



Dietary Response of Chimpanzees and Cercopithecines to Seasonal Variation in Fruit Abundance. I. Antifeedants

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In order to understand dietary differentiation among frugivorous primates with simple stomachs, we present the first comparison of plant diets between chimpanzees and cercopithecine monkeys that controls for food abundance. Our aim was to test the hypothesis that monkeys have a more diverse diet as a result of their dietary tolerance for chemical antifeedants. Our study species are chimpanzees, blue monkeys, redtail monkeys, and gray-cheeked mangabeys living in overlapping ranges in Kibale National Park, Uganda. We indexed food abundance by the percentage of trees having ripe fruit within the range of each group; it varied widely during the year. Chimpanzees spent almost 3 times as much of their feeding time eating ripe fruits as the monkeys did and confined their diets almost exclusively to ripe fruits when they were abundant. Monkeys maintained a diverse diet at all times. When ripe fruit was scarce chimpanzee and monkey diets diverged. Chimpanzees relied on piths as their main fallback food, whereas monkeys turned to unripe fruits and seeds. For each primate group we calculated the total weighted mean intake of 5 antifeedants; condensed tannins (CT), total tannins assayed by radial diffusion (RD), monoterpenoids (MT), triterpenoids (TT), and neutral-detergent fiber (NDF). Monkeys had absolutely higher intakes of CT, RD, MT, and TT than those of chimpanzees, and their intake of NDF did not differ from that of chimpanzees, appearing relatively high given their lower body weights. However contrary to expectation, dietary divergence during fruit scarcity was not

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associated with any change in absolute or relative intake of antifeedants. For example, fruit scarcity did not affect the relative intake of antifeedants by cercopithecines compared to chimpanzees. Our results establish chimpanzees as ripe-fruit specialists, whereas cercopithecines are generalists with a higher intake of antifeedants. The low representation of ripe fruits in the diets of cercopithecines has not been explained. An important next step is to test the hypothesis that the difference between Kibale chimpanzees and cercopithecines represents a more general difference between apes and monkeys.

KEY WORDS: diet; ape; monkey; terpenoids; tannins; fiber; seasonality.

INTRODUCTION

Secondary plant chemicals are potentially important contributors to dietary separation in primate communities (Ganzhorn 1989). We investigated their role in separating chimpanzees and cercopithecines.

Several lines of evidence suggest that chimpanzees (*Pan troglodytes*) are ripe-fruit specialists compared to cercopithecine monkeys. For example, when ripe fruit is scarce, chimpanzee foraging parties often become small (Chapman *et al.*, 1994, 1995; Wrangham *et al.* 1996), whereas under the same conditions in the same forests, foraging group sizes of arboreal cercopithecines are stable (Rudran, 1978a; Butynski, 1990; Struhsaker and Leyland, 1979; Struhsaker, 1980; Waser, 1975, 1976, 1977). This comparison suggests that the cercopithecines have alternative sources of food not available to chimpanzees. In line with this proposal, differences in the social organization and ecology of frugivorous apes and monkeys conform to apes having restricted diets (Gaulin and Konner, 1977; Temerin and Cant, 1983). Thus apes have a relatively low population density, a low biomass, and large home ranges (Clutton-Brock and Harvey, 1979). Finally, dietary studies support the idea that chimpanzees eat more ripe fruit than cercopithecines do (Clutton-Brock, 1977; Ghiglieri, 1984; Rudran, 1978a, b; Struhsaker, 1978; Waser, 1975, 1976, 1977). For example in Kibale National Park, Uganda, the reported percentage of feeding time spent eating ripe fruits varies between 71.7% (Wrangham *et al.*, 1991) and 78% (Ghiglieri, 1984). Lower figures are reported for sympatric cercopithecines (43.6% for red-tailed monkeys (*Cercopithecus ascanius*); 42.7% for blue monkeys (*C. mitis*), and <58.8% for gray-cheeked mangabey (*Lophocebus albigena*) (Struhsaker, 1978).

These suggestive comparisons are weakened by the fact that no study has directly compared the diets of chimpanzees and cercopithecines under the same conditions of fruit availability. To solve this problem, we compared diets of chimpanzees and cercopithecines from the same period and

overlapping ranges, indexed to our own synchronous measure of food availability. We studied chimpanzees and three species of frugivorous cercopithecines: red-tailed monkeys, blue monkeys, and gray-cheeked mangabays in the Kanyawara area of Kibale National Park.

In theory, diets of sympatric competitors could either converge or diverge during periods of fruit scarcity. However, in a review of three communities of frugivorous forest primates, Waser (1987) found divergence to be more common: Krau, Malaysia; Makokou, Gabon; and Manu, Peru. Waser's survey included 23 specific pairs. In 21 pairs, diets diverged during the dry season (when fruit was apparently scarce). Depressed fruit availability was also associated with greater dietary differentiation among monkeys of French Guiana (Guillotin *et al.*, 1994). Based on these observations, we expected that when preferred foods were scarce, diets would be more different.

To understand the source of dietary differences, we investigated both antifeedant and nutrient composition of plant food items. Primate diets discriminate finely among food species, individual organisms, and plant parts (Milton, 1980; Glander, 1982). However, Old World primates have remarkably similar neural and physiological responses to sugars and sugar-mimics (Rolls *et al.*, 1996), suggesting that responses to nutrients may not vary widely among species. We report on nutrient composition of our study species diets in a companion paper (Conklin-Brittain *et al.*, 1998).

Antifeedant concentration in plant items can influence diets importantly (Lindroth, 1989; Harborne, 1993; Provenza and Cincotta, 1993), including those of primates (Oates *et al.*, 1977, 1980; Milton, 1979; Waterman *et al.*, 1980; Wrangham and Waterman, 1983; McKey *et al.*, 1981; Calvert, 1985; Davies *et al.*, 1988; Marks *et al.*, 1988; Kinzey and Norconk, 1993; Leighton, 1993; Rogers *et al.*, 1992). Ganzhorn (1989) reported differences in tolerance of antifeedants among some primate species, and Wrangham (1980) suggested that cercopithecines may be more tolerant of them than chimpanzees are. However, we are unaware of any relevant data on physiological differences between forest cercopithecines and chimpanzees.

Accordingly, we tested the following hypotheses.

Hypothesis 1: Chimpanzees eat more ripe fruit than cercopithecines do.

Hypothesis 2: When ripe-fruit pulp is not eaten, the diets of chimpanzees and cercopithecines diverge.

Hypothesis 3: In the diet as a whole, cercopithecines ingest more antifeedants than chimpanzees do.

Hypothesis 4: When ripe fruit is scarce, both chimpanzees and cercopithecines ingest more antifeedants.

Hypothesis 5: When ripe fruit is scarce, cercopithecines ingest higher loads of antifeedants than chimpanzees do.

The antifeedants that we discuss are ones that we were able to analyze quantitatively: condensed tannins (CT), total tannins assayed by radial diffusion (RD), monoterpenoids (MT), and triterpenoids (TT). Their functions as feeding deterrents vary. In general, condensed tannins are digestion-inhibitors, whereas terpenoids are more often toxic (Lindroth, 1989; Gershenson and Croteau, 1991). However, their roles as antifeedants depend on several factors, including the taste system, salivary glands, and digestive system of the forager. We refer to both digestion-inhibitors and toxins as antifeedants. In addition to the four classes of secondary compounds, we present data on a fifth antifeedant, neutral-detergent fiber (NDF), which although not a secondary compound, also serves as a digestion-inhibitor (Oates *et al.*, 1977, 1980; Milton, 1980; Davies *et al.*, 1988; Rogers *et al.*, 1992; van Soest, 1994).

