



Dietary Response of Chimpanzees and Cercopithecines to Seasonal Variation in Fruit Abundance. II. Macronutrients

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In a continuation of our study of dietary differentiation among frugivorous primates with simple stomachs, we present the first comparison of differences in dietary macronutrient content between chimpanzees and cercopithecine monkeys. Previously we have shown that chimpanzee and monkey diets differ markedly in plant part and species content. We now examine whether this diet diversity is reflected in markedly different dietary macronutrient levels or the different feeding strategies yield the same macronutrient levels in their diets. For each primate group we calculated the total weighted mean dietary content of 4 macronutrients: crude lipid (lipid), crude protein (CP), water-soluble carbohydrates (WSC), and total nonstructural carbohydrates (TNC). We also calculated 4 fiber fractions: neutral-detergent fiber (NDF), which includes the subfractions hemicellulose (HC), cellulose (Cs), and sulfuric acid lignin (Ls). The HC and Cs are potentially fermentable fibers and would contribute to the energy provided by plant food, depending on the hind gut fermenting capacity of the individual primate species. The chimpanzee diet contained higher levels of WSC and TNC because during times of fruit abundance the chimpanzees took special advantage of ripe fruit, while the monkeys did not. The monkey diets contained higher levels of CP because the monkeys consumed a constant amount of leaf throughout the year. All four primate species consumed diets with similar NDF levels. However, the chimpanzees also took advantage of periods of ripe fruit abundance to decrease their Ls levels and to increase their

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HC levels. Conversely, the monkey diets maintained constant levels of the different fiber fractions throughout the year. Nevertheless, despite these differences, the diets of the 4 frugivores were surprisingly similar, considering the substantial differences in body size. We conclude that the chimpanzee diet is of higher quality, particularly of lower fiber content, than expected on the basis of their body size.

KEY WORDS: diet; ape; monkey; protein; lipid; fiber; sugar; seasonality.

INTRODUCTION

This paper is the second in a series on dietary separation among four sympatric frugivorous primates; one ape (chimpanzee, *Pan troglodytes schweinfurthi*) and three cercopithecine monkeys (red-tailed monkey, *Cercopithecus ascanius schmidti*; blue monkey, *C. mitis stuhlmanni*; gray-cheeked mangabey, *Lophocebus albigena johnstoni*, (Wrangham *et al.*, 1998). Our aim is to compare the chemistry, nature, and distribution of food items so as to answer two kinds of question. First, how do the diets differ? Second, what role do phylogenetic history, body size, and/or species-specific adaptations play in generating the dietary differences? In particular, what dietary differences distinguish chimpanzees from cercopithecines?

In general, chimpanzees have been considered to be ripe-fruit specialists and therefore have relatively high-quality diets, but few quantitative data have been available to examine this idea or to identify the nature of the difference between chimpanzees and other primates (Wrangham *et al.*, 1998). Here we assume that primate feeding behavior is best understood through a detailed analysis of nutritional and chemical ecology. Though single-species descriptions exist for many primate diets (Milton, 1979; Oates *et al.*, 1980; Glander, 1981; McKey *et al.*, 1981; Estrada, 1985; Calvert, 1985; Ganzhorn *et al.*, 1985; Marks *et al.*, 1988; Beeson, 1989; Nash and Whitten, 1989; Rogers *et al.*, 1990; Kool, 1992; Malenky and Stiles, 1991; Wrangham *et al.*, 1991, 1993; Leighton, 1993; Hamilton and Galdikas, 1994; Kar-Gupta and Kumar, 1994; Sterling *et al.*, 1994; Hill and Lucas, 1996; Mowry *et al.*, 1996; Yeager *et al.*, 1997), cross-specific comparisons are few (Hladik, 1971, 1977a; Milton 1981; Baranga, 1982, 1983; Simmen and Sabatier, 1996).

Assessing dietary quality across species is difficult because what may be good for one species may not be good for others. Therefore the indices of dietary quality are both the fiber content, which is expected to be inversely related to digestibility (Van Soest, 1994), and the presence of easily digested macronutrients: sugars, proteins, and lipids. In particular, the combination of macronutrients is considered more important than the abundance or lack of any one nutrient.

Two major classes of important plant antifeedant chemicals—tannins and terpenoids—occur at higher concentrations in the diets of cercopithecines than of chimpanzees (Wrangham *et al.*, 1998). A third major antifeedant—fiber, assayed as neutral-detergent fiber (NDF)—occurred at essentially the same level in the diets of all 4 primates (32.0–33.6%). Since larger animals are generally expected to eat lower-quality diets, the fact that the large-bodied chimpanzee (weight, 40–50 kg) consumed diets containing no more NDF than the small-bodied monkeys (weights, 3–10.5 kg) supports the hypothesis that chimpanzees selected a relatively high-quality diet.

Further evidence for chimpanzee selectivity is that they ate relatively more ripe fruit than the monkeys did, both in general and specifically during periods of fruit abundance (Wrangham *et al.*, 1998). Such observations raise the possibility that the diets of sympatric frugivores differ not only in antifeedants, but also in macronutrients such as protein, lipids, sugars, and fermentable fiber fractions. Little, however, is known about the macronutrient intake of our study species in the wild, other than one study of heavily provisioned chimpanzees in Gabon (Hladik, 1977b) and one of a second subspecies of *Cercopithecus mitis* in a southern Africa subtropical forest with little fruit available (Beeson, 1989).

Accordingly, we examined how dietary macronutrients differ among our 4 study species. Specifically, we examined whether the differences in specific diets are correlated with differences in dietary macronutrient or with any of the fiber subfractional levels.

Because competition among species is expected to be driven by specialization for nonpreferred resources (Boag and Grant, 1981; Robinson and Wilson, 1998), we consider the specific differences in macronutrient intake in the context of seasonal variation in food abundance. For frugivores, the overall level of food abundance is expected to be determined primarily by the availability of ripe fruits. We therefore expect that when more ripe fruit is available, dietary quality should increase and converge in all species. Conversely, specific differences in the macronutrient content of fallback foods—eaten more and contribute significantly more to the diet when ripe fruits are scarce—are expected to increase during periods of fruit scarcity.

The prediction of seasonal variation in dietary quality applies equally to macronutrients and to antifeedants. Contrary to expectation, in our previous study we found no rise in antifeedant intake by our 4 study species when fruit was scarce (Wrangham *et al.*, 1998). Possibly, therefore, all of them optimized their intake of antifeedants throughout the year. A foraging strategy that maximizes energy intake may necessarily incorporate a high level of antifeedants, up to a species-specific ceiling.

Nevertheless, since the macronutrients, fiber and other antifeedant contents of a plant are not necessarily linked, we still expect seasonality in

the macronutrient content of the diet. In addition to the major macronutrients, we consider distinguishing different NDF fractions according to their fermentability, to test the idea that more fermentable fractions are eaten when fruit is abundant.

Our study is accordingly organized around 4 hypotheses, as follows.

Hypothesis 1: When ripe fruit is scarce, the diet of both chimpanzees and cercopithecines is of lower macronutrient quality than when fruit is abundant.

Hypothesis 2: On a percentage basis, the macronutrient levels in the diets of our study species should be consistent with their body size differences. Because the cercopithecines are smaller than chimpanzees, cercopithecine diets are predicted to contain higher levels of macronutrients.

Hypothesis 3: As a corollary to Hypothesis 2, the high antifeedant content of the cercopithecine diet is expected to be associated with a higher percentage of macronutrients than that of chimpanzees.

Hypothesis 4: The fallback foods for each species, or the plant food items or parts consumed when ripe fruits are scarce, will make a significant contribution to the overall macronutrient or fiber content of the diet. Thus the macronutrient composition of the fallback diet will help to explain the overall nutritional differences of the diets.

