2	52	0	4	6
1/98	0	14	8	20	42	39	0	39	0	11	9
2/98	21	19	2	34	75	14	1	15	0	5	6

Table III shows the monthly variation in time spent feeding on all food items by both groups. Monthly time spent feeding on whole fruit ranged from 23 to 81% in T-group and from 14 to 67% in O-group. T-group spent more time feeding on whole fruit than O-group did during 11 of the 12 months. This monthly difference in level of frugivory between the two groups is significant (Wilcoxon Signed Ranks Test $p = .003$). Monthly time spent feeding on leaves ranged from 17 to 69% in T-group and from 23 to 80% in O-group. Over the course of the study, O-group spent more time feeding on leaves than T-group did during 10 of the 12 months. This disparity in time spent feeding on leaves between the two groups is significant (Wilcoxon Signed Ranks Test $p = .028$).

The annual diets of both groups in terms of plant parts of different species are presented in Tables IV.A and IV.B. Both groups fed on 28 positively identified species, though they also fed on several unidentified vine species and several unidentified tree species. Including both identified and unidentified species, the total number of species consumed during feeding scan samples is unlikely to have exceeded 35–40 for each group.

Table IV.A. Percent of time spent feeding on specific food items (n = 2211) by T-group between March 1997 and February 1998

Species	Family	Leaf Buds	Young Leaves	Mature Leaves	Unclassified Leaves	Fruit	Seeds	Flowers	Bark	Urid	Total
<i>Prunus africana</i>	Rosaceae		4.79	2.35	12.39			0.09	0.05	0.18	19.86
<i>Ficus exasperata</i>	Moraceae		1.31		0.54	10.04				0.18	12.08
<i>Teclea nobilis</i>	Rutaceae		1.94		0.05	7.73		0.50		1.49	11.71
<i>T. madagascariense</i> *	Moraceae				0.18	8.73				1.63	10.54
<i>Antiaris toxicaria</i>	Moraceae					9.77			0.05		9.81
<i>Celtis africana</i>	Ulmaceae	0.86	8.19	0.09	0.32		1.45		0.14	0.09	9.68
<i>Albizia gummifera</i>	Mimosaceae		2.17								3.62
<i>Morus mesozygia</i>	Moraceae	1.67	0.23			1.04				0.09	3.03
<i>Aningeria altissima</i>	Sapotaceae					2.89				0.05	2.94
<i>Piper guineense</i>	Piperaceae		0.23	1.63	1.09						2.94
<i>Zanthoxylum gillettii</i>	Rutaceae		1.13	0.05	0.45			0.14			1.76
<i>Eucalyptus</i> sp.	Myrtaceae								1.09		1.09
<i>Sapium ellipticum</i>	Euphorbiaceae					0.90					0.90
<i>Srombosia scheffleri</i>	Oleaceae			0.36	0.41					0.09	0.86
<i>Ficus sur</i>	Moraceae					0.68					0.68
<i>Olea capensis</i>	Oleaceae		0.05	0.05	0.45						0.54
<i>Markhamia lutea</i>	Bignoniaceae		0.23		0.18						0.41
<i>B. oblanceolatum</i> *	Sapotaceae					0.23				0.09	0.32

(Continued)

Table IV.A. (Continued)

Species	Family	Leaf		Mature Leaves	Unclass Leaves	Fruit	Seeds	Flowers	Bark	Urd	Total
		Buds	Young Leaves								
<i>Ficus lutea</i>	Moraceae		0.09		0.23					0.09	0.32
<i>Maesopsis eminii</i>	Rhamnaceae		0.18							0.05	0.27
<i>Croton syriaticus</i>	Euphorbiaceae		0.14							0.05	0.18
<i>Ficus thonningii</i>	Moraceae			0.05	0.14						0.18
<i>Alangium chinense</i>	Alangiaceae			0.09							0.14
<i>Celtis gomphophylla</i>	Ulmaceae			0.05							0.05
<i>Funtumia africana</i>	Apocynaceae								0.05		0.05
<i>Polyscias fulva</i>	Araliaceae								0.05		0.05
<i>Premna angolensis</i>	Verbenaceae		0.05								0.05
<i>Strychnos usambarensis</i>	Loganiaceae		0.05								0.05
unidentified <i>Ficus</i> spp.	Moraceae		0.18			0.18				0.09	0.54
type of plant unidentified	Unidentified		0.27	0.09					0.05	1.00	2.85
unidentified vines	Unidentified		0.23	0.14						0.27	1.31
unidentified trees	Unidentified		0.27		0.41	0.23				0.32	1.22

T. madagascariense* = *Trilepisium madagascariense*.B. oblanceolatum* = *Bequartiodendron oblanceolatum*.

Table IV.B. Percent of time spent feeding on specific food items (n = 2043) by O-group between March 1997 and February 1998