METHODS

We studied 4 primate species in the Kanyawara sector of Kibale National Park, Uganda, from July 1992 to June 1993. Observations were focused in two adjacent compartments of Kibale, K14 (lightly logged in the 1960s) and K30 (not commercially logged). Together with a team of locally trained field assistants, we observed the Kanyawara community of chimpanzees, *Pan troglodytes schweinfurthii*, which ranged not only in K14 and K30, but also in several other compartments (Chapman and Wrangham, 1993). In each month we also observed two groups of each monkey species, one in K14 and one in K30. We thus observed one group of chimpanzees and 6 groups of monkeys, as follows: chimpanzees (C); blue monkeys, *Cercopithecus mitis stuhlmanni*, in K14 and K30 (B14 and B30, respectively); red-tailed monkeys, *Cercopithecus ascanius schmidtii*, in K14 and K30 (R14 and R30); and gray-checked mangabeys, *Lophocebus albigena johnstoni*, in K14 and K30 (M14 and M30). Monkey groups that were located in K14 sometimes moved during the observation day to K30, and vice versa. For example, although B14, R14, and M14 were observed primarily in K14, they were sometimes recorded in K30 also.

Chimpanzees were well habituated, allowing uninterrupted observation when they were in trees. When on the ground, most adult males allowed observers to sit about 5 m away, but even so, thick vegetation made viewing of terrestrial foods difficult at times. None of the monkeys was as well habituated as the chimpanzees, but all allowed observation of feeding with-

out moving out of sight, and all groups could be followed all day without being lost.

We observed the monkeys during three 12-hr periods per group per month, each one week apart. The protocol required a pair of observers to locate a group in the appropriate compartment, observe it until nightfall, and resume recording the next day at dawn; on that second day, observations were terminated at the same time as they began on the first day. Chimpanzees could not be located and followed predictably. Therefore, we observed them whenever they could be found. The total number of plant-food records was 10,338 (mean \pm SD per month: B14, 114.6 \pm 28.4; B30, 96.0 \pm 31.1; M14, 120.6 \pm 65.2; M30, 130.3 \pm 55.9; R14, 98.5 \pm 41.3; R30, 94.6 \pm 37.0; C, 207.0 \pm 115.4).

We recorded feeding observations by instantaneous, focal-animal sampling. Observations of focal individuals rotated through all individuals that could be observed in the feeding party, changing targets every 10 min. At the end of a 10-min focal-animal session, the observer located a new target individual, the behavior of which had not been recorded for at least 20 min. After a target was selected, it was observed for 60 sec, at the end of which its instantaneous behavior was recorded. Feeding was defined as picking, handling or chewing a food item. When feeding was recorded, we noted the food item as insect or plant part (fruit: ripe or unripe pulp, ripe or unripe seed), leaf (young or mature, petiole, bud, or blade), flower (age and part, e.g., ovule, petal), pith, bark, root, and wood. All new plant items, such as unripe fruits of a species whose ripe fruits had not been eaten previously, were brought back to the research camp for discussion and evaluation. Plant species were identified by collection of specimens.

Potential sources of error include habituation, interobserver variance, and sampling schedule. First, the 6 cercopithecine groups were not as fully habituated as chimpanzees. However, given our results on ripe-fruit-eating, the direction of error seems wrong. Lack of habituation might be expected to lead to overestimation of ripe fruits in the diet because monkeys might be most easily found and observed at dense concentrations of food, such as fruiting trees. It is harder to see why it should lead to underestimating the ripe-fruit component. Secondly, discrepancy could have occurred among observers. To prevent this, food-coding by field assistants was checked regularly by Hunt and Wrangham; field assistants worked in pairs, checking each other; and new foods were brought back to base camp and examined by all field assistants working with the different groups. Thirdly, ripe-fruit eating by chimpanzees may have been overestimated by the fact that observations were not distributed as evenly with respect to time of day as were those of cercopithecines. Any effect appears small.

Chemical Analysis

We collected samples of as many foods as possible and dried them for complete nutritional analysis. Chemical assays were performed at Harvard University. Methods for assaying CT (condensed tannins), RD (total tannins assayed by radial diffusion), and NDF (neutral detergent fiber) followed Conklin and Wrangham (1994). The CT method (butanol/HCl) is a chemical assay, with no index of biological activity. The RD method complements this by measuring tanning activity (protein-binding), including both condensed and hydrolyzable tannins (Hagerman, 1987). Additional methods were developed to index monoterpenoids and triterpenoids. Monoterpenoids (MT) were extracted in petroleum ether and reextracted in methylene chloride (DCM). The DCM extract was spotted on aluminum-backed, silica gel thin-layer chromatography plates and developed for 30 min in a 50:50 mix of toluene:chloroform. The developed plates were sprayed with vanillin-sulfuric acid reagent and viewed with a densitometer. The standard spotted with each plate was anise. The quantity of MTs was calculated as the sum of the optical densities for all bands from a given sample spot. This was then expressed as a percentage of the optical density of the anise band.

Triterpenoids (TT) were extracted from the plant residue remaining after the above petroleum ether extraction, with hot 100% methanol. The methanol was evaporated until only 1 ml remained. Using as solvent a 50:50 mix of hexane:ethyl acetate, the concentrated extract was spotted, developed and quantified as described above. The plates were sprayed with Liebermann-Burchard reagent and the standard was squalene.

We measured antifeedant (AF) concentrations in 194 plant items, representing 60.8% of all plant items recorded as food. We calculated weighted mean intake of antifeedants (WMIAF) in each month as $WMIAF = \Sigma(p_i * c_i) / \Sigma(p_i)$, where p_i is the percentage of the total plant-feeding time spent eating the i th item for which the concentration of antifeedant was known, and c_i is the concentration of antifeedant in the i th item. Mean values for $\Sigma(p_i)$ across 12 months averaged 94.3% of plant-feeding time across primate groups and antifeedants, with ranges as follows: CT, 90.5% (R14) to 96.9% (B30); MT, 90.9% (C) to 96.6% (R14); NDF, 90.1% (C) to 96.9% (B30); and TT, 90.1% (C) to 96.1% (B30).

Measuring Food Availability

To index food availability, once per month we monitored the presence of ripe fruits, unripe fruits, flowers, young leaves, and mature leaves in 48

permanently marked phenological transects (each 200×10 m = 0.2 ha). The phenology transect system was that described by Chapman *et al.* (1995), except that we added 22 transects to the 26 established previously, in order to intensify the sampling rate for each monkey group. We recorded phenophases for all trees >10 cm DBH. For the purpose of analysis, we noted the geographic range occupied by each monkey group during the observation year and recorded food availability for it using only transects that occurred within its range. This procedure yielded the following number of trees and transects monitored monthly per group: B14, 2539 trees, 24 transects; B30, 2887, 28; C, 4560, 48; M14, 3511, 34; M30, 3713, 36; R14, 2974, 27; and R30, 3609, 36.

We calculated monthly fruit abundance indices (FAI) as the percentages of trees containing ripe fruits. FAIs that assayed all fruiting species range from 0.51% (R14; May 1993) to 4.51% (R30; November 1992), and were closely correlated across all primate groups (r^2 varied from 0.71 (C–B30) to 1.00 (M14–M30; all P 's < 0.001). However, such FAIs, which assay all tree species, include species of fruits not eaten by some primates and are therefore a weak measure of food availability. Therefore, for analyses conducted separately on each primate group, we calculated FAIs using only the tree species whose ripe fruits were eaten by the relevant group at least once during the study period. These FAIs are also closely correlated across primate groups: r varied from 0.98 to 0.99; P < 0.001 for all comparisons. FAIs and sample sizes using this method are in Table I. Sometimes it was desirable to use a single FAI that applied to all 7 primate groups; for this purpose, we calculated the mean FAI per month across the 7 primate groups (Table I).