We quantified the following macronutrients and fibers: crude lipid, crude protein (CP), water-soluble carbohydrates or simple sugars (WSC), total nonstructural carbohydrates (TNC), which includes polysaccharides and the WSCs, and two neutral-detergent fiber (NDF) fractions—hemicellulose and cellulose. The insoluble cell, wall or NDF, is generally considered a digestion inhibitor, especially the lignin subfraction (Oates, 1977; Oates *et al.*, 1980; Milton *et al.*, 1980; Calvert, 1985; Davies *et al.*, 1988; Hill and Lucas, 1996). However, the two other principal fractions of NDF, namely hemicellulose and cellulose, are partial sources of energy for species capable of hindgut fermentation, such as chimpanzees and cercopithecines (Bruorton and Perrin, 1988; Milton and Demment, 1988; Van Soest, 1994). Therefore, we regard them as potential macronutrients. In addition, however, all of the principal insoluble fiber fractions can bond chemically with macronutrients such as starch and protein, thereby slowing or preventing their digestion (Van Soest, 1994).

METHODS

We collected behavioral data and plant food samples from July 1992 to June 1993. We observed 2 monkey groups per species, whose ranges lay

in one of two adjacent compartments (designated K14 and K30) of the Kanyawara sector of Kibale National Park, Uganda, monthly. The chimpanzee ranges overlapped with both compartments K14 and K30 and extended beyond them. We observed monkeys during three 12-hr periods per group per month, each 1 week apart, and chimpanzees whenever they could be found. Details of behavioral and phenological observation are in Wrangham *et al.* (1998).

Chemical Analysis

We analyzed 408 plant food samples of 215 observed plant food items for macronutrient and fiber levels, which provided duplicate sampling of many species. The 215 items represented 68.5% of all plant items recorded as food, and 95.9% of all plant-feeding time across primate species (Wrangham *et al.*, 1998).

We collected samples of the plant food items and air-dried them in the field. We removed pulp from seeds and dried it separately. Our drying room is on the back of the kitchen in order to take advantage of the heat from the back of the fireplaces and the chimney. The roof is corrugated metal with a large panel of translucent corrugated fiberglass. The drying rack has thin plywood sides and 3 wire mesh (<1-cm² holes) shelves. Two-by-fours held the whole rack about 1 m off the ground. During rainy weather we placed 1–3 kerosene lamps under the rack, especially at night. The drying temperatures never exceeded 37°C. We used sheets of thin aluminum foil as drying trays. During the drying process we stirred the samples at least once per day. We closely monitored samples that tended to mold quickly, often because of a high sugar content, stirred them several times during the first day, and kept them in the warmest section of the drier. After drying, we placed the samples in labeled paper envelopes and stored them in large baskets hanging from the rafters, over the drying rack, near the chimney. This system was very successful; even during rainy weather samples would dry within a day or 2. By storing them in paper and keeping them in a warm, dry area of the room—the ceiling—no mold developed during storage of 1–4 months.

Chemical assays were performed in the nutritional ecology laboratory at Harvard University, Anthropology Department. We used samples that we used in the antifeedant study (Wrangham *et al.*, 1998). We determined crude protein (CP), water-soluble carbohydrates (WSC), lipid, fibers, and ash per Conklin and Wrangham (1994). In the fiber analysis (Van Soest, 1994), the total cell wall or neutral-detergent fiber (NDF) analysis measures all of the insoluble fibers: cellulose, hemicellulose, and lignin (and cutin if

present) together. The NDF is then subjected to an acid-detergent fiber (ADF) analysis, which solubilizes the hemicellulose (HC) fraction, which is then determined by subtraction: $NDF - ADF = HC$, and the ADF still contains the cellulose and lignin. The ADF is then subjected to 72% sulfuric acid, which solubilizes the cellulose (Cs) fraction, which is then determined by subtraction: $ADF - Ls = Cs$, and the resulting residue contains only lignin (Ls) and cutin, if present. Total nonstructural carbohydrates is also calculated $TNC = 100 - \% NDF - \% lipid - \% CP - \% ash$.

We present each macronutrient and fiber category as a weighted average per month, with the percentage of feeding time for each food item as the weighting coefficient. Kurland and Gaulin (1987) explained how weight-based intake estimates were more accurate than temporally-based estimates. However, it was the consumption of animal matter that seriously compromised their estimates. In this paper, we consider only the plant component of the diet, which shows a tighter relationship between temporal and weight-based estimates. In addition, the majority of the fruit seen eaten during the study required no manipulation before consumption.

We report values as percentage of room temperature (20°C) dry matter (aka air dry matter), rather than as percentage of 100°C dry matter (also referred to as 100% dry matter), which is the dry matter value commonly used in agricultural work. The exact nature of the dry matter determination is frequently not reported in primatological or ecological journals, but unfortunately it has an effect on the comparability of data among different publications. Room-temperature dry matter means that the samples have been dried initially at 40–60°C, the lower temperatures being preferable in order not to damage secondary plant compounds. The sample then equilibrates at room temperature and is ground up and weighed out for the various procedures. This dry matter is susceptible to atmospheric fluctuations in humidity, but when sample sizes are small, the determination of 100% dry matter takes second place to using the available sample for nutrient analysis. In addition, if an outside lab is performing the analyses, dry matter determination probably incurs an additional cost. Consequently, values are frequently reported as simply a percentage of room-temperature dry matter. The 100% dry matter is determined by weighing out a small subsample of <1 gram and drying it at 100°C for 8 hr (AOAC, 1984). This value is then multiplied times each subsample weight for the different analyses as a correction factor to remove the effect of atmospheric humidity fluctuations on the final values obtained. Normally 100% dry matter values are 2–3 percentage units higher than the room-temperature dry matter values. Hence the confusion when comparing values from different publications that have not specified which type of dry matter determination was used; it is important to be specific.

We used analysis of variance and Scheffé's multiple contrasts to determine differences among primate species. The accepted probability for the Scheffé's test is $P < 0.05$. We performed simple regressions to compare fruit availability to the chemical content of the diet. The sample size is 12 for each species, representing the 12 weighted-average, monthly diets per species. Two-tailed significance is used throughout.

RESULTS

Hypothesis 1: When Ripe Fruit Is Scarce, the Diet of Both Chimpanzees and Cercopithecines Has Lower Macronutrient Quality Than When Fruit Is Abundant.

The mean annual percentages for the chemical fractions in the diets are in Table I. Ripe fruit availability indices are shown in Table II. Figures 1–9 show the month-to-month variation in macronutrient or fiber levels in the diets of by the different primate groups. A list of the ripe fruit species eaten by the primates is in Wrangham *et al.*, 1998.

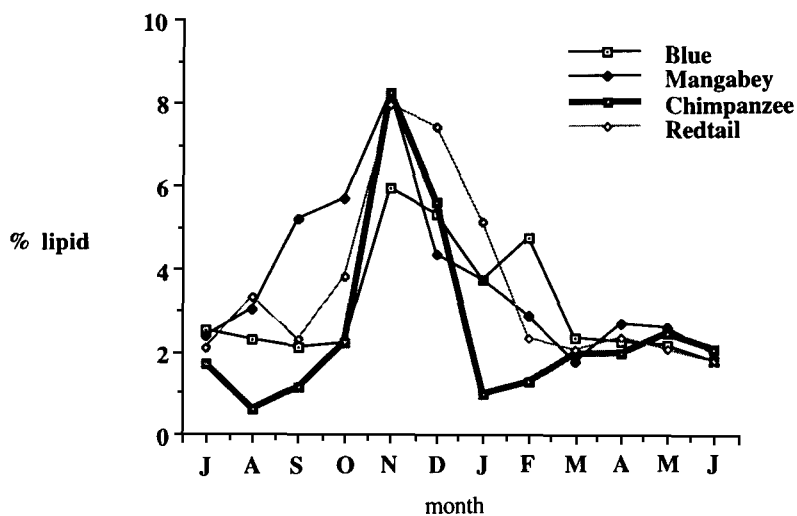


Fig. 1. Lipid content of primate diets as a percentage of the total dry matter in monthly diets.