Species	Family	Leaf Buds	Young Leaves	Mature Leaves	Unclass Leaves	Fruit	Seeds	Flowers	Bark	Uid	Total
<i>Prunus africana</i>	Rosaceae		1.03	2.45	15.03					0.05	18.55
<i>T. madagascariense</i> *	Moraceae				0.20	11.11				1.47	12.78
<i>Ficus exasperata</i>	Moraceae		1.22		0.54	5.97				0.39	8.13
<i>Celtis africana</i>	Ulmaceae		5.43		1.17				0.05		6.66
<i>Antiaris toxicaria</i>	Moraceae					6.31			0.15		6.46
<i>Teclea nobilis</i>	Rutaceae		0.83		0.05	4.31				0.59	5.78
<i>Piper guineense</i>	Piperaceae		0.54	3.03	1.71					0.05	5.34
<i>Morus mesozygia</i>	Moraceae	4.06	0.93							0.05	5.04
<i>Albizia gummifera</i>	Mimosaceae		3.33	0.10	0.20		0.54		0.15	0.05	4.36
<i>Celtis gomphophylla</i>	Ulmaceae		1.47	1.42	0.54						3.43
<i>Callistemon sp.</i>	Myrtaceae								2.30		2.30
<i>Sapium ellipticum</i>	Euphorbiaceae			0.05		1.81				0.20	2.06
<i>Olea capensis</i>	Oleaceae				1.42					0.15	1.57
<i>Zanthoxylum gillettii</i>	Rutaceae		1.03	0.05	0.10		0.10		0.05	0.20	1.52
<i>B. oblanceolatum</i> *	Sapotaceae					1.37					1.37
<i>Spathodea campanulata</i>	Bignoniaceae		0.29	0.15	0.54			0.20			1.17
<i>Markhamia lutea</i>	Bignoniaceae		0.73		0.10						0.83
<i>Alangium chinense</i>	Alangiaceae		0.24		0.24	0.10			0.05		0.64

(Continued)

Table IV.B. (Continued)

Species	Family	Leaf Buds	Young Leaves	Mature Leaves	Undclass Leaves	Fruit	Seeds	Flowers	Bark	Urd	Total
<i>Eucalyptus</i> sp.	Myrtaceae								0.59		0.59
<i>Ficus thomningii</i>	Moraceae									0.34	0.34
<i>Maesopsis eminii</i>	Rhamnaceae			0.10		0.24				0.05	0.34
<i>Strombosia scheffleri</i>	Oleaceae		0.05		0.10	0.10					0.29
<i>Bridelia micrantha</i>	Euphorbiaceae					0.29					0.29
<i>Polyscias fulva</i>	Araliaceae					0.24					0.24
<i>Albizia grandibracteata</i>	Mimosaceae		0.20								0.20
<i>Anungeria altissima</i>	Sapotaceae					0.15					0.15
<i>Ficus lutea</i>	Moraceae		0.10								0.10
<i>Bischoffia javanica</i>	Euphorbiaceae					0.05					0.05
unidentified <i>Ficus</i> spp.	Moraceae			0.05	0.83					0.05	0.93
type of plant unidentified	Unidentified		0.29	0.44	0.73				0.05	1.62	3.13
unidentified vines	Unidentified		1.32	0.44	1.86		0.39			0.34	4.36
unidentified trees	Unidentified		0.10	0.29	0.29				0.15	0.20	1.03

T. madagascariense* = *Trilepisium madagascariense*.B. oblanceolatum* = *Bequartiodendron oblanceolatum*.

The top items in the diets of both groups were the leaves of *Prunus africana*, which accounted for 19.5% of the diet of T-group and 18.5% of the diet of O-group. Nine species appeared among the top 10 species in the diets of both groups. In addition, 23 of the 28 identified species in the diets of each group were fed on by both groups during the study.

O-group fed on fruit from 13 plant species, while T-group fed on fruit from ≥ 12 plant species. Only 7 of these fruit species were eaten by both groups. The only species for which seeds appeared to be the primary fruit item being consumed were *Albizia gummifera*, *Zanthoxylum gillettii*, and one unidentified species of vine with winged seeds (probably *Hippocratea* sp.). Many of the tree species from which guerezas consumed whole fruits or seeds, including the four most heavily exploited species—(*Antiaris toxicaria*, *Ficus exasperata*, *Teclea nobilis*, and *Trilepisium madagascariense*)—are characterized by relatively strong intraspecific synchrony of fruit production at Kakamega.

For several of the most heavily exploited fruit species, e.g., *Antiaris toxicaria*, *Trilepisium madagascariense*, *Ficus exasperata*, guerezas began eating fruits when they were unripe and approaching full size. At least one guenon species, *Cercopithecus mitis*, did not begin eating the fruits of *Trilepisium madagascariense* (and possibly *Antiaris toxicaria* and *Ficus exasperata* as well) for at least another 1–2 mo until they became ripe (K. Pazol, pers. comm.). Once fruits were ripe, guerezas appeared to decrease fruit consumption so that competition for important fruit species with *Cercopithecus mitis* appeared to be minimal for *Colobus guereza*. Dasilva (1994) noted a similar trend at Tiwai where *Colobus polykomos* fed on unripe whole fruit well before *Cercopithecus* spp. began to exploit it.

The top species-specific food items for each month in the two study groups are in Table V. In 9 of the 12 mo, the two groups shared the same primary species-specific food item. Total monthly dietary overlap between the groups in terms of species-specific food items ranged from 31.6 to 72.7% (Mean = 54.4%, $n = 12$ months).