RESULTS

Hypothesis 1: Chimpanzees Eat More Ripe Fruit Than Cercopithecines Do

During the study period there were two peaks of ripe fruit availability (Fig. 1). The levels of fruit availability differed little between primate groups (Table I). However, across months the patterns of feeding differed strikingly between chimpanzees and cercopithecines (Table II).

Ripe fruits were much more frequent items for chimpanzees than for cercopithecines. In every month, chimpanzees had more ripe fruit in their diets than in that of any of the 6 cercopithecine groups (Fig. 1). Averaged over the year, chimpanzees spent about three times as much of their feeding time on ripe fruit as cercopithecines did (74.6 vs. 24.7%; Table II).

Table I. Fruit Availability Indices (FAI's)^a

Month	C	B14	B30	M14	M30	R14	R30	Mean FAI
July 1992	0.3	0.5	0.5	0.4	0.3	0.5	0.4	0.4
Aug 1992	1.2	2.3	1.7	1.4	1.2	2.3	1.4	1.6
Sept 1992	2.0	2.3	3.4	2.8	2.2	2.3	2.8	2.5
Oct 1992	5.9	7.7	9.8	8.5	6.8	8.8	8.6	8.0
Nov 1992	8.2	10.5	12.8	10.8	8.5	12.3	11.5	10.6
Dec 1992	6.0	8.5	9.7	7.7	6.1	8.4	8.3	7.8
Jan 1993	4.6	5.3	7.9	5.2	4.3	5.6	7.1	5.7
Feb 1993	3.0	4.6	5.8	3.7	3.2	4.5	4.8	4.2
Mar 1993	1.7	2.4	3.4	2.0	1.8	2.3	2.4	2.3
Apr 1993	1.9	3.1	4.4	2.7	2.3	2.9	3.1	2.9
May 1993	1.4	1.4	2.9	1.6	1.7	1.4	2.3	1.8
June 1993	6.0	7.9	12.0	8.3	7.0	8.4	9.2	8.4
Mean	3.5	4.7	6.2	4.6	3.8	5.0	5.2	4.7

^aCells show mean percentage, across food-tree species, of trees having ripe fruit in each month. A food-tree species is one whose ripe fruit was eaten by that primate group at least once during the study year. Sample sizes for food-trees are: C, 17 species, 1252 trees; B14, 11 tree species, 841 trees; B30, 10 species, 1188 trees; M14, 12 species, 1004 trees; M30, 15 species, 1252 trees; R14, 11 species, 890 trees; and R30, 12 species, 1501 trees. Mean FAI shows mean FAI across the 7 primate groups. Primates: C, chimpanzee; B14, blue monkeys in compartment K14; B30, blue monkeys in compartment K30; M mangabey (M14 and M30 in K14 and K30, respectively); R red-tailed monkeys (R14 and R30 in K14 and K30, respectively).

This comparison was made simultaneously for the 7 primate groups in overlapping areas of forest. However, chimpanzees used a larger area than those of the monkeys, and the areas used by each group of cercopithecines were different. This means that each primate group experienced its own unique pattern of fruit availability. Therefore, to check for possible effects of differential fruit availability, we regressed the ripe-fruit component of the diet against the mean percentage of trees having ripe fruit eaten by each primate within its own range (Fig. 2). At all levels of fruit availability, chimpanzees had a higher proportion of ripe fruit in the diet than that of any of the 6 groups of monkeys. Thus, chimpanzees ate more ripe fruits than cercopithecines did in relation to fruit availability. Accordingly, Hypothesis 1 is supported, because cercopithecines spent less time eating ripe fruit than chimpanzees did in relation to availability.

Why did chimpanzees eat ripe fruits more than cercopithecines did? One possibility is that chimpanzees include in their diet species of ripe fruits that are unavailable to cercopithecines, e.g., fruits that are difficult

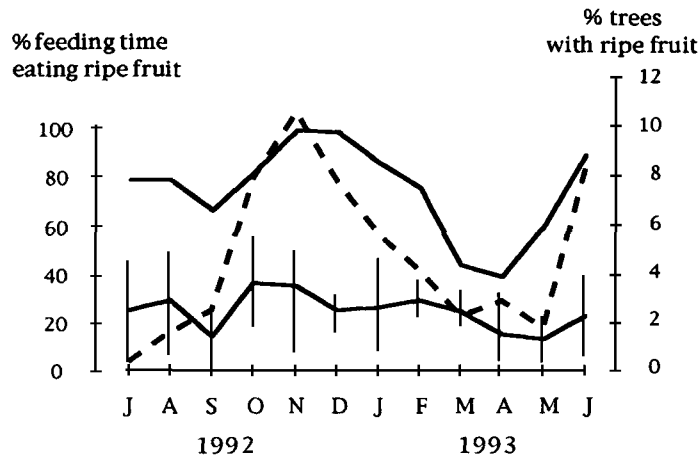


Fig. 1. Ripe fruit in ape vs. cercopithecine diets: seasonal variation. Solid lines, and left-hand scale, show percentage of feeding time (on plant items) spent eating ripe fruit (upper line, chimpanzees; lower line, mean and ranges for 6 monkey groups). Dashed line, and right-hand scale, shows mean percentage of trees with ripe fruit for samples from the 7 primate groups (i.e., mean FAI).

Table II. Chimpanzee vs. Cercopithecine Diets: Composition by Plant Part

	C	B14	B30	M14	M30	R14	R30	Monkey mean
Ripe fruit	74.6	27.4	26.7	25.1	24.2	21.8	22.8	24.7
Unripe fruit	3.9	23.5	21.5	21.4	21.4	35.4	31.1	25.7
Seed	0.1	3.1	7.1	9.9	13.8	3.7	6.2	7.3
Flower	0.6	3.6	4.2	2.8	3.3	0.6	2.3	2.8
Leaf	9.3	42.3	40.6	37.4	33.3	38.5	37.5	38.3
Pith/stem	10.8	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Bark	0.4	0.0	0.0	3.2	3.9	0.0	0.0	1.2
Root	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Wood	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	99.9	99.9	100.1	100	99.9	100	99.9	100

^aCells show the mean percentage (across 12 months, July 1992 to June 1993) of feeding observations spent eating each plant part. Fruit includes pulp or some other nonseed part of the fruit (e.g., pod), without destroying the seed. Seed includes all records of seed predation. Monkey mean gives the average for the 6 monkey groups (B14, B30, M14, M30, R14, R30).

for the monkeys to open, or are palatable only to chimpanzees. In other words, cercopithecines might have eaten as much as chimpanzees did from