Table 1. Chemical Fractions in the Diets as a Percentage of Room-Temperature (20°C) Dry Matter^a

	Lipid	CP	WSC	TNC	NDF	ADF	HC	Cs	Ls
Chimpanzee									
Mean	2.5	9.5 a	14.9 a	38.8 a	33.6	19.6	13.7	11.8	7.8
SD	2.2	3.0	8.3	7.8	4.5	5.8	4.4	4.7	2.3
B14									
Mean	3.5	17.6 b	8.7 b	35.3 a	32.3	20.2	11.8	12.3	7.9
SD	1.8	1.1	1.3	2.4	2.9	2.2	1.1	1.6	1.2
B30									
Mean	2.6	16.2 b	11.3 b	38.0 a	33.2	19.9	13.4	11.6	8.3
SD	1.5	2.3	2.2	2.7	3.7	2.3	2.2	1.8	1.4
M14									
Mean	3.9	16.3 b	9.8 b	34.0 b	32.0	19.8	12.0	11.9	7.9
SD	2.1	2.1	1.9	4.1	3.3	2.0	1.8	1.7	1.0
M30									
Mean	3.4	15.7 b	10.3 b	33.9 b	33.9	21.0	12.6	12.4	8.6
SD	2.0	2.1	2.0	5.4	4.6	3.3	1.9	1.7	2.2
R14									
Mean	3.6	17.6 b	9.9 b	36.5 a	31.3	19.7	11.4	11.6	8.1
SD	2.3	1.3	2.4	3.6	4.0	3.3	0.8	1.8	1.6
R30									
Mean	3.4	16.6 b	11.6 b	37.6 a	31.7	19.0	12.8	11.0	8.1
SD	2.5	1.8	2.6	4.4	3.1	2.5	1.1	1.5	1.2

^aThe values are means of 12 monthly percentages. Values followed by different letters (a, b) were significantly different across species ($P < 0.05$). Each mean is calculated from 12 monthly weighted averages per chemical fraction. CP, crude protein; WSC, water-soluble carbohydrates; TNC, total nonstructural carbohydrates; NDF, neutral-detergent fiber; ADF, acid-detergent fiber; HC, hemicellulose; Cs, cellulose; Ls, sulfuric acid lignin. B14, M14, and R14 are blue monkey, mangabey, and red-tailed monkey troops, respectively, in the K14 compartment of Kibale Forest. B30, M30, and R30 are blue monkey, mangabey, and red-tailed monkey troops, respectively, in the K30 compartment of Kibale Forest.

Table II. Fruit Availability Indices (FAIs) from Wrangham *et al.* (1998)^a

Month	C	B14	B30	M14	M30	R14	R30	Mean
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	10.7
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 the 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" shows mean FAI across the seven primate groups. B14, M14, and R14 are blue monkey, mangabey, and red-tailed monkey troops, respectively, in the K14 compartment of Kibale Forest. B30, M30, and R30 are blue, mangabey, and red-tailed monkey troops, respectively, in the K30 compartment of Kibale Forest.

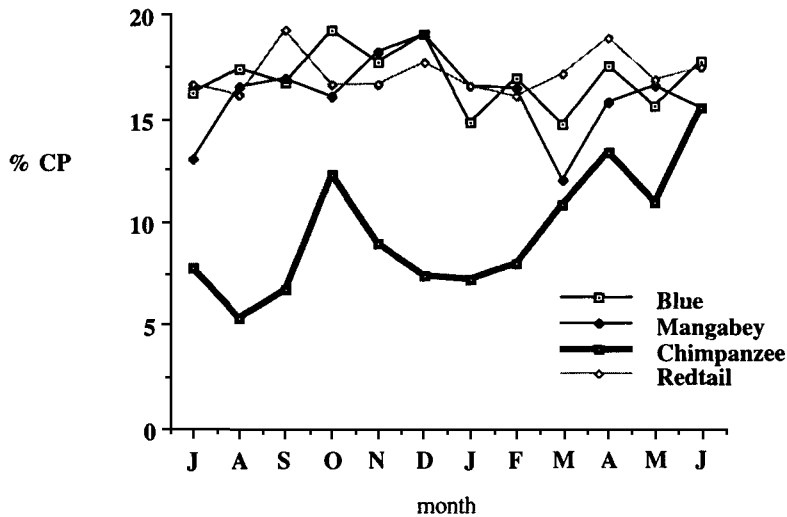


Fig. 2. Crude protein (CP) content of primate diets as a percentage of the total dry matter in monthly diets.

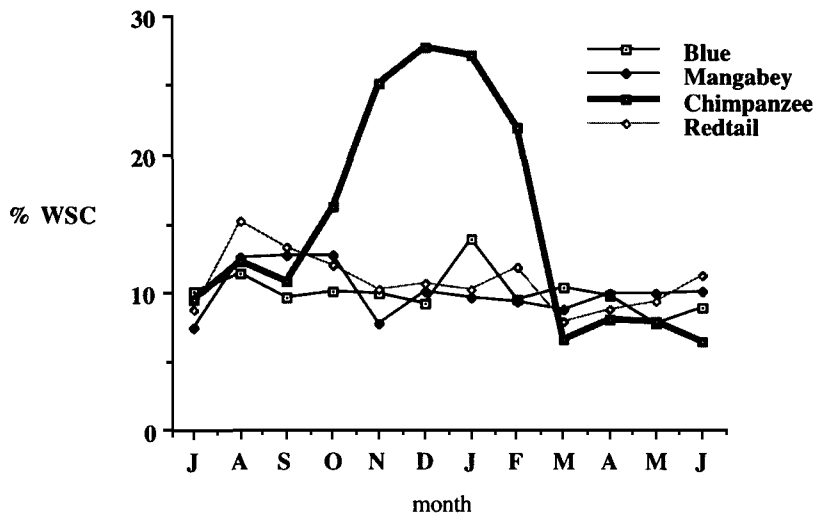


Fig. 3. Water-soluble carbohydrate (WSC) content of primate diets as a percentage of the total dry matter in monthly diets.

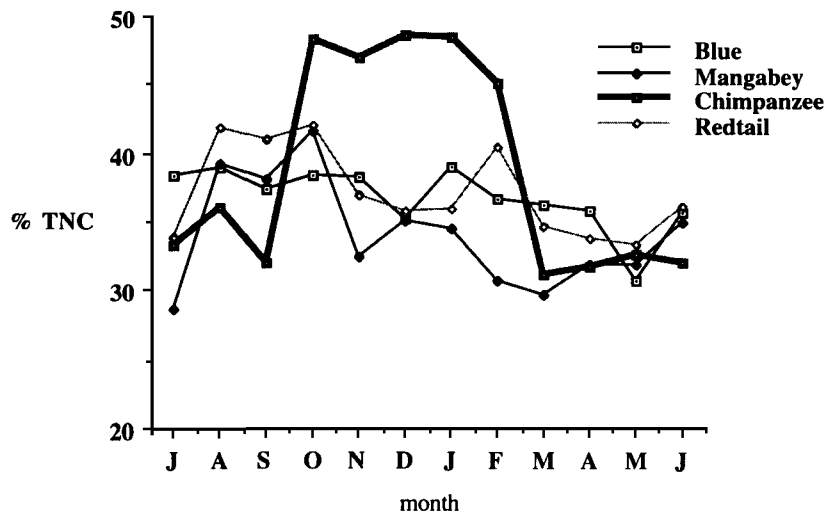


Fig. 4. Total non-structural carbohydrate (TNC) content of primate diets as a percentage of the total dry matter in monthly diets.