Dietary Diversity and Food Choice

The mean of the 12 monthly Shannon-Weaver indices of food species diversity (H') is 1.61 (range: 0.97–2.15) for T-group and 1.73 (range: 1.32–2.15) for O group. The mean of the 12 monthly Shannon-Weaver indices of food species evenness (J) is 0.71 (range: 0.50–0.84) for T-group and 0.72 (range: 0.60–0.81) for O-group. There is no significant difference over the 12 mo of study in food species diversity (Wilcoxon Signed Ranks Test, $p = .119$) or evenness (Wilcoxon Signed Ranks Test, $p = .647$) between the two groups.

Table V. The top species-specific food items for each month in groups T and O, the top item of dietary overlap between the groups for each month, and the total dietary overlap between the groups for each month

Month	Primary food item		Top overlap item	Total diet overlap
	T-group	O-group		
3/97	<i>Antiaris toxicaria</i> fruit (23%)	<i>Antiaris toxicaria</i> fruit (20%)	<i>Antiaris toxicaria</i> fruit (20%)	56%
4/97	<i>Antiaris toxicaria</i> fruit (27%)	<i>Celtis africana</i> leaves (28%)	<i>Celtis africana</i> leaves (23%)	55%
5/97	<i>Prunus africana</i> leaves (34%)	<i>Ficus exasperata</i> fruit (31%)	<i>Ficus exasperata</i> fruit (31%)	70%
6/97	<i>Ficus exasperata</i> fruit (27%)	<i>Ficus exasperata</i> fruit (23%)	<i>Ficus exasperata</i> fruit (23%)	44%
7/97	<i>Prunus africana</i> leaves (42%)	<i>Prunus africana</i> leaves (50%)	<i>Prunus africana</i> leaves (42%)	55%
8/97	<i>Prunus africana</i> leaves (37%)	<i>Prunus africana</i> leaves (35%)	<i>Prunus africana</i> leaves (35%)	60%
9/97	<i>Teclea nobilis</i> fruit (38%)	<i>Teclea nobilis</i> fruit (24%)	<i>Teclea nobilis</i> fruit (24%)	54%
10/97	<i>Teclea nobilis</i> fruit (24%)	<i>Albizia gummifera</i> leaves (31%)	<i>Prunus africana</i> leaves (15%)	32%
11/97	<i>T. madagascariense</i> [‡] fruit (69%)	<i>T. madagascariense</i> [‡] fruit (56%)	<i>T. madagascariense</i> [‡] fruit (56%)	73%
12/97	<i>T. madagascariense</i> [‡] fruit (55%)	<i>T. madagascariense</i> [‡] fruit (49%)	<i>T. madagascariense</i> [‡] fruit (49%)	59%
1/98	<i>T. madagascariense</i> [‡] fruit (25%)	<i>T. madagascariense</i> [‡] fruit (38%)	<i>T. madagascariense</i> [‡] fruit (25%)	41%
2/98	<i>Morus lactea</i> leaves (21%)	<i>Morus lactea</i> leaves (28%)	<i>Morus lactea</i> leaves (21%)	56%

[‡]*T. madagascariense* = *Trilepisium madagascariense*.

The selection ratios for food species accounting for $\geq 1\%$ of the annual diets of the study groups are in Table VI. Using a selection ratio based on stem density, *Prunus africana* is by far the most selected for species in the diets of both groups. Employing a selection ratio based on basal area, *Teclea nobilis* is by far the most selected for species by T-group and *Morus mesozygia* is by far the most selected for species by O-group.

Based on a series of Spearman rank-order correlations between dietary variables and phenological variables it was possible to determine which plant items were eaten in accordance with their abundance and which were not. The only plant item whose percentage of monthly representation in the diet exhibited a significant correlation with its monthly FAI scores is whole fruit (Table VII.A). This relationship between whole fruit consumption and availability existed for both study groups (Figure 4). Similarly, when FAI scores are based solely on those phenology tree species that contributed $\geq 1\%$ to the annual diet for a given plant part, the only significant correlation is between

Table VI. Selection ratios (S.R.) for species accounting for $\geq 1\%$ of the annual diet. D/N/A = did not appear along the tree enumeration transects. S.D. S.R. = Selection ratio based on stem density. B.A. S.R. = Selection ratio based on basal area