Table III. Ripe-Fruit Species Eaten by Chimpanzees and Cercopithecines^a

Species	Form	Eaten by	CT	RD	MT	TT	NDF
<i>Celtis africana</i>	T	C, B, M, R	0.1	0.0	4.2	1.7	15.7
<i>Celtis durandii</i>	T	C, B, M, R	0.1	0.0	62.8	1.8	18.9
<i>Ficus brachylepis</i>	T	C, B, M, R	0.4	2.8	8.4	123.8	30.8
<i>Ficus exasperata</i>	T	C, B, M, R	0.3	0.5	8.9	0.3	30.3
<i>Ficus natalensis</i>	T	C, R	0.7	1.8	5.0	5.6	52.3
<i>Linociera johnsonii</i>	T	C, M, R	0.6	3.5	7.3	21.8	39.8
<i>Mimusops bagshawei</i>	T	C, B, M, R	1.0	0.2	0.7	10.8	35.5
<i>Pseudospondias microcarpa</i>	T	C, B, M, R	0.9	7.8	1.9	1.1	44.6
<i>Teclea nobilis</i>	T	C, B, M, R	0.1	0.0	4.5	38.3	22.1
<i>Uvariopsis congensis</i>	T	C, B, R	0.0	0.0	6.7	10.9	39.3
<i>Vangueria apiculata</i>	T	C, R	4.1	3.5	1.3	23.6	46.6
<i>Aframomum</i> spp.	H	C	0.9	0.3	3.0	7.0	25.8
<i>Aphania senegalensis</i>	T	C	6.3	5.0	0.9	7.4	37.0
<i>Cordia abyssinica</i>	T	C					
<i>Cordia millenii</i>	T	C					
<i>Dichrostachys glomerata</i>	T	C	16.3	26.4	1.4	7.5	29.5
<i>Drypetes battiscombei</i>	T	C	4.3	5.5	1.3	2.9	60.7
<i>Euadenia</i> spp.	T	C	1.9	3.8	0.6	4.9	35.7
<i>Ficus brachypoda</i>	T	C	7.8	13.9	19.1	240.6	30.1
<i>Ficus capensis</i>	T	C	7.4	5.3	8.1	8.2	40.6
<i>Ficus cyathistipula</i>	T	C	1.1	0.0	27.7	14.8	39.0
<i>Ficus dawei</i>	T	C	2.0	3.0	14.4	29.1	44.9
<i>Ficus stipulifera</i>	T	C	3.7	2.8	15.4	19.2	38.5
<i>Ficus urceolaris</i>	S	C	0.2	0.2	13.0	25.4	16.7
Unidentified herb 153	H	C					
Unidentified tree 264	T	C					
<i>Tabernaemontana</i> spp.	T	C	1.2	0.0	122.4	21.5	18.7
<i>Balanites wilsoniana</i>	T	M	0.2	4.7	0.2	10.2	13.6
<i>Casearia engleri</i>	T	M, R	0.2	0.2	41.2	5.5	33.3
<i>Celtis zenkeri</i>	T	R					
<i>Chaetacme aristata</i>	T	B, R	18.2	22.2	1.6	6.6	22.5
<i>Chrysophyllum gorungosanum</i>	T	B, M	5.3	6.2	260.9	23.4	51.6
Unidentified liana 65	L	M					
<i>Diospyros abyssinica</i>	T	B, M, R	1.3	16.6	14.1	28.0	36.6
<i>Dombeya mukole</i>	T	M					
<i>Fagaropsis angolensis</i>	T	B, M	0.1	0.7	13.9	14.8	16.2
Unidentified fig 76	T	B					
<i>Funtumia africana</i>	T	B, R					
<i>Pancovia turbinata</i>	T	B, M, R	2.0	16.7	0.6	11.0	26.0
<i>Polyscias fulva</i>	T	M					
<i>Rauvolfia oxyphylla</i>	T	B					
<i>Strychnos mitis</i>	T	B, M, R	0.0	0.6	62.7	9.4	45.7
<i>Symphonia globulifera</i>	T	B	11.7	13.9	24.2	75.9	37.2
Unidentified tree 322	T	B, R					

^aAll species recorded during the study period are shown, listed alphabetically in three groups (eaten by both chimpanzees and monkeys, by chimpanzees only, and by monkeys only). Form: H, herb; L, liana; S, shrub; T, tree. Cells show antifeedant concentrations. CT (condensed tannin) and RD (total tannins) are expressed as % quebracho dry matter units. NDF (neutral-detergent fiber) is % dry matter. MT (monoterpene) and TT (triterpene) figures are scaled as described under Methods. Empty cells mean that no assays were performed. Primates: C, chimpanzee, B, blue monkey; M, mangabey; R, red-tailed monkey.

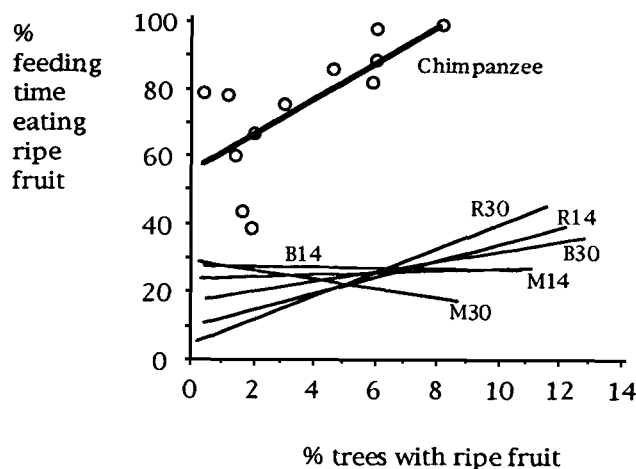


Fig. 2. Ripe fruit in diets in relation to fruit availability. Graph shows the percentage of feeding time spent eating ripe fruit in each month, plotted in relation to fruit availability (% trees with ripe fruit). Least-squares regression lines are shown for chimpanzees (upper bold line, with monthly data points shown) and 6 monkey groups. Chimpanzee $r = 0.70$, $N = 12$ months, $P < 0.05$. Monkey groups, $r = -0.04$, P ns (B14), 0.44 , P ns (B30), 0.08 , P ns (M14), -0.22 , P ns (M30), 0.72 , $P < 0.05$ (R14), and 0.80 , $P < 0.01$ (R30). The percentage of trees with ripe fruit was calculated separately for each primate group.

certain ripe-fruit (RF) species shared by both taxa, while forgoing other chimpanzee-specific RF species, which might have been of lower quality: Hypothesis 1A.

A first test of Hypothesis 1A is whether cercopithecine RF diets were merely a subset of the chimpanzee ripe-fruit diet. Among a total of 44 RF species, only 11 (25%) were eaten by both chimpanzees and cercopithecines (Table III). However, of the remainder, even more were eaten by cercopithecines only (17 species; 38.6%) than by chimpanzees only (16 species; 36.4%). Thus, cercopithecine RF diets are not merely a subset of the chimpanzee diet.

A second test of Hypothesis 1A is whether the RF species uniquely eaten by chimpanzees contributed disproportionately to the total RF feeding time of chimpanzees. They did not (Table IV). In fact, RF species that were unique to each primate group contributed very little to total feeding time (8.5% for chimpanzees, mean of 4.3% for cercopithecines; Table IV). Conversely, RF species that were shared between chimpanzees and cercopithecines were eaten at a disproportionately high frequency. For

Table IV. Overlap in Ripe-Fruit Diets: Percentage Time Feeding^a

RF eaten by	C	B14	B30	M14	M30	R14	R30	Monkey mean
Focal only	8.5	1.8	0.8	11.0	11.3	0.8	0.0	4.3
C	100	79.7	60.6	74.0	66.8	77.1	72.8	71.8
C, B, M, R	75.9	71.7	55.9	66.4	64.2	76.0	71.2	67.6

^aRF, ripe fruit. Cells show the percentage, of the total time eating ripe fruit, that was spent eating ripe fruits of the category shown. Fruit-species categories: focal only—species eaten only by the primate group listed; C—species eaten by chimpanzees; C, B, M, R—species eaten by all four primates during the study period. Data are for July 1992 to June 1993, averaged across 12 months. Monkey mean is the average for the 6 monkey groups (R14, B30, M14, M30, R14, R30).

example, RF species eaten by chimpanzees accounted for a mean of 71.8% of monkey RF feeding time.