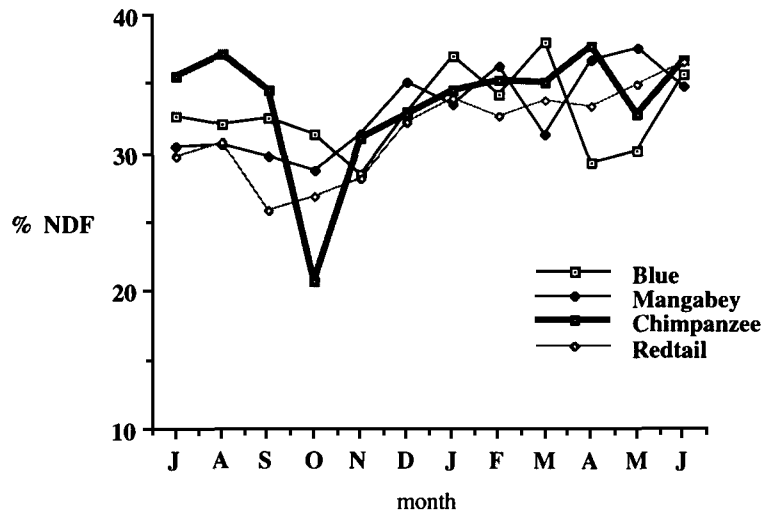


Fig. 5. Neutral-detergent fiber (NDF) content of primate diets as a percentage of the total dry matter in monthly diets.

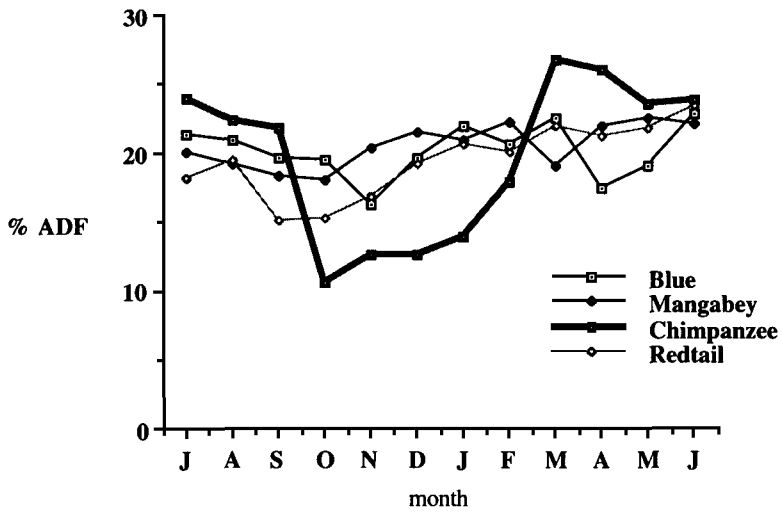


Fig. 6. Acid-detergent fiber (ADF) content of primate diets as a percentage of the total dry matter in monthly diets.

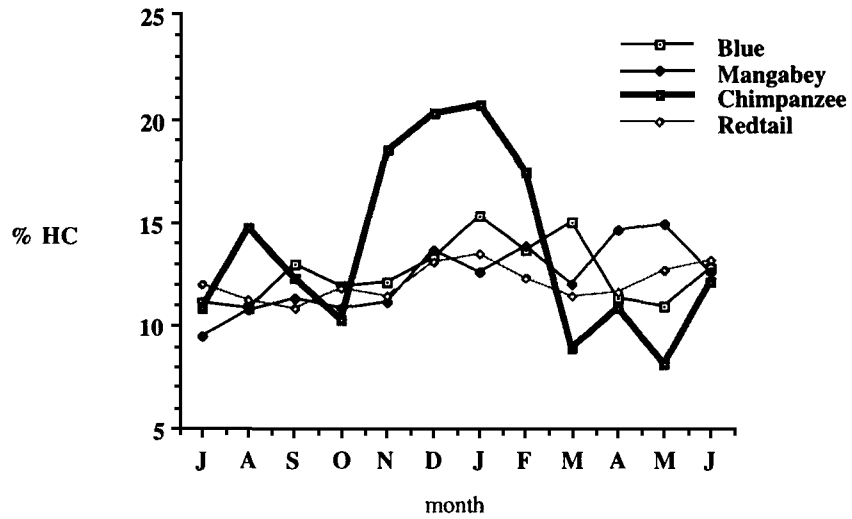


Fig. 7. Hemicellulose (HC) content of primate diets as a percentage of the total dry matter in monthly diets.

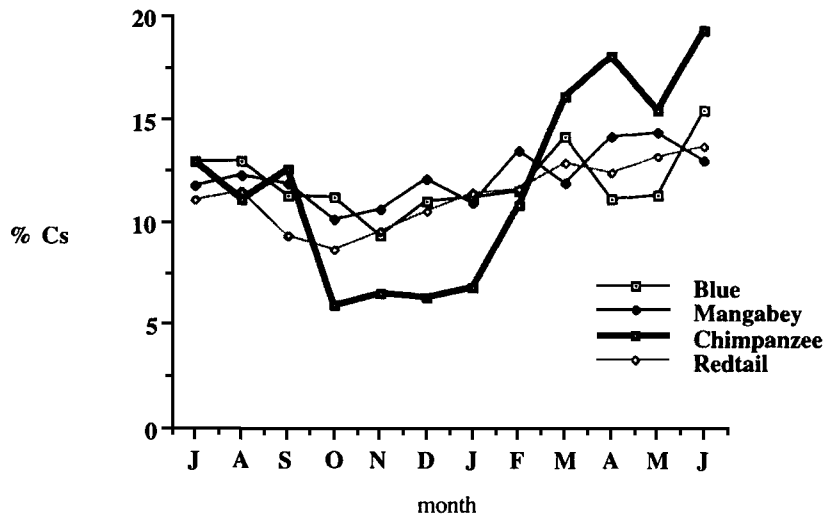


Fig. 8. Cellulose (Cs) content of primate diets as a percentage of the total dry matter in monthly diets.

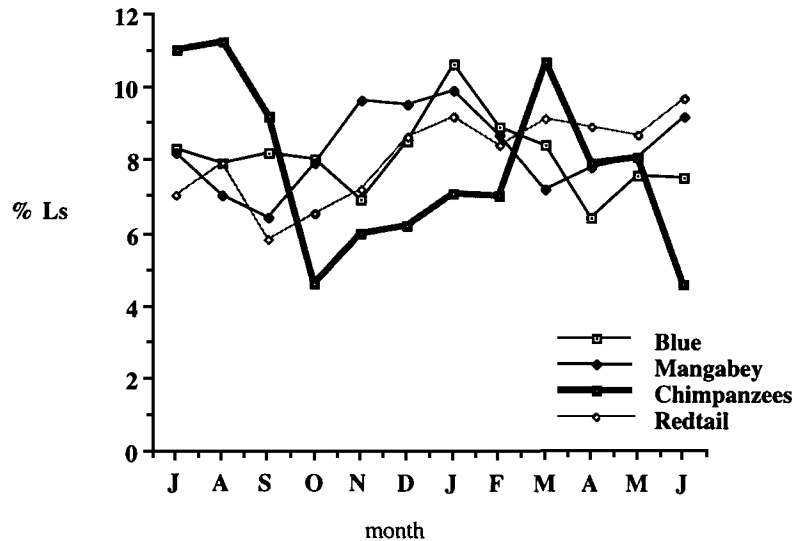


Fig. 9. Lignin (Ls) content of primate diets as a percentage of the total dry matter in monthly diets.

Overall, for the 4 primate species, the lipid fraction was the only macronutrient that showed seasonality in relation to ripe fruit availability. The chimpanzees, mangabeys in K30, and red-tailed monkeys in K30 consumed a diet significantly higher in lipid during times of ripe fruit abundance ($r^2 = 0.49$ and $P = 0.01$, $r^2 = 0.40$ and $P = 0.03$; $r^2 = 0.60$, $P = 0.003$, respectively). At those times, the blue monkeys in K30 and the mangabeys in K14 consumed a diet marginally higher in lipid ($P < 0.1$) ($r^2 = 0.31$, $P = 0.06$; $r^2 = 0.32$, $P = 0.06$, respectively).