Species	T-Group			Species	O-Group		
	S.D. S.R. (Rank)	B.A. S.R. (Rank)	% of diet (Rank)		S.D. S.R. (Rank)	B.A. S.R. (Rank)	% of diet (Rank)
<i>Prunus africana</i>	12.4 (1)	5.9 (3)	19.9 (1)	<i>Prunus africana</i>	93.0 (1)	16.0 (2)	18.6 (1)
<i>Teclea nobilis</i>	4.9 (2)	18.6 (1)	11.7 (3)	<i>Sapium ellipticum</i>	10.5 (2)	2.9 (7)	2.1 (12)
<i>Celtis africana</i>	3.3 (3)	1.8 (6)	9.7 (6)	<i>Morus mesozygia</i>	8.3 (3)	63.0 (1)	5.0 (8)
<i>Morus mesozygia</i>	3.0 (4)	4.6 (4)	3.0 (8)	<i>Teclea nobilis</i>	4.5 (4)	14.5 (3)	5.8 (6)
<i>Ficus exasperata</i>	2.5 (5)	0.7 (10)	12.1 (2)	<i>T. madagascariense*</i>	2.7 (5)	1.2 (9)	12.8 (2)
<i>Aningeria altissima</i>	2.2 (6)	7.7 (2)	2.9 (tie 9)	<i>Albizia gummifera</i>	1.7 (tie 6)	0.6 (11)	4.4 (9)
<i>T. madagascariense*</i>	1.9 (7)	1.1 (8)	10.5 (4)	<i>Celtis africana</i>	1.7 (tie 6)	1.3 (8)	6.7 (4)
<i>Albizia gummifera</i>	2.0 (8)	0.9 (9)	3.6 (7)	<i>B. oblanceolatum*</i>	1.6 (8)	6.0 (5)	1.4 (15)
<i>Antiaris toxicaria</i>	1.6 (9)	1.2 (7)	9.8 (5)	<i>Ficus exasperata</i>	1.4 (9)	0.7 (10)	8.1 (3)
<i>Zanthoxylum gillettii</i>	0.5 (10)	3.4 (5)	1.8 (11)	<i>Zanthoxylum gillettii</i>	1.2 (10)	11.7 (4)	1.5 (14)
<i>Eucalyptus</i> sp.	D/N/A	D/N/A	1.1 (12)	<i>Antiaris toxicaria</i>	1.1 (11)	1.6 (8)	6.5 (5)
<i>Piper guineense</i> †	—	—	2.9 (tie 9)	<i>Olea capensis</i>	0.9 (12)	0.4 (12)	1.6 (13)
				<i>Celtis gomphophylla</i>	0.6 (13)	4.8 (6)	3.4 (10)
				<i>Callistemon</i> sp.	D/N/A	D/N/A	2.3 (11)
				<i>Spathodea nilotica</i>	D/N/A	D/N/A	1.2 (16)
				<i>Piper guineense</i> †	—	—	5.3 (7)

* *T. madagascariense* = *Trilepisium madagascariense*

**B. oblanceolatum* = *Bequariodendron oblanceolatum*

† *Piper guineense* is a climber

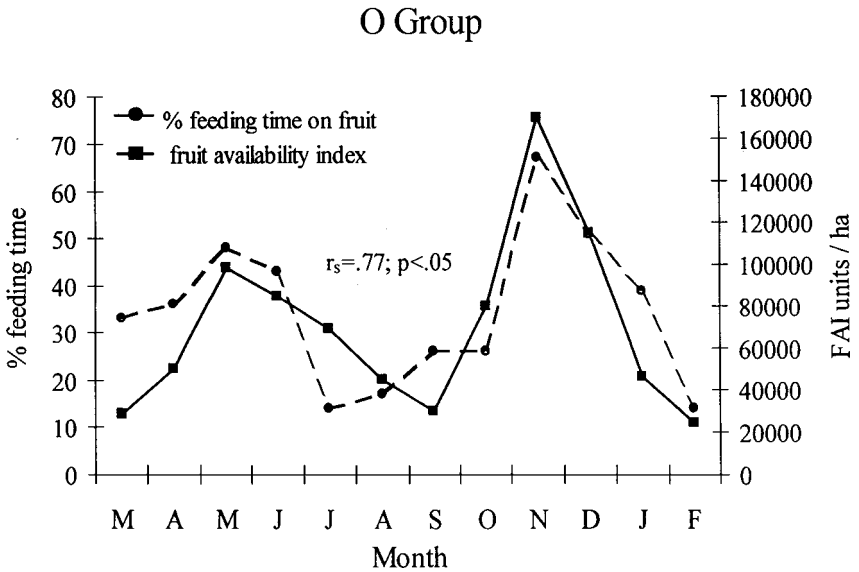
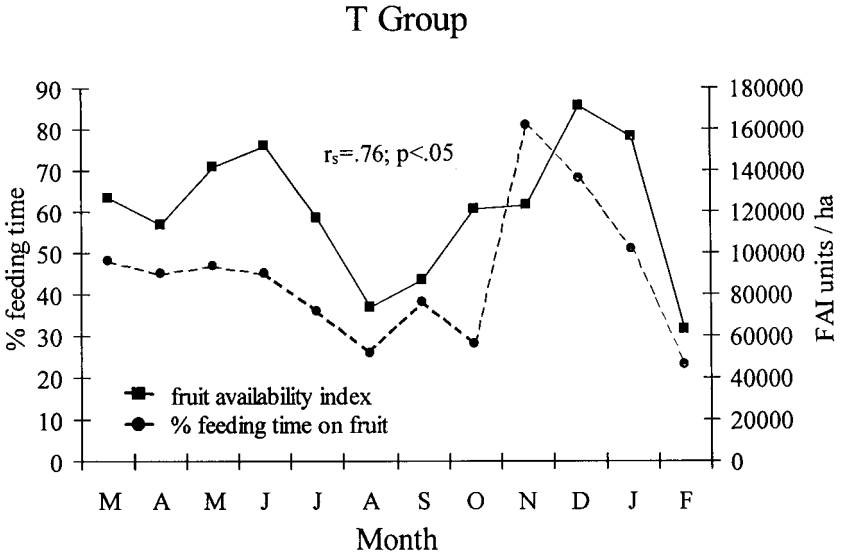


Fig. 4. Comparison of how whole fruit consumption varies with changes in whole fruit availability for groups T and O.