A third test of Hypothesis 1A is whether RF species shared by chimpanzees and cercopithecines are higher-quality than those eaten by chimpanzees only. There is limited support for this: CT was lower in RF species eaten by both taxa than in those eaten by chimpanzees only ($t = 2.59$, $n_1 = 12$, $n_2 = 11$, $P < 0.02$). There is no other difference (Table V).

In sum, Hypothesis 1A receives no support from the list of RF species eaten or the time spent eating RF species, and only limited support from the antifeedant content of ripe fruits. There was no subset of RF species that cercopithecines ate as much as chimpanzees. Cercopithecines simply ate less ripe fruit in general than chimpanzees did.

Hypothesis 2: When Ripe-Fruit Pulp Is Not Eaten, the Diets of Chimpanzees and Cercopithecines Diverge

Hypothesis 2 is supported (Table II). When not eating ripe fruits, chimpanzees and cercopithecines tended to have strongly divergent diets. Chimpanzees ate piths and stems of terrestrial herbs more than cercopithecines did (10.8% versus 0 %, Table II). Conversely, there were three major classes of plant part that all six cercopithecine groups ate more than chimpanzees did: unripe fruits (25.7%), seeds (7.3%), and leaves (38.3%) versus 3.9, 0.1, and 9.3%, respectively (Table II).

To find out which of these items were particularly important as fallback foods during periods of ripe-fruit scarcity, we regressed the percentage of feeding time spent on different items against the fruit availability index (FAI) for each group. Items examined are ripe fruits, unripe fruits, leaves, seeds, piths, and flowers. We also created three larger categories: unripe

Table V. Antifeedant Concentrations in Ripe Fruits^a

	All RF species	Eaten by		
		Chimpanzees only	Monkeys only	Chimpanzees and monkeys
CT	3.1	4.4	4.3	0.8
RD	5.5	5.5	9.1	1.9
MT	23.7	18.9	46.6	10.2
TT	25.4	32.4	20.5	21.8
NDF	33.6	34.8	31.4	34.2
<i>N</i>	32	12	9	11

^aRF species, ripe-fruit species. Cells show mean concentrations across plant species; see Table IV for units. *N* = number of species with chemical data. Antifeedant levels were compared among RF species eaten by chimpanzees only, by monkeys only, or by both taxa.

fruits plus seeds (UF+S), leaves plus piths (L+P), and bark plus wood plus root (B+W+R). Fallback foods are items for which percentage of time feeding is negatively correlated with the fruit availability index (FAI) ($P < 0.05$, 2-tailed).

Using this criterion, we identified fallback foods for three groups.

For chimpanzees, they were piths ($r = -0.66$, $n = 12$ months, $P < 0.05$) or leaves plus piths ($r = -0.67$, $P < 0.05$).

For guenons, they were unripe fruits and seeds. For blue monkeys in K30 (B30), they were unripe fruits plus seeds (UF+S) ($r = -0.63$, $P = 0.05$). For red-tailed monkeys in K30 (R30), they were unripe fruits ($r = -0.75$, $P < 0.02$) or UF+S ($r = -0.78$, $P < 0.01$). Unripe fruits and seeds were also eaten less when FAI was high for B14 and R14 ($r = -0.35$ and -0.50 , respectively, ns). Accordingly, for blue monkeys and red-tailed monkeys, Hypothesis 2 is supported by evidence that when ripe fruits were scarce, their diets differed increasingly from those of chimpanzees, with chimpanzees using more vegetative matter (leaves and piths), while the guenons ate more unripe fruits and seeds.

For mangabeys there was no evidence of any particular class of plant items acting as fallback foods.

A seasonal shift toward a particular class of plant items is not the only kind of response that has been documented to fruit scarcity. For chimpanzees, it has also been shown that dietary diversity increases when ripe fruit is scarce (Basuta, 1989; Wrangham *et al.*, 1991). We therefore compared chimpanzees and cercopithecines by plotting dietary diversity, measured by the distribution of time spent eating different items, against group-specific FAIs (Fig. 3). When fruit was abundant, dietary diversity was low for chimpanzees. As fruit became scarcer, chimpanzee diets became more diverse (r

= -0.64, $n = 12$ months, $P < 0.02$). In contrast, in all months cercopithecines had diverse diets, i.e., they spread their feeding time as widely as chimpanzees did when fruit was scarce. This analysis shows that with respect to the distribution of feeding time across different food items, Hypothesis 2 is rejected: chimpanzees and cercopithecines converged on a similar level of high dietary diversity when fruit was scarce. Nevertheless, Hypothesis 2 is supported in terms of the particular items eaten.

Hypothesis 3: In the Diet as a Whole, Cercopithecines Ingest More Antifeedants Than Chimpanzees Do

To test Hypothesis 3 we assayed levels of antifeedants (AF) in as many food items as possible (Table VI) and combined them with monthly data on time spent eating each item to yield a weighted mean intake of antifeedants (WMIAF).

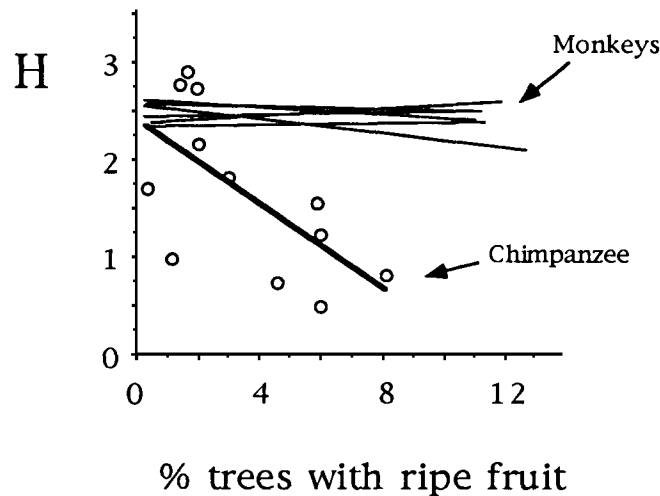


Fig. 3. Feeding-time diversity in relation to fruit availability. H is the Shannon-Weiner diversity index, i.e., $H = \Sigma(p_i(\log p_i))$, where p_i is the proportion of feeding time spent on the i th plant food item. The percentage of trees with ripe fruit was calculated separately for each primate group. Least-squares regression lines are shown for chimpanzees (bold, with monthly data points shown) and 6 monkey groups. Chimpanzees: $r = -0.64$, $n = 12$ months, $P < 0.05$. Monkey groups: $r = -0.42$ (B14), -0.51 (B30), -0.08 (M14), -0.03 (M30), $+0.01$ (R14), and $+0.04$ (R30); none of the monkey regressions is statistically significant.

In the diet as a whole, chimpanzees had lower intake than any of the cercopithecines for four classes of antifeedant (Table VII). ANOVA comparisons are significant for CT, RD, and MT (CT, $F = 3.496$, $p = 0.01$; RD, $F = 3.984$, $p < 0.01$; MT, $F = 2.708$, $p < 0.05$). For TT, differences are not significant by ANOVA. However, TT intake was lower for chimpanzees than for the 6 cercopithecine groups as a whole ($t = 8.29$, $n_1 = 1$, $n_2 = 6$, $p < 0.001$).

For the fifth antifeedant, NDF chimpanzees and monkeys ingested comparable levels throughout the year.