Seasonal variation in the other nutrient fractions varied among the species. Chimpanzees were the only species that consumed a diet higher in simple sugars when ripe fruit was more abundant ($r^2 = 0.38$, $P = 0.032$). The chimpanzee diet was also the only one higher in total nonstructural carbohydrates during ripe fruit abundance ($r^2 = 0.48$ and $P = 0.01$), although the mangabeys in K14 showed a tendency in the same direction ($r^2 = 0.31$, $P = 0.06$).

For crude protein only, the blue monkeys in K14 consumed a diet significantly higher in protein during ripe fruit abundance at the $P < 0.05$ level ($r^2 = 0.65$, $P = 0.002$) and the mangabeys in K30 did so at the $P < 0.1$ level ($r^2 = 0.27$, $P = 0.08$).

The fiber fractions are distinguished by the general lack of seasonality. Surprisingly no species decreased the NDF content of their diet during

peak ripe fruit abundance. However, the chimpanzee diet varied with regard to the different fiber subfractions. During fruit abundance they decreased the dietary content of ADF (containing both cellulose, which is somewhat fermentable, and lignin, which is not fermentable) ($r^2 = 0.57$, $P = 0.004$), whereas they marginally increased the content of hemicellulose (a fermentable fiber) ($r^2 = 0.29$, $P = 0.07$). The combination of these trends explains why the chimpanzee total NDF level stayed the same. Chimpanzees also decreased cellulose content at the $P < 0.1$ level ($r^2 = 0.26$, $P = 0.09$) but what really caused the significant decrease in ADF content is the decrease in lignin present during peak ripe fruit abundance ($r^2 = 0.72$, $P = 0.0005$). Meanwhile, only mangabeys in K14 consumed a diet with less cellulose at the $P < 0.1$ level ($r^2 = 0.29$, $P = 0.07$) but surprisingly increased the lignin content of their diet at the $P < 0.05$ level ($r^2 = 0.36$, $P = 0.04$). No other primate changed the fiber levels in their diets throughout the year.

In conclusion, the chimpanzee was the only species that improved dietary quality during times of ripe fruit abundance. The only nutrient fraction the chimpanzees did not increase was crude protein, which stayed fairly level at a monthly average about 9.5% of dry matter. Accordingly hypothesis 1 is supported in the case of chimpanzees, but rejected for cercopithecines.

Hypothesis 2: On a Percentage Basis, the Macronutrient Levels in the Diets of Our Study Species Should Be Consistent with Their Body Size Differences. Because the Cercopithecines Are Smaller Than Chimpanzees, Cercopithecine Diets Are Predicted to Contain Higher Levels of Macronutrients.

Statistical comparisons of the macronutrient content of the diet using Scheffé's multiple contrasts are summarized in Table I. In spite of the considerable body size differences between chimpanzees and cercopithecines, there was no significant difference among species in the dietary levels of any fiber fraction, and crude protein was the only nutrient that the monkeys as a group consumed at higher levels than chimpanzees did ($F = 22.6$, $P = 0.0001$). In fact, the chimpanzees consumed a diet significantly higher in water-soluble carbohydrates (WSCs) compared to those of the monkeys ($F = 3.5$, $P = 0.004$) during peak ripe fruit abundance. There was no significant difference in WSC's among the monkeys, and when peak abundance months were excluded there was no difference between monkeys and chimpanzees ($F = 0.8$, $P = 0.60$). In addition, the chimpanzee diet contained somewhat more total nonstructural carbohydrates than were in the monkey

diet at the $P < 0.1$ level ($F = 2.1$, $P = 0.06$), though again, when peak abundance months were excluded there was no difference between monkeys and chimpanzees ($F = 0.9$, $P = 0.51$).

Thus, contrary to Hypothesis 2, body weight did not predict total macronutrient density in the diet.

Hypothesis 3: The High Antifeedant Content of the Cercopithecine Diet Is Expected to Be Associated with a Higher Percentage of Macronutrients Than That of Chimpanzees.

Because it provides amino acids, protein is potentially an important resource for use in detoxification, and may therefore be expected to be higher in the diets of species eating more antifeedants. As shown in the above discussion of Hypothesis 2, all 3 monkey diets contain significantly more crude protein than was in the chimpanzee diet.

However, the diets contained similar energy levels, reflecting the similar lipid and fiber levels in all diets. The calculated energy level of the chimpanzee diet (215.2 ± 42.9 kcal/g) was somewhat lower, but not significantly, than those of the monkeys [blue monkeys (B14, 243.6 ± 21.4 ; B30, 240.8 ± 21.4), red-tailed monkeys (R14, 249.0 ± 19.6 ; R30, 247.8 ± 29.0), and mangabeys' (M14, 236.5 ± 35.6 ; M30, 229.3 ± 32.0)]. We calculated these energy values via the human metabolizable energy conversion factors of 4 kcal/g of carbohydrate or protein and 9 kcal/g of fat (RDA, 1980), without considering any contribution from potentially fermentable fibers, and with no allowance for rates of intake.

In summary, the monkeys' diets contained more protein, as expected from a detoxification hypothesis, but there was no evidence that they experienced overall increases in energy availability.

Hypothesis 4: The Fallback Foods for Each Species, or Those Plant Food Items or Parts Consumed When Ripe Fruits Are Scarce, Will Make a Significant Contribution to the Overall Macronutrient or Fiber Content of the Diet. Thus the Macronutrient Composition of the Fallback Diet Will Contribute to Explaining the Overall Nutritional Differences of the Diets

We determined the principal (or preferred) foods, and fallback foods, by regressing the intake of ripe fruit, unripe fruit and seed, leaf, or pith against the availability of ripe fruit. We assayed ripe fruit availability by the mean percentage of fruit trees having ripe fruit in each month. It was calculated separately for each primate group, depending on the species of

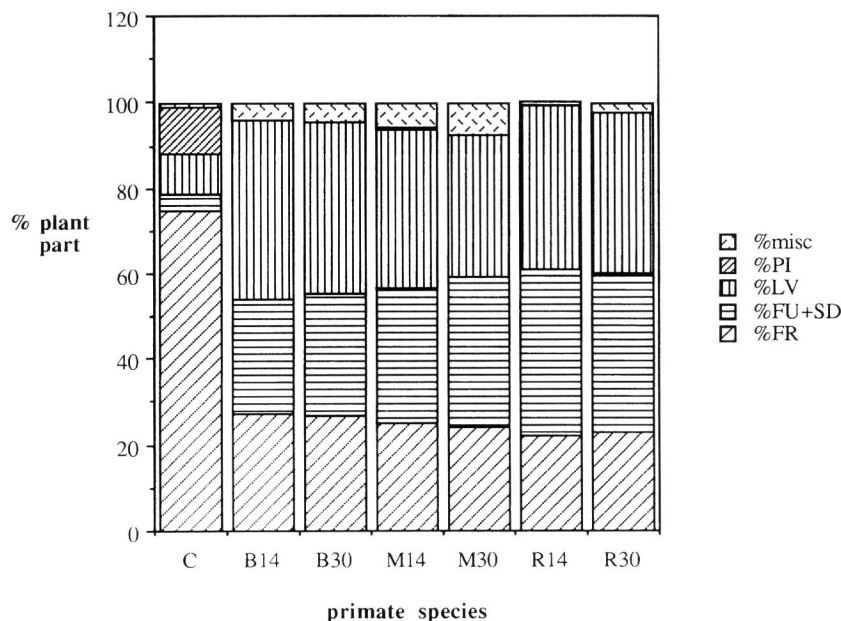


Fig. 10. Percentages of plant parts consumed per primate species annually. B14, M14, and R14 are blue monkey, mangabey, and red-tailed monkey troops, respectively, in the K14 compartment of Kibale Forest. B30, M30, and R30 are blue, mangabey, and red-tailed monkey troops, respectively, in the K30 compartment of Kibale Forest. C, chimpanzees; PI, pith; LV, leaves; FU + SD, unripe pulp and seeds; FR, ripe pulp.

fruits that they include in their diet and on the home range that they used, (Table II).