Table VII. Spearman correlation coefficient (r_s) values for comparisons of plant item availability versus plant item consumption in groups T and O across 12 months. * = $p < .05$; ** = $p < .01$; Av. = (availability units/ha); Dt. = Diet

A. Comparison of the availability of a plant item (for all phenology species) versus the consumption of a plant item.

Group	% L Bds vs. L Bds Av.	% Y Lvs vs. Y Lvs Av.	% M Lvs vs. M Lvs Av.	% Fruit vs. Fruit Av.	% Flow vs. Flow Av.	% Seeds vs. Seeds Av.
T	0.430	0.368	0.021	0.762*	0.164	0.424
O	0.358	0.182	-0.007	0.767*	0.131	0.055

B. Comparison of the availability of a plant item (only for those species in which the plant item accounted for at least 1% of the annual diet) versus the consumption of a plant item.

Group	% L Bds vs. L Bds Av.	% Y Lvs vs. Y Lvs Av.	% M Lvs vs. M Lvs Av.	% Fruit vs. Fruit Av.	% Flow vs. Flow Av.	% Seeds vs. Seeds Av.
T	0.186	0.529	0.168	0.685*	—	0.424
O	0.442	0.434	-0.056	0.921**	—	—

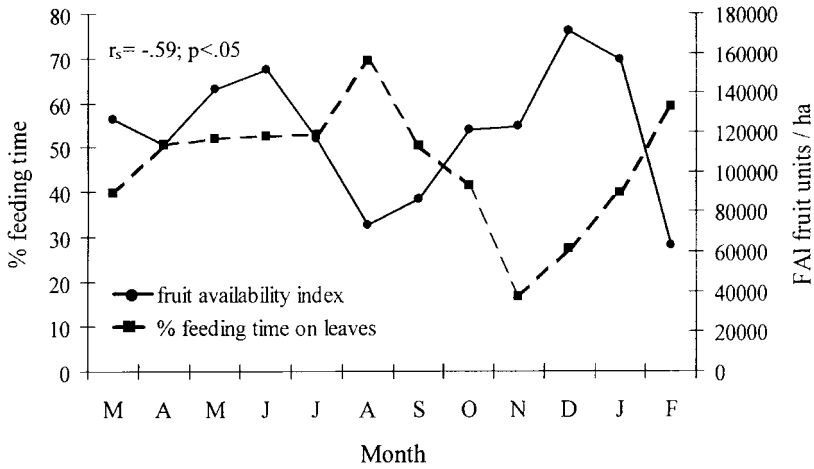
whole fruit consumption and whole fruit availability (Table VII.B). Again, this correlation exists for both study groups. There is also a significant negative correlation between leaf consumption and whole fruit availability for both study groups (Figure 5; T: $r_s = -.594$, $p = .049$; O: $r_s = -.650$, $p = .031$).

DISCUSSION

Forest Composition

The Moraceae had the highest stem density of any tree family, and dominated the tree family biomass, in the ranges of both study groups at Kakamega. Dominance by members of the Moraceae does not occur at the other two major guereza study sites: Ituri Forest, D.R. Congo and Kibale Forest, Uganda. Trees of the Moraceae appear to be uncommon at Ituri where individuals ≥ 30 cm DBH of all the *Ficus* species combined achieved a density of only 1.5 stems per hectare (Bocian, 1997). Conversely, individuals ≥ 30 cm DBH of *Ficus* species at Kakamega reached densities of 8.2 stems per hectare and 7.7 stems per hectare in the ranges of groups T and O, respectively. At Kibale, trees of the Moraceae ≥ 50 cm DBH achieved a density of 12.3 stems per hectare (Oates, 1974). In contrast, trees of Moraceae ≥ 50 cm GBH at Kakamega had stem densities of 81.8 stems per hectare in T-group's range and 64.6 stems per hectare in O-group's range.

Several other colobine study sites in Africa and Asia also have low stem densities and biomasses of *Ficus* spp. or trees in the Moraceae relative to



O Group

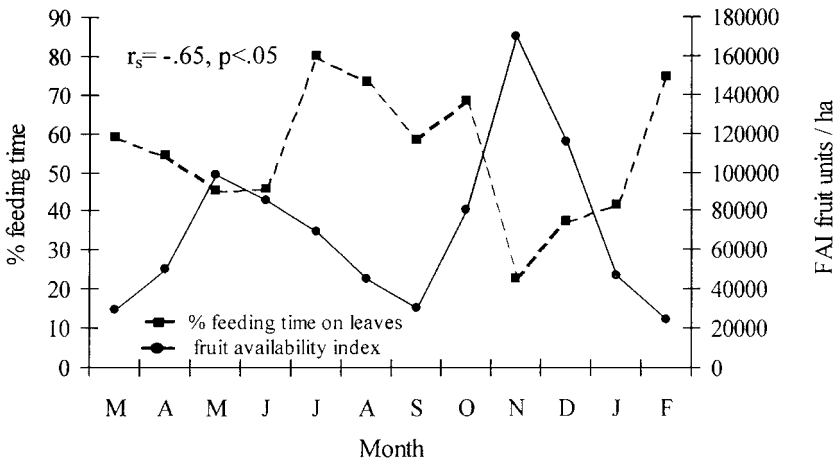


Fig. 5. Comparison of how leaf consumption varies with changes in whole fruit availability for groups T and O.