In summary, Hypothesis 3 is supported for condensed tannins (CT), total tannins (RD), monoterpenoids (MT), and triterpenoids (TT) but not for neutral-detergent fiber (NDF).

Hypothesis 4: When Ripe Fruit Is Scarce, Both Chimpanzees and Cercopithecines Ingest More Antifeedants

To test Hypothesis 4, we regressed monthly WMIAF against fruit availability indices (FAI) for each primate group (Table I). A negative correlation of WMIAF with FAI would support Hypothesis 4.

Hypothesis 4 is not supported. Only 1 of the 35 regressions (5 antifeedants \times 7 primate groups) of WMIAF versus FAI was significantly negative (RD, for chimpanzees: $r = -0.66$, $df = 11$, $P < 0.02$), whereas five of them, all for monkeys, were significantly positive (for RD, B30, M14, and R14, $p < 0.01$; for MT, M14 and R14, $p < 0.01$).

It is possible that this overall rejection of Hypothesis 4 masks important differences in the seasonal intake of antifeedant classes. At one extreme, the clearest rejection of Hypothesis 4 is provided by MT, for which all slopes were positive, including strong correlations for M14 ($r = 0.78$)

Table VI. Antifeedant Concentrations by Plant Part^a

	RF	UF	L	S	P	FL
CT	3.1	4.7	5.8	3.6	0.5	6.2
RD	5.2	6.1	6.9	3.5	0.7	6.1
MT	23.7	17.3	5.9	9.6	1.1	8.2
TT	25.4	22.8	28.6	13.3	8.4	25.1
NDF	33.6	38.7	40.7	46.1	40.0	35.5
<i>N</i>	32	35	75	18	12	18

^aRF, Ripe fruit; UF, unripe fruit (pulp, not seed); L, leaf (including petioles, young leaf, and mature leaf), S, seed; P, pith; FL, flower. Antifeedant concentrations as in Table V. *N* = number of species.

Table VII. Mean WMIAF (Weighted Mean Intake of Antifeedants)^a

	CT	RD	MT	TT	NDF
C	1.2 ± 0.7	1.9 ± 1.8	5.4 ± 3.5	9.7 ± 6.8	33.6 ± 4.5
B14	2.0 ± 1.3	3.9 ± 1.2	13.8 ± 5.9	13.8 ± 4.8	32.3 ± 2.9
B30	1.7 ± 0.8	3.7 ± 1.3	13.1 ± 7.8	13.2 ± 3.8	33.2 ± 3.7
M14	2.1 ± 0.8	3.8 ± 0.9	13.7 ± 6.2	13.3 ± 5.2	32.0 ± 3.3
M30	3.2 ± 1.9	4.2 ± 1.7	12.7 ± 6.9	13.5 ± 6.0	33.9 ± 4.6
R14	1.9 ± 0.9	3.5 ± 1.1	11.4 ± 6.0	13.2 ± 5.0	31.3 ± 4.0
R30	2.8 ± 1.8	4.4 ± 1.8	12.6 ± 5.7	12.6 ± 4.5	31.7 ± 3.1

^aCells show means ± standard deviations, across 12 months (July 1992 to June 1993).

R30 ($r = 0.68$). This suggests that monoterpenes may be particularly high in the fruit component of the diet, as Table VI confirms.

In contrast to MT, all 7 primate groups ate more CT when fruit was scarce. Although the correlation was not statistically significant for any of the groups, the uniformly negative slopes mean that overall, intake of CT declined with increasing fruit abundance, in support of the hypothesis (Sign test, $P < 0.02$) and in line with the result for chimpanzee intake of RD.

Hypothesis 5: When Ripe Fruit Is Scarce, Cercopithecines Ingest Relatively Higher Loads of Antifeedants Than Chimpanzees Do

The rejection of Hypothesis 4 means that Hypothesis 5 is unlikely to be supported, though in theory it still could be. For each of the antifeedants, we tested Hypothesis 5 by subtracting chimpanzee WMIAF's from cercopithecine WMIAF's. Our prediction was that this cercopithecine-chimpanzee difference would be higher in months when ripe fruits were scarce. Ripe-fruit availability was indexed by the mean FAI.

The result is clear. Whether chimpanzee WMIAFs were compared with the WMIAF for each monkey group separately, or with the mean WMIAF across monkey groups, the cercopithecine-chimpanzee difference never increased when fruits were scarce. Thus, Hypothesis (5) is rejected for all 5 antifeedants.

DISCUSSION

Dietary separation among species of the same guild within primate communities is normally discussed in terms of body size. Chimpanzees,

which are larger than cercopithecines, might be expected to have a lower-quality diet. We found the opposite.

The first major difference was in plant parts. Chimpanzees spent more time eating ripe fruits than cercopithecines did, and their time spent eating ripe fruit was more closely related to its availability than it was for blue monkeys or mangabeys (Fig. 2). Conversely, chimpanzees spent little time eating unripe fruit or seeds, whereas these were fallback foods for blue and red-tailed monkeys and were major items in the diets of all cercopithecines. Fruits selected by chimpanzees were scarcer than those selected by monkeys. These results are the first simultaneous comparisons of the diets of sympatric chimpanzees and cercopithecines. Because they take account of differences in fruit availability, the 1992–1993 data provide the first controlled evidence for ripe-fruit specialization by chimpanzees.

Further data from other sites and other years will test our conclusions. For example, in other years in Kibale we have recorded chimpanzees eating unripe fruit of figs more than was recorded in this study, though apparently not enough to challenge the principle of the difference seen here. In general, the 1992–1993 diets of Kibale chimpanzees and cercopithecines appear typical of those since our observations of chimpanzees began in 1987.

The conclusion that chimpanzees are indeed ripe-fruit specialists compared to cercopithecines is somewhat surprising because there is no obvious reason why ripe fruits that are palatable to chimpanzees should not be equally attractive to cercopithecines. Cercopithecines can sometimes eat more ripe fruits than reported here, e.g., blue monkeys, 54.6% of feeding time; red-tailed monkeys, 61.3%; Kakamega Forest, Kenya (Cords, 1986, 1987). However, even when ripe fruits were abundant and widely distributed, Kanyawara cercopithecines maintained high dietary diversity and spent less time than chimpanzees eating ripe fruits. For example, in June 1993 there was a high density of *Uvariopsis congensis* fruit throughout K30, yet no monkey group ate it as much as chimpanzees did. It appears that cercopithecines were not prevented by fruit distribution from having a high intake of ripe fruit. Instead, they were less interested in selecting ripe fruit than chimpanzees were. It is not clear why this should be.

The second major difference was in dietary chemistry. For four classes of chemicals assumed to be antifeedants, cercopithecines had absolutely higher intakes: condensed tannins (CT), total tannins (RD), monoterpenes (MT) and triterpenes (TT). For the fifth (NDF), intake did not differ between chimpanzee and cercopithecine diets (Table VII), but because smaller animals are expected to eat less NDF, chimpanzees appear to have had a relatively low NDF intake. Thus, although little is known about the relative ability of chimpanzees and cercopithecines to digest fiber (Milton and Demment, 1988; Maisels, 1993), among ruminants larger species tend

to eat more NDF (van Soest, 1994). Our study cercopithecines were much smaller than chimpanzees (estimated body weights (female-male): chimpanzees, 40–50 kg; blue monkeys, 3–6 kg; red-tailed monkeys, 3–4 kg; mangabeys, 7–10.5 kg (Kerbis Peterhans *et al.*, 1992; Struhsaker and Leland, 1979). Antifeedant intake by cercopithecines thus appears relatively high for all five classes analyzed.