For the chimpanzee, ripe fruit was confirmed as the preferred food, because its intake increased significantly with the increase in ripe fruit abundance ($r^2 = 0.48$, $P = 0.01$). Pith (mainly from terrestrial herbs) was the principal fallback food, because its intake significantly increased as ripe fruit abundance decreased ($r^2 = 0.44$, $P = 0.02$). The intake of unripe fruit and seeds or leaves by chimpanzees was low and did not change significantly as ripe fruit abundance varied.

For the red-tailed monkeys, ripe fruit was also the principal food ($r^2 = 0.76$, $P = 0.0002$), and their principal fallback food is "unripe fruit and seed" ($r^2 = 0.43$, $P = 0.02$). Intergroup differences in monkey diets are small, and we ignored them for the sake of simplicity (Wrangham *et al.*, 1998). Red-tailed monkey intake of leaves did not change significantly with ripe fruit abundance, and we saw them consume no pith.

Table III. Chemistry of Food Categories Eaten by Primates^a

	% DM					
	Ripe fruit	Unripe fruit	Leaf	Seed	Pith	Flowers
Lipid	4.9	3.1	1.4	8.4	1.3	2.5
CP	9.5	12.0	22.1	14.3	11.1	20.8
WSC	13.9	8.0	5.3	9.8	11.0	8.5
NDF	33.6	38.7	40.7	46.1	40.0	35.5
ADF	23.8	27.1	27.5	30.7	26.7	24.5
HC	9.7	11.8	13.1	15.3	13.4	11.0
Cs	13.3	15.9	14.9	17.3	22.8	12.1
Ls	10.5	11.2	12.6	13.3	3.9	12.4
No. spp.	32	35	75	18	12	18

^aLipid, crude protein (CP), water-soluble carbohydrates (WSC), neutral-detergent fiber (NDF), acid-detergent fiber (ADF), hemicellulose (HC), cellulose (Cs), and sulfuric acid lignin (Ls) as a percentage of dry matter (DM).

The blue monkeys, though typically classified as frugivorous (Rudran, 1979; Cords, 1986), did not consume ripe fruit as their principal food. Their principal food was leaves, and they ate remarkably more leaves when fruit was abundant ($r^2 = 0.53$, $P = 0.007$). Their fallback food was unripe fruit or seeds ($r^2 = 0.32$, $P = 0.05$). Their intake of ripe fruit did not vary significantly with ripe fruit abundance, and they consumed no pith.

The mangabeys, also normally classified as frugivorous, did not change their intake of any food category significantly compared to ripe fruit abundance. They ate ripe fruit, unripe fruit and seeds, and leaves at the same levels throughout the year.

The contributions, in terms of feeding time, by different plant parts to the subjects' diets is shown in Fig. 10, specifically this is dietary content based on time spent feeding. Chimpanzees ate proportionately much more fruit than the monkeys did ($F = 11.4$, $P = 0.0001$) and compared to the other food categories ($F = 92.9$, $P = 0.0001$). Among the monkeys there was no significant difference in the annual diet of the different plant parts. Considering each monkey group separately, only red-tailed monkey diet in K14 included more leaf and unripe fruit and seeds compared to ripe fruit (Scheffé F -test = 3.4, $P < 0.05$) and blue monkeys in K14 included more leaf compared to ripe fruit (Scheffé F -test = 7.1, $P < 0.05$), or unripe fruit and seeds (Scheffé F -test = 8.0, $P < 0.05$). The other monkey groups consumed diets with statistically similar amounts of all three food categories on an annual basis.

The simple averages for nutrient content of different plant parts are in Table III. The contributions of macronutrients and fiber obtained from the different plant parts over 12 months are in Table IV. The majority of the protein in the monkeys' diets came from leaves, with unripe fruit and

Table IV. Percentage of Each Nutrient Fraction Provided by Different Plant Parts, Given the Percentage Contribution of Each Plant Part to the Diet (Fig. 10) and the Chemical Composition of Each Plant Part Category (Table III)^a

	RP	UP + SD	LV	PI	Conclusion
Crude protein (CP)					
R14	16.5 ± 10.1 a	38.0 ± 21.6 b	45.1 ± 16.9 b		CP from LV & UP + SD
R30	14.8 ± 12.8 a	35.0 ± 21.8 b	49.5 ± 18.3 b		CP from LV & UP + SD
M14	19.7 ± 12.6 a	31.1 ± 15.8 ab	45.4 ± 14.8 b		CP from LV & UP + SD
M30	17.9 ± 17.6 a	34.3 ± 15.6 ab	41.9 ± 18.2 b		CP from LV & UP + SD
B14	22.9 ± 8.8 a	26.1 ± 9.7 a	48.7 ± 8.4 b		CP from LV
B30	17.8 ± 10.0 a	27.2 ± 17.3 a	51.5 ± 15.8 b		CP from LV
C	74.9 ± 23.0 a	3.9 ± 5.1 b	15.6 ± 17.8 b	5.3 ± 5.6 b	CP from RP
Lipid					
R14	35.7 ± 25.7 a	47.8 ± 21.9 a	16.1 ± 8.4 b		lipid from RP & UP + SD
R30	29.7 ± 29.5 a	49.2 ± 24.8 a	20.5 ± 15.4 b		lipid from RP & UP + SD
M14	44.9 ± 26.4 a	37.3 ± 22.6 ab	15.8 ± 10.7 b		lipid from RP & UP + SD
M30	35.2 ± 27.5 ab	44.0 ± 23.6 a	15.7 ± 9.7 b		lipid from RP & UP + SD
B14	50.2 ± 20.0 a	31.0 ± 16.3 b	18.1 ± 5.9 b		lipid from RP & UP + SD
B30	33.8 ± 25.9 ab	41.3 ± 23.0 a	19.0 ± 7.3 b		lipid from RP & UP + SD
C	87.5 ± 10.6 a	7.5 ± 10.4 b	3.0 ± 3.6 b	1.8 ± 2.1 b	lipid from RP
Cell wall fiber (NDF)					
R14	18.2 ± 11.4 a	35.9 ± 21.3 ab	45.5 ± 17.1 b		NDF from LV & UP + SD
R30	21.9 ± 13.3 a	36.3 ± 18.4 ab	41.2 ± 16.8 b		NDF from LV & UP + SD
M14	20.0 ± 11.6 a	31.5 ± 15.9 ab	44.6 ± 14.1 b		NDF from LV & UP + SD
M30	19.8 ± 16.5 a	36.6 ± 15.5 b	38.5 ± 14.4 b		NDF from LV & UP + SD
B14	22.8 ± 8.7 a	23.7 ± 11.2 a	51.6 ± 10.4 b		NDF from LV
B30	22.9 ± 14.5 a	27.8 ± 16.6 a	45.6 ± 15.8 b		NDF from LV
C	79.1 ± 18.7 a	4.6 ± 5.8 b	6.2 ± 6.9 b	9.5 ± 11.5 b	NDF from RP
Nonstructural carbohydrates (TNC)					
R14	23.7 ± 15.5 a	43.2 ± 23.4 b	32.7 ± 14.7 ab		TNC from all
R30	26.0 ± 17.6 a	43.2 ± 22.2 a	30.2 ± 12.4 a		TNC from all
M14	25.9 ± 14.0 a	35.2 ± 15.6 a	31.8 ± 12.5 a		TNC from all
M30	26.6 ± 19.3 a	37.8 ± 16.5 a	27.4 ± 13.8 a		TNC from all
B14	30.9 ± 12.2 a	31.5 ± 12.6 a	35.9 ± 7.1 a		TNC from all
B30	32.5 ± 16.7 a	31.3 ± 19.2 a	32.8 ± 13.4 a		TNC from all
C	83.7 ± 17.6 a	4.0 ± 4.1 b	5.6 ± 7.6 b	6.3 ± 8.2 b	TNC from RP

^aIn rows, values followed by different letters (a, b) are significantly different ($P < 0.05$). RP, ripe pulp; UP + SD, unripe pulp and seed; LV, leaf; PI, pith. B14, M14, and R14 are blue monkey, mangabey, and red-tailed monkey troops, respectively, in the K14 compartment of Kibale Forest. B30, M30, and R30 are blue, mangabey, and red-tailed monkey troops, respectively, in the K30; C, chimpanzees.