Kakamega (McKey *et al.*, 1981; Waterman *et al.*, 1988). Two factors sometimes invoked to explain high densities of *Ficus* spp. and Moraceae—habitat disturbance and edge effects—may be responsible for the abundance of these trees at Kakamega (Gautier-Hion and Michaloud, 1989). The study site at Kakamega is bordered on two sides by human use areas, and humans

currently illegally exploit the site to some extent for charcoal production, honey gathering, and the collection of building materials (Fashing 1999b). However, if habitat disturbance and edge effects resulted in the current dominance of Moraceae at Kakamega, then the forest must have endured sustained disturbance over a long period of time. Whether such long-term sustained habitat disturbance has occurred at Kakamega is unknown. Furthermore, habitat disturbance and edge effects cannot always be invoked to explain high densities of Moraceae. For example, at Tangkoko DuaSudara on Sulawesi, fig densities are lower in secondary forest (8.3 canopy-sized figs/ha), and significantly lower in regenerating agricultural areas (5.3 canopy-sized figs/ha), than they are in primary forest (10.3 canopy-sized figs/ha; Kinnaird *et al.*, 1996). Therefore, it cannot necessarily be assumed that the high densities of figs and Moraceae at Kakamega resulted from habitat disturbance or edge effects.

Dietary Diversity

Guereza groups at Kakamega, Kibale, and Ituri consumed between 28 and 43 total plant food species, which are low values relative to those for most other colobines (Table VIII). Monthly dietary diversity as calculated by the Shannon-Weaver index (H') is also low for guereza groups at all sites. Average monthly H' was 1.72 at Kibale over 14 months (Oates, 1974), 1.90 at Ituri over 11 months (Bocian, 1997), and 1.61 and 1.73 at Kakamega over 12 months in groups T and O, respectively. In comparison, average monthly H' was 1.83 among *Colobus angolensis* at Ituri (Bocian, 1997) and 2.61 among *Procolobus badius* at Kibale (Struhsaker and Oates, 1975).

Guerezas appear to be adapted to feed on relatively few food species and to maintain a low dietary species diversity even in species-rich rain forest environments. This finding supports Oates' (1977a, pers. comm.) contention that guerezas are adapted to gallery or dry forest environments where relatively few plant species exist, and that even in rain forests, they continue to live as though in these environments. If population density is considered the best indicator of a species' success in an area, then guerezas indeed appear to do better in gallery and dry forests than in rain forests (Oates, 1974; Rose, 1978; Dunbar, 1987; Bocian, 1997; Fashing and Cords, 2000).

Colobus angolensis also inhabit dry and gallery forests (Groves, 1973; Moreno-Black and Maples, 1977), and, like *C. guereza*, consume a low number of total food species and exhibit low dietary species diversity in the Ituri rain forest (Bocian, 1997). However, *Colobus angolensis* does not reach the high densities in gallery and dry forests that are reached by *C. guereza* in similar environments. For example, the population density of *Colobus*

Table VIII. Diets from long-term colobine field studies. LB = leaf buds; YL = young leaves; ML = mature leaves; UL = unclassified leaves; TotL = total leaves; TotFr = total fruit (fruit + seeds); Flow = flowers + flower buds; # spp. = number of species in diet

Species	LB	YL	ML	UL	TotL	Fruit	Seeds	TotFr	Flow	Bark	Other	# spp.	Site	References
<i>Colobus guereza</i> (T)	2.5	21.7	4.6	19.3	48.1	42.6	1.4	44.0	0.7	1.4	7.1	28+	Kakamega, Kenya	this study
<i>Colobus guereza</i> (O)	4.1	19.1	8.6	25.6	57.4	32.1	1.0	33.1	0.2	3.5	9.2	28+	Kakamega, Kenya	this study
<i>Colobus guereza</i>	4.0	57.7	12.4	2.5	76.6	—	—	13.6	2.1	1.1	6.6	43	Kibale, Uganda	Oates (1977a)
<i>Colobus guereza</i>	3.5	26.2	3.8	24.2	57.9	2.6	22.0	24.6	2.9	—	14.5	31	Ituri, D.R. Congo	Bocian (1997)
<i>Colobus angolensis</i>	2.4	23.5	2.4	22.0	51.1	5.4	22.1	27.5	7.2	0.0	14.0	37	Ituri, D.R. Congo	Bocian (1997)
<i>Colobus angolensis</i>	—	21	6	0	27	17	50	67	6	0	0	46	Salonga, D.R. Congo	Maisels <i>et al.</i> (1994)*
<i>Colobus polykomos</i>	—	29.7	26.4	0.0	56.1	2.9	31.7	34.6	1.7	—	7.6	56	Tiwai, Sierra Leone	Dasilva (1994); Oates (1994)
<i>Colobus satanas</i>	0.8	19.7	18.1	0.0	38.6	0.0	53.2	53.2	3.3	0.0	4.9	84	Douala-Edea, Cameroon	McKey <i>et al.</i> (1981)
<i>Colobus satanas</i>	—	23	3	0	26	4	60	64	5	—	4	65	Lope, Gabon	Harrison in Oates (1994) ^f
<i>Procolobus badius</i>	14.5	27.2	23.7	8.0	73.4	4.2	1.4	5.6	15.9	0.0	5.1	57	Kibale, Uganda	Struhsaker (1978)
<i>Procolobus badius</i>	16.4	36.0	11.5	0.9	64.8	24.1	0.9	25.0	6.2	0.2	3.8	22	Tana (Mchelelo), Kenya	Marsh (1981)
<i>Procolobus badius</i>	4.4	56.8	2.2	0.0	63.4	—	—	21.7	13.3	—	1.6	28	Tana (Mchelelo), Kenya	Decker (1994)
<i>Procolobus badius</i>	2.4	43.5	1.3	0.0	47.2	—	—	25.6	26.7	—	0.5	26	Tana (B.S.), Kenya	Decker (1994)
<i>Procolobus badius</i>	17.5	24.0	5.4	0.0	46.9	17.4	18.5	35.9	8.7	3.7	4.8	39	Fathala, Senegal	Gatinot (1978); Oates (1994)