Is there a cost of antifeedants to cercopithecines, and if so, how can they afford it? Unfortunately, it is difficult to predict how costly a particular chemical is or how it will influence food selectivity (Freeland and Saladin, 1989). The differences in antifeedant intake between chimpanzees and cercopithecines are most easily explained by assuming that cercopithecines pay a cost that chimpanzees avoid, but why the costs should differ among primates is unknown.

There are at least three possibilities. First, costs of antifeedant intake may be reduced partly by behavior. For instance, by eating small amounts at one time, animals can dilute the harmful effect of a particular antifeedant, i.e., cafeteria-style feeding (Kingsbury, 1978). Thus, the higher diversity of cercopithecine diets may contribute to allowing high antifeedant intake.

Secondly, morphological adaptations are potentially relevant. For example, cercopithecines have molars with high cusps and crowns, long shearing blades, and large crushing surfaces relative to body mass (Kay and Hylander, 1978). This may enable them to utilize NDF relatively effectively through fine comminution of vegetable matter. In support of this idea, particle size in feces appears to be smaller in cercopithecines than in chimpanzees (personal observation). However, tooth morphology provides only equivocal support for this interpretation. All three of our cercopithecines fall below a regression line for shearing crest length, well among the frugivores (Kay, 1984). Red-tailed and blue monkeys fall closer to folivores than to chimpanzees in a regression of incisor breadth and body mass, but mangabeys are if anything farther into the frugivore zone than chimpanzees (Kay and Hylander, 1978). Thus the adaptive significance of NDF differences in the diets of the Kibale frugivores remains to be explored.

Thirdly, physiological adaptations for high antifeedant intake are likely to be important. For example, in herbivorous mammals proline-rich salivary proteins (PRP's) protect against the nitrogen-reducing properties of dietary tannins (Mole *et al.*, 1990). Unfortunately differences in PRPs are unknown for chimpanzees versus cercopithecines. Detoxification mechanisms can vary adaptively and may do so among prosimians (Ganzhorn 1988) but are unstudied for chimpanzees versus cercopithecines.

Understanding such adaptations is important to resolve the effects of antifeedants on the evolution of metabolic strategies. For example, contrary to expectation, antifeedant intake did not vary systematically with ripe-fruit abundance (except for RD in chimpanzee diets), even though food items appeared to be lower-quality when fruit was scarce. This suggests that antifeedant intake levels were maintained close to a physiological maximum at all times, and therefore that the ecological role of antifeedant adaptations is to set dietary breadth, rather than to modulate dietary costs. In other words, the costs of eating antifeedants should be paid by evolutionary adaptations, not by energetic losses at the time of eating (Andrews, 1981). The high-quality diet of chimpanzees has been argued to allow them to fuel a large brain (Aiello and Wheeler, 1995). Thus, specific differences in antifeedant adaptations may be responsible for important issues in energy allocation.

In sum, our data support the hypothesis that chimpanzees are ripe-fruit specialists, whereas cercopithecines eat a lower-quality diet including higher antifeedant intake. Such differences are significant for understanding ecological separation within the frugivore community, socioecological influences on grouping patterns, and evolutionary adaptations including metabolic allocation strategies. An important next step is to find out whether the chimpanzee–cercopithecine difference reported here occurs in other African forests and, if so, whether it is an example of a more generalized difference between apes and cercopithecines.

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REFERENCES.

- Aiello, L. C., and Wheeler, P. (1995). The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. *Curr. Anthropol.* 36: 199-221.
- Andrews, P. J. (1981). Species diversity and diet in monkeys and apes during the Miocene. In Stringer, C. B. (ed.), *Aspects of Human Evolution*, Taylor and Francis, London, pp. 25-41.
- Basuta, G. I. (1989). Feeding ecology of chimpanzees in the Kibale Forest, Uganda. In Heltne, P. G., and Marquardt, L. A. (eds.), *Understanding Chimpanzees*, Harvard University Press, Cambridge, MA, pp. 116-127.
- Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecol. Monog.* 60: 1-26.
- Calvert, J. J. (1985). Food selection by western gorillas (*G. g. gorilla*) in relationship to food chemistry. *Oecologia* 65: 236-246.
- Chapman, C. A., and Wrangham, R. W. (1993). Range use of the forest chimpanzees of Kibale: implications for the understanding of chimpanzee social organization. *Am. J. Primatol.* 31: 263-273.
- Chapman, C. A., White, F., and Wrangham, R. W. (1994). Party composition and tree-fruit parameters in chimpanzees and bonobos. In Wrangham, R. W., McGrew, W. C., de Waal, F. B., and Heltne, P. G. (eds.) *Chimpanzee Cultures*, Harvard University Press, Cambridge, MA, pp. 41-58.
- Chapman, C. A., Wrangham, R. W., and Chapman, L. J. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behav. Ecol. Sociobiol.* 32: 199-209.
- Clutton-Brock, T. H. (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In Clutton-Brock, T. H. (ed.) *Primate Ecology: Studies of Feeding and Ranging in Lemurs, Monkeys, and Apes*, Academic Press, London, pp. 539-556.
- Clutton-Brock, T. H., and Harvey, P. H. (1979). Home range size, population density and phylogeny in primates. In Bernstein, I. S., and Smith, E. O. (eds.), *Primate Ecology and Human Origins*, Garland Press, New York, pp. 201-214.
- Conklin, N. L., and Wrangham, R. W. (1994). The value of figs to a hind-gut fermenting frugivore: A nutritional analysis. *Biochem. Syst. Ecol.* 22:137-151.
- Conklin-Brittain, N. L., Wrangham, R. W., and Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *Int. J. Primatol.* 19: 971-997.
- Cords, M. (1986). Interspecific and intraspecific variation in diet of 2 forest guenons, *Cercopithecus ascanius* and *C. mitis*. *J. Anim. Ecol.* 55: 811-827.
- Cords, M. (1987). *Mixed-Species Association of Cercopithecus Monkeys in the Kakamega Forest, Kenya*, University of California Publications in Zoology, Vol. 117.
- Davies, A. G., Bennett, E. L., and Waterman, P. G. (1988). Food selection by two South-East Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biol. J. Linn. Soc.* 34: 33-56.
- Freeland, W. J., and Saladin, L. R. (1988). Choice of mixed diets by herbivores: The idiosyncratic effects of plant secondary compounds. *Biochem. Syst. Ecol.* 17: 493-497.
- Ganzhorn, J. U. (1988). Food partitioning among Malagasy primates. *Oecologia* 75: 436-450.
- Ganzhorn, J. U. (1989). Primate species separation in relation to secondary plant chemicals. *Hum. Evol.* 4: 125-132.
- Gaulin, S. J. C., and Konner, M. (1977). On the natural diet of primates, including humans. In Wurtman, R. and Wurtman, J. (eds.), *Nutrition and the Brain, Vol. I*, Raven Press, New York, pp. 1-86.
- Gautier-Hion, A. (1980). Seasonal variations of diet related to species and sex in a community of *Cercopithecus* monkeys. *J. Anim. Ecol.* 49: 237-269.
- Gershenson, J., and Croteau, R. (1991). Terpenoids. In Rosenthal, G. A., and Berenbaum, M. R. (eds.) *Herbivores, Their Interactions With Secondary Plant Metabolites. Vol. 1. The Chemical Participants*, Academic Press, San Diego, pp. 165-219.