Table V. Percentages of Each Antifeedant Fraction Provided by Different Plant Parts, Based on the Percentage Contribution of Each Plant to the Diet, shown in Fig. 10 and Wrangham *et al.* (1998)^a

	RP	UP + SD	LV	PI	Conclusion
Condensed tannin (CT)					
R14	12.7 ± 18.2 a	24.4 ± 28.6 a	62.7 ± 31.7 b		CT from LV
R30	9.9 ± 10.9 a	48.3 ± 27.4 b	41.7 ± 26.3 b		CT from LV & UP + SD
M14	5.0 ± 4.2 a	35.5 ± 28.6 b	55.6 ± 29.2 b		CT from LV & UP + SD
M30	5.0 ± 5.2 a	31.3 ± 20.2 b	56.7 ± 23.4 c		CT from LV & UP + SD
B14	6.7 ± 7.9 a	12.6 ± 12.5 a	79.7 ± 16.1 b		CT from LV
B30	10.4 ± 10.4 a	32.2 ± 32.2 ab	56.5 ± 30.4 b		CT from LV & UP + SD
C	61.3 ± 32.2 a	9.5 ± 19.2 b	25.5 ± 29.5 b	0.5 ± 0.8 b	CT from RP
Total tannin (RD)					
R14	8.9 ± 11.4 a	22.9 ± 25.4 a	68.1 ± 25.0 b		RD from LV
R30	14.0 ± 13.8 a	34.0 ± 20.8 b	51.9 ± 24.9 b		RD from LV & UP + SD
M14	7.3 ± 7.9 a	28.6 ± 24.9 a	62.2 ± 26.3 b		RD from LV
M30	10.4 ± 10.5 a	27.1 ± 15.6 b	56.7 ± 20.0 c		RD from LV & UP + SD
B14	11.0 ± 14.8 a	12.6 ± 10.6 a	76.0 ± 17.9 b		RD from LV
B30	15.3 ± 21.1 a	20.4 ± 21.5 a	63.7 ± 27.2 b		RD from LV
C	58.3 ± 34.0 a	11.2 ± 24.1 b	29.3 ± 31.0 ab	0.5 ± 1.6 b	RD from RP & LV
Monoterpenoids (MT)					
R14	22.5 ± 16.5 a	40.6 ± 23.9 a	36.7 ± 15.4 a		MT from all
R30	23.1 ± 22.9 a	37.3 ± 25.2 a	39.5 ± 18.4 a		MT from all
M14	31.5 ± 18.9 a	27.3 ± 17.8 a	39.5 ± 18.6 a		MT from all
M30	32.0 ± 27.3 a	33.0 ± 20.1 a	31.5 ± 19.5 a		MT from all
B14	33.9 ± 11.9 a	20.0 ± 12.2 b	45.9 ± 10.1 a		MT from all
B30	34.8 ± 24.7 a	26.2 ± 17.8 a	34.2 ± 18.2 a		MT from all
C	83.8 ± 14.7 a	8.9 ± 11.7 b	6.4 ± 12.6 b	0.7 ± 1.0 b	MT from RP
Triterpenoids (TT)					
R14	14.9 ± 14.7 a	29.0 ± 24.2 a	55.5 ± 21.1 b		TT from LV
R30	14.0 ± 10.4 a	33.0 ± 20.9 b	52.8 ± 18.9 c		TT from LV & UP + SD
M14	13.9 ± 13.2 a	23.3 ± 18.3 a	58.4 ± 21.3 b		TT from LV
M30	17.9 ± 17.4 a	24.7 ± 17.6 a	49.0 ± 17.1 b		TT from LV
B14	17.0 ± 15.0 a	18.8 ± 13.1 a	62.9 ± 15.7 b		TT from LV
B30	21.0 ± 15.8 a	18.8 ± 9.2 a	50.7 ± 19.3 b		TT from LV
C	76.5 ± 20.8 a	7.7 ± 10.3 b	7.9 ± 10.5 b	7.2 ± 9.4 b	TT from RP

^aIn rows, values followed by different letters (a, b, c) are significantly different ($P < 0.05$). RP, ripe pulp; UP + SD, unripe pulp and seed; LV, leaf; PI, pith. B14, M14, and R14 are blue monkey, mangabey, and red-tailed monkey troops, respectively, in the K14 compartment of Kibale Forest. B30, M30, and R30 are blue, mangabey, and red-tailed monkey troops, respectively, in the K30; C, chimpanzees.

seeds generally secondary. Ripe fruit provided significantly less of the total protein in the diet. Ripe fruit, however, provided the greatest proportion of protein in the chimpanzee diet.

Leaves also provided the majority of the fiber in the monkey diets, with unripe fruit and seeds again secondary; ripe fruit provided significantly less. Ripe fruit, again, provided the bulk of the fiber in the chimpanzee diet. The majority of the lipid in the diets of the 4 species came from ripe or unripe fruit. Ripe fruit provided the majority of lipid in the chimpanzee diet.

Total nonstructural carbohydrates (TNC), including sugars, starch, and nonstarch polysaccharides, were provided in equal proportions by ripe fruit, unripe fruit and seeds, and leaves in the monkey diets. Predictably, ripe fruit provided the majority of the TNC in the chimpanzee diet.

In conclusion, the chimpanzee fallback food—pith—did not significantly influence the macronutrient or fiber content of the chimpanzee diet. For the red-tailed monkeys, the protein, lipid, and fiber content of their diet derives significantly from their fallback food of unripe fruit and seed. For the blue monkeys the results were somewhat ambiguous but unripe fruits and seeds did not seem to have significantly influenced the macronutrient content of the diet, which tends to be dominated by leaves. Mangabeys did not have any clear-cut fallback food, but leaves dominated their dietary chemistry via protein and fiber content.

In summary, Hypothesis 4 is supported for cercopithecines but not for chimpanzees.

DISCUSSION

In at least four ways, the macronutrient composition of the diets of chimpanzees and cercopithecines conformed to expectations. Overall nutrient composition of the diet is rather similar across the four species, reflecting their generally similar frugivorous diets. Cercopithecines ate more protein than chimpanzees did, which is consistent with their smaller body mass and greater detoxification needs. Macronutrient differences among diets of the four species are most pronounced between chimpanzees and the three cercopithecine species than among the cercopithecines. Finally, our findings of seasonal differences in dietary composition, mostly for the chimpanzees, support the prediction that periods of fruit abundance would lead to higher-quality diets.

The quantitative details of these patterns were surprising, however. First, only chimpanzees improved their dietary quality when ripe fruit was abundant, especially in terms of reducing the less digestible fiber fractions

and increasing more digestible carbohydrates. This is not easily understood, since all species are expected to take advantage of better foraging conditions. There may be nonnutritional factors preventing the monkeys from changing and improving their diets. Alternatively, the cercopithecines may have digestive adaptations that differ from those of chimpanzees or among the monkey species, which means that ripe fruits are not always preferred items in their diet.

Second, the degree of similarity in the diets, especially fiber content, of the four primates is greater than expected from body weight differences. Body weights are substantially larger for chimpanzees [34–40 kg (female), 43–50 kg (male)] than for cercopithecines [gray-cheeked mangabeys, 6–7 kg (female) and 8–10.5 kg (male); blue monkeys, 3–4 kg (female) and 6 kg (male); red-tailed monkeys, 3 kg (female) and 4 kg (male)] (Wrangham *et al.*, 1998; Smith and Jungers, 1997). This could mean that chimpanzee diets are as expected, while the cercopithecines had particularly low-quality diets; or, alternatively, that chimpanzees eat exceptionally high-quality diets. Consideration of other species favors the latter explanation.