<i>Procolobus badius</i>	14.6	32.1	7.3	7.3	61.3	—	—	31.7	10.6	1.9	0.4	63	Jozani, Zanzibar	Mturi (1993)
<i>Procolobus badius</i>	21.6	31.8	6.3	5.6	65.3	—	—	31.2	5.4	1.1	0.2	62	Jozani, Zanzibar	Mturi (1993)
<i>Procolobus badius</i>	—	54.3	6.4	0.0	60.7	7.1	30.8	37.9	1.4	0.0	0.0	84	Salonga, D.R.Congo	Maisels <i>et al.</i> (1994)
<i>Procolobus badius</i>	8.7	26.2	11.7	0.1	46.7	38.8	2.9	41.7	8.6	0.0	3.0	89	Abuko, Gambia	Starin (1991)
<i>Procolobus badius</i>	—	32	20	0.0	52	6	25	31	16	—	1	—	Tiwai, Sierra Leone	Davies <i>et al.</i> (1999) ^f
<i>Trachypithecus johnii</i>	<5.7	25.5	26.8	4.2	62.2	—	—	25.1	9.3	—	3.4	107+	Kakachi, India	Oates <i>et al.</i> (1980)
<i>Trachypithecus pileatus</i>	4.9	10.9	42.0	0.0	57.8	24.4	9.3	33.7	7.0	0.0	1.5	35	Madhupur, Bangladesh	Stanford (1991)
<i>Trachypithecus obscura</i>	—	36	22	0	58	32	3	35	7	0	0	87	Kuala Lompat, Malaysia	Curtin (1980) ^f
<i>Trachypithecus senex</i> [†]	—	—	—	60	60	—	—	28	12	0	0	—	Polonnaruwa, Sri Lanka	Hiadik (1977) ^f
<i>Semnopithecus entellus</i> [†]	—	—	—	48	48	—	—	45	7	0	0	—	Polonnaruwa, Sri Lanka	Hiadik (1977) ^f
<i>Semnopithecus entellus</i>	2.8	11.5 ^{††}	34.9	2.4	51.6	—	—	24.4	9.5	—	14.5	53	Kanha, India	Newton (1992)
<i>Presbytis melalophos</i>	—	26	7	0	33	20	26	46	17	—	4	—	Kuala Lompat, Malaysia	Bennett in Kool (1989) ^f
<i>Presbytis melalophos</i>	—	24	11	0	35	48	8	56	6	—	2	137	Kuala Lompat, Malaysia	Curtin (1980) ^f
<i>Presbytis rubicunda</i>	—	36.5	1.1	0.0	37.6	19.2	30.1	49.3	11.1	—	2.0	103+	Sepilok, Malaysia	Davies (1991)
<i>Presbytis hoesii</i> (1)	—	—	—	59.7	59.7	18.8	21.3	40.1	0.2	0.0	0.0	—	Lipad, Malaysia	Mitchell (1994)
<i>Presbytis hoesii</i> (4)	—	—	—	77.8	77.8	2.8	16.7	19.5	2.8	0.0	0.0	—	Lipad, Malaysia	Mitchell (1994)
<i>Nasalis larvatus</i>	—	—	—	51.9	51.9	—	—	40.3	3.0	—	4.8	47	Tanjung Puting, Indonesia	Yeager (1989)

— = data not available.

() = group identity for sites where more than one group studied.

^f Reported percentages only as whole numbers (in at least some cases because n < 1000).

* 8-month study.

** Occasions when leaf buds and young leaves were ingested simultaneously are grouped with young leaves.

† Occasions when young leaves and mature leaves were ingested simultaneously are grouped with unclassified leaves.

‡ Dietary data based on wet weight of food ingested.

†† Unlike Newton (1992), I include "open leaf buds" with young leaves rather than leaf buds.

angolensis in the coastal forest at Diani Beach, Kenya, was estimated at only 23 animals/km² (J. Anderson, pers. comm.), while population densities of *C. guereza* in the gallery forests at Lake Naivasha, Kenya and Bole, Ethiopia were reported to be as high as 396 animals/km² (Rose, 1978) and 370 animals/km² (Dunbar, 1987), respectively. *Colobus polykomos* and *C. vellerosus* also inhabit gallery forests in West Africa, but are less typically found in this environment than are *C. guereza* in East Africa (Oates, 1994). Therefore, because guerezas appear to have a wider geographic distribution in gallery and dry forests than the other species, and because they attain very high population densities in these forests, guerezas are probably better adapted to life in gallery forests and dry forests than are other black-and-white colobus. This contention requires further evaluation, however, since most black-and-white colobus species have barely been studied in gallery and dry forest environments.