- Ghiglieri, M. P. (1984). *The Chimpanzees of Kibale Forest*, Columbia University Press, New York.
- Glander, K. E. (1982). The impact of plant secondary compounds on primate feeding behavior. *Yrbk. Phys. Anthropol.* 25: 1-18.
- Guillotin, M., Dubost, G., and Sabatier, D. (1994). Food choice and food competition among the three major primate species of French Guiana. *J. Zool. (Lond.)* 233: 551-579.
- Hagerman, A. E. (1987). Radial diffusion method for determining tannin in plant extracts. *J. Chem. Ecol.* 13: 437-449.
- Harborne, J. B. (1993). *Introduction to Ecological Biochemistry*, 4th ed., Academic Press, London.
- Kay, R. F. (1984). On the use of anatomical features to infer foraging behavior in extinct primates. In Rodman, P. S., and J. G. H. Cant (eds.), *Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismal Biology of Prosimians, Monkeys and Apes*, Columbia University Press, New York, pp. 21-53.
- Kay, R. F., and Hylander, W. L. (1978). The dental structure of mammalian folivores with special reference to Primates and Phalangerioidea (Marsupialia). In Montgomery, G. G. (ed.), *The Biology of Arboreal Folivores*, Smithsonian Institution Press, Washington, DC, pp. 173-191.
- Kerbis Peterhans, J., Wrangham, R. W., Carter, M. L., and Hauser, M. D. (1994). A contribution to tropical rain forest taphonomy: Retrieval and documentation of chimpanzee remains from Kibale Forest, Uganda. *J. Hum. Evol.* 25: 485-514.
- Kingsbury, J. M. (1978). Ecology of poisoning. In Keeler, R. F., Van Kampen, K. R., and James, L. F. (eds.), *Effects of Poisonous Plants on Livestock*, Academic Press, New York.
- Kinzey, W. G., and Norconk, M. A. (1993). Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venequela. *Int. J. Primatol.* 14: 207-227.
- Leighton, M. (1993). Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. *Int. J. Primatol.* 14: 257-313.
- Lindroth, R. L. (1989). Mammalian herbivore-plant interactions. In Abrahamson, W. G. (ed.), *Plant-Animal Interactions*, McGraw-Hill, New York, pp 163-206.
- Maisels, F. (1993). Gut passage rate in guenons and mangabeys: Another indicator of a flexible feeding niche? *Folia Primatol.* 61: 35-37.
- Marks, D. L., Swain, T., Goldstein, S., Richard, A., and Leighton, M. (1988). Chemical correlates of rhesus monkey food choice: The influence of hydrolyzable tannins. *J. Chem. Ecol.* 14: 213-235.
- McKey, D. B., Gartlan, J. S., Waterman, P. G., and Choo, G. M. (1981). Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biol. J. Linn. Soc.* 16: 115-146.
- Milton, K. (1979). Factors influencing leaf choice by howler monkeys: A test of some hypotheses of food selection by generalist herbivores. *Am. Nat.* 114: 362-378.
- Milton, K. (1980). *The Foraging Strategy of Howler Monkeys*, Columbia University Press, New York.
- Milton, K., and Demment, M. W. (1988). Chimpanzees fed high and low fiber diets and comparison with human data. *J. Nutr.* 118: 1082-1088.
- Mole, S., Butler, L. G., and Iason, G. (1990). Defense against dietary tannin in herbivores: A survey for proline-rich salivary proteins in mammals. *Biochem. Syst. Ecol.* 18: 287-293.
- Oates, J. F., Swain, T., and Zantovska, J. (1977). Secondary compounds and food selection by colobus monkeys. *Biochem. Syst. Ecol.* 5: 317-321.
- Oates, J. F., Waterman, P. G., and Choo, G. M. (1980). Food selection by the south Indian leaf-monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* 45: 45-56.
- Provenza, F. D., and Cincotta, R. P. (1993). Foraging as a self-organizational learning process: accepting adaptability at the expense of predictability. In Hughes, R. N. (ed.) *Diet Selection: An Interdisciplinary Approach to Foraging Behaviour*, Blackwell Scientific Publications, Oxford, pp. 78-101.
- Rogers, M. E., Maisels, F., Williamson, E. A., Tutin, C. E. G., and Fernandez, M. (1992). Nutritional aspects of Gorilla food choice in the Lopé reserve, Gabon. In Matano, S.,

- Tuttle, R. H., Ishida, H., and Goodman, M. (eds.), *Topics in Primatology*, University of Tokyo Press, Tokyo, pp. 255-266.
- Rolls, E. T., Critchley, H. D., Wakeman, E. A., and Mason, R. (1996). Responses of neurons in the primate taste cortex to the glutamate ion and to inosine 5'-monophosphate. *Physiol. Behav.*, 59: 991-1000.
- Rudran, R. (1978a). Socioecology of the blue monkeys (*Cercopithecus mitis stuhlmanni*) of the Kibale Forest, Uganda. *Smithsonian Contributions to Zoology*, Smithsonian Institution Press, Washington, DC, Vol. 249, pp. 1-88.
- Rudran, R. (1978b). Intergroup dietary comparisons and folivorous tendencies of two groups of blue monkeys (*Cercopithecus mitis stuhlmanni*). In Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores*, Smithsonian Institution Press, Washington, DC, pp. 483-503.
- Struhsaker, T. T. (1978). Food habits of five monkey species in the Kibale Forest, Uganda. In Chivers, D. J., and Herbert, J. (eds.), *Recent Advances in Primatology, Vol. 1.*, Academic Press, New York, pp. 225-248.
- Struhsaker, T. T. (1980). Comparison of the behaviour and ecology of red colobus and redtail monkeys in the Kibale Forest, Uganda. *Afr. J. Ecol.* 18:33-51.
- Struhsaker T. T., and Leland, L. (1979). Sociobiology of five sympatric monkey species in Kibale forest, Uganda. *Adv. Study Behav.* 9:159-227.
- Temerin, L. A., and Cant, J. G. H. (1983). The evolutionary divergence of old world monkeys and apes. *Am. Nat.* 122(3): 335-351.
- van Soest, P. J. (1994). *Nutritional Ecology of the Ruminant*, Cornell University Press, Ithaca, NY.
- Waser, P. M. (1975). Monthly variations in feeding and activity patterns of the mangabey, *Cercocebus albigena*. *E. Afr. Wild. J.* 13: 249-263.
- Waser, P. M. (1976). *Cercocebus albigena*: site attachment, avoidance, and intergroup spacing. *Am. Nat.* 110: 911-935.
- Waser, P. M. (1977). Feeding, ranging, and group size in the mangabey *Cercocebus albigena*. In Clutton-Brock, T. H. (ed), *Primate Ecology*, Academic Press, London, pp. 183-222.
- Waser, P. M. (1987). Interactions among primate species. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, Chicago University Press, Chicago, pp. 210-226.
- Waterman, P. G., Mbi, C. N., McKey, D. B., and Gartlan, J. S. (1980). African rainforest vegetation and rumen microbes: Phenolic compounds and nutrients as correlates of digestibility *Oecol.* 47: 22-33.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour* 75: 262-299.
- Wrangham, R. W., and Waterman, P. G. (1983). Condensed tannins in fruits eaten by chimpanzees. *Biotropica* 15: 217-233.
- Wrangham, R. W., Conklin, N. L., Chapman, C. A., and Hunt, K. D. (1991). The significance of fibrous foods for Kibale Forest chimpanzees. *Phil. Trans. R. Soc. Lond. B* 334: 171-178.
- Wrangham, R. W., Chapman, C. A., Clark, A. P., and Isabirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: Implications for understanding the costs of great ape groups. In McGrew, W. C., Marchant, L. F., and Nishida, T. (eds.), *Great Ape Societies*, Cambridge University Press, Cambridge, pp.45-57.