In general, smaller animal species are expected to consume diets higher in digestibility (and lower in fiber) because they have higher per kilogram body mass energy requirements per day, but have neither alimentary capacity nor a sufficiently slow passage rate to hold and ferment dietary fiber in order to extract the energy in these fibers (Parra, 1979; Demment and Van Soest, 1985). These observations apply to both ruminants and non-ruminants. There is a particularly pronounced drop in the consumption of fibrous plant parts by animals weighing less than 15 kg (Cork, 1994). Some small species can survive on higher-fiber diets. For example, the diets of laboratory rats, weighing <1 kg, and having no special digestive tract adaptations, must contain $\leq 40\%$ fiber (Keys *et al.*, 1970), and meadow voles, which have special gut adaptations, have a limit of 50–55% NDF (Keys and Van Soest, 1970). Since even the smallest of our subjects, the red-tailed monkeys (3–4 kg), consumed diets containing about 31% NDF, they clearly have a relatively low-fiber, high-quality diet compared to rodents. Supporting the notion of a high-quality diet, those of all our subjects had low fiber levels compared to western lowland gorillas (*Gorilla gorilla*), which weigh 71–170 kg (Smith and Jungers, 1997). The mean dietary fiber content, including soluble fibers, of 31 of the most commonly consumed gorilla foods is $74.0 \pm 12.9\%$ (Popovich *et al.*, 1997). This is not a weighted mean, and differences in intake were not considered, but it is much higher than the simple mean of $38.2 \pm 12.6\%$ NDF for 78 plant foods consumed by Kibale chimpanzees.

Accordingly, these comparisons suggest that both cercopithecines and chimpanzees have high-quality diets compared to other mammalian herbi-

vores. Furthermore, it seems likely that they are able to use the fiber that they ingest. The dietary NDF values in our study are slightly lower than those in an experimental high-fiber diet (34% NDF) that Milton and Dement (1988) fed to chimpanzees, which digested 54.3% of it, indicating a substantial capacity to extract energy from fiber. We found no comparable report on the capacity to cercopithecines to digest fiber. However, Maisels (1993) showed that cercopithecines have passage times similar to those of folivorous howlers (*Alouatta* sp.), suggesting again that retention would be adequate for effective fermentation, since folivorous monkeys in captivity digested 42.3–81.3% of fibrous diets (Milton *et al.*, 1980; Watkins *et al.*, 1985; Sakaguchi *et al.*, 1991). Thus, current data suggest that the NDF component of natural diets may provide frugivorous primates with significant amounts of energy.

Nevertheless, chimpanzee diets are relatively higher in quality than those of cercopithecines when body mass is taken into account. Specifically, the four primate diets contain similar levels of virtually all of the fiber fractions; and in months when there were specific differences in the dietary percentage of simple sugars and other easily digested or fermented carbohydrates, chimpanzees ate more of them than did cercopithecines.

Third, the protein composition of the monkey diets is higher than probably required. Given the relatively slow rate at which most primates mature, it has been predicted that they have low protein requirements (Case, 1978), and this has been confirmed for the few primates tested (Oftedal, 1991). Our results for chimpanzees, averaging 9.5% CP over the year (Conklin-Brittain *et al.*, 1997), also supports the theory. Although these particular species have not been tested in nitrogen balance studies, Beeson (1989) found that the diet of blue monkeys in Malawi contained only about 8.5% crude protein. Kibale blue monkey diets contain almost twice that amount. It is unclear, of course, whether the high protein intake at Kibale is an incidental result of the plant parts that are being consumed or the result of monkeys seeking out high protein foods. Assuming that their protein requirements are not >8–10% CP, it is difficult to support an argument that protein requirements are driving them to seek high protein foods.

Our fourth hypothesis concerns which plant food items provided the majority of the different macronutrient categories for the different primate species. Many primates derive a substantial part of their diets from ripe fruit, so that niche specialization is based on where they obtain the minor fraction of the diet (Gartlan *et al.*, 1978; Wrangham *et al.*, 1998). For Kibale chimpanzees, ripe fruit provides the great majority of the diet and also dominates the chemical composition of the diet. Their fallback food—pith, does not significantly influence the overall chemical composition of the diet. Contrarily, for the monkeys, leaves, whether or not they are significant fall-

back foods, influence the chemical composition of the diets. In particular, leaves significantly increase the crude protein and NDF contents of the diets. Overall the monkeys consumed practically equal proportions of ripe pulp, unripe pulp and seeds, and leaves over the course of 12 months. Consequently the leaves, containing more protein and fiber on average, could dominate those two nutrient categories. Lipid intake was so low that, while fruit dominated that category, its contribution to the diet is so small that it cannot explain selectivity.

Why did these reputedly frugivorous monkeys consume so much leaf? Evolutionarily they may be adapted to do so. Proximately, one possibility is that the protein provided by leaves is needed for detoxification reactions. Sulfur-containing amino acids—methionine and cysteine—provide sulfur in the liver for general detoxification reactions, particularly phenolics and tannins (Mandel, 1971). Specific amino acids are used intact in various conjugation or acetylation detoxification pathways, for example glycine, cysteine, glutamine, and the aromatic amino acids (Williams, 1959). Methyl groups, which can be supplied by amino acids, are used in methylation reactions to detoxify especially alkaloids (Williams, 1959).

However, leaves are also the source of the greatest concentration of secondary plant compounds or allelochemicals compared to other plant parts (Foley and McArthur, 1994; Cork and Foley, 1991). To see what effect this has we examined (Table V) the sources of antifeedants by plant part, using data from Wrangham *et al.* (1998). Condensed tannins, total tannins, and triterpenoids in the monkeys diets all come significantly more from leaves, only occasionally from unripe fruit and seeds, and least from ripe fruits. Monoterpenoids come equally from all plant food categories. For the chimpanzees, most antifeedants in the diet come from ripe fruit, but leaves also contribute significantly to the total tannin load. We did not quantify alkaloids in these food samples, but Gartlan *et al.* (1980) showed that Kibale Forest leaves contain significantly more alkaloids than those in the Douala-Edea Forest Reserve of Cameroon. Therefore, eating more leaves in order to obtain more amino acids for detoxification pathways is unlikely to be effective because of the increased secondary plant compound load from leaves. High protein intake may be simply a by-product of the monkey's attempt to maintain a diverse, mixed diet that leads to a dilution of any particular toxin (Kingsbury, 1978).

The chimpanzees had what most human nutritionists would call a very healthy diet, containing low fat, low protein, and high carbohydrate. Like the cercopithecines, they increased the lipid level in their diet during peak ripe fruit abundance. However, even the peak lipid percentage in the diets

was only about 6.0–8.5%DM. While this is above the level suggested for an adequate supply of essential fatty acids and fat soluble vitamins (RDA, 1980), it is low compared to the 15–20%DM lipid levels consumed by modern, Western humans. The protein value is similar to human protein requirements (Oftedal, 1991; RDA, 1980). The fiber intake is higher than recommended for humans. Thus, even during periods of fruit abundance, neither chimpanzees nor cercopithecines consumed a diet that could be called nutrient-dense.

In conclusion, our analysis of the macronutrient content of the plant component of Kibale primate diets suggests remarkably little overall difference in absolute levels among the four frugivores. Despite major differences in plant items eaten (Wrangham *et al.*, 1998), all species had a diet close to the mean of 2.5–4% lipid, 16–18% CP, 10–15% WSC, and 31–34% NDF. The only exception was that chimpanzees had a lower protein diet (9.5%). In general, therefore, body mass and phylogenetic history appear to have had little impact on nutrient composition of the diet. Nevertheless, there is a major difference between chimpanzees and cercopithecines in their response to fruiting seasonality, with chimpanzees taking greater nutritional advantage of temporary abundance. This difference remains to be understood, but the other main difference between chimpanzees and cercopithecines has clear significance. In relation to body weight, chimpanzees have a strikingly higher dietary quality than cercopithecines, which suggests a difference between apes and cercopithecines that could explain niche differentiation and evolutionary history in other ecosystems (Temerin and Cant, 1984).

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