Colobine Dietary Strategies

The facts that guerezas (1) ate whole fruit in proportion to its abundance, (2) did not eat young leaves in proportion to their abundance, and (3) ate leaves most when whole fruit was scarce and least when whole fruit was abundant, raise the possibility that whole fruit may have been the preferred food item for guerezas at Kakamega. However, since preference can only really be tested when all possible food items are equally abundant and accessible (criteria that are virtually impossible to meet in primate field studies), my study can only suggest, rather than demonstrate, that guerezas at Kakamega prefer whole fruit over all other food items.

Although whole fruit may be the "preferred" food item for guerezas at Kakamega, guerezas in both study groups spent more time feeding on leaves than fruit over the annual cycle. The top species in the annual diets of both groups, *Prunus africana*, was a relatively rare tree exploited almost exclusively for its leaves. Despite its relative rarity, *Prunus africana* was among the top 5 monthly food species during 11 of 12 months for T-group and 10 of 12 months for O-group. It would therefore be overly simplistic to assume that just because guerezas at Kakamega ate fruit in accordance with its abundance, that leaves, especially those of *Prunus africana*, are not essential to their diet as well.

The importance of leaves notwithstanding, the finding that both groups at Kakamega spent much of their feeding time on whole fruit, especially when it was abundant, contrasts with the conclusion that guerezas are specialist folivores at Ituri (Bocian, 1997) and Kibale. At Kibale, fruit (primarily whole) accounted for only 13.6% of the annual diet and was mainly

consumed during months when young leaf availability was low (Oates, 1977a). At Ituri, fruit (primarily seeds) comprised 24.6% of the annual diet, but, as at Kibale, was consumed by guerezas most in those months when young leaf availability was low (Bocian, 1997).

What accounts for the different dietary strategies of the Kakamega guerezas relative to those of the Kibale and Ituri guerezas? One obvious ecological difference between Kakamega and the other two sites is that: unlike at Kibale and Ituri, trees of the Moraceae family dominate the vegetational composition at Kakamega. Trees of Moraceae were not only by far the most common trees in the forest but also accounted for 71.8% and 72.9% of the whole fruits consumed by groups T and O, respectively. Furthermore, overall fruit consumption exhibits a significant positive correlation with Moraceae fruit availability in both groups (T: $r_s = .68$, $p < .05$; O: $r_s = .80$, $p < .05$). Therefore, it is probable that the dominance of Moraceae at Kakamega is responsible for the high level of fruit consumption by guerezas at this site. Similarly, at Pangandaran, Indonesia, where Moraceae also dominate the tree family biomass, fruits of Moraceae make up a substantial part of the diet of another colobine monkey, the ebony langur (*Trachypithecus auratus*; Kool, 1989).

The reliance on seeds by several Central African, West African, and Southeast Asian colobine monkey species also appears to be related to the abundance of a particular tree family in their habitats. At several sites where leguminous trees, especially those of Caesalpinaceae, are common, colobine monkeys tend to include high proportions of seeds in their diets (Table VIII; Davies, 1984; Harrison, 1986; Dasilva, 1994; Maisels *et al.*, 1994). These high levels of granivory have been linked to the abundance of leguminous seeds, the poor nutritional quality of mature foliage, and/or the high levels of secondary compounds in mature foliage at these sites.

Table VIII is a synthesis of colobine monkey diets at 20 long-term study sites, from which it is clear that colobines range from folivores (Oates, 1977a; Struhsaker, 1978; Mitchell, 1994) to folivore/frugivores (Starin, 1991; this study), to granivores (McKey *et al.*, 1981; Harrison, 1986; Maisels *et al.*, 1994) with many populations falling somewhere in between these designations. Some of the dietary complexity revealed in the table can probably be attributed to certain phylogenetic or ecological factors. Trends such as the higher level of whole fruit consumption and lower level of seed consumption in *Trachypithecus* spp. relative to *Presbytis* spp. appear to be related more to phylogeny than to ecology. Conversely, the tendencies for whole fruit consumption to be high in Moraceae-rich forests and for seed consumption to be high in legume-rich forests appear to have more to do with ecology than with phylogeny.

My study of guerezas at Kakamega suggests that they are yet another colobine species that exhibits dietary flexibility both across their geographic range, e.g. *Procolobus badius* (Struhsaker, 1978; Starin, 1991; Decker, 1994), and over time at a single site, e.g. *Trachypithecus pileata* (Stanford, 1991), and *Colobus polykomos* (Dasilva, 1994). The Moraceae-rich forest at Kakamega provides guerezas with the opportunity to expand beyond the specialist folivore niche that they occupy at Kibale and Ituri (Oates, 1977a; Bocian, 1997) and to subsist on large quantities of whole fruit when it is available. This dietary flexibility may be a major reason why guerezas are able to inhabit such a wide variety of habitat types across equatorial Africa.

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