



## The Value of Figs to Chimpanzees

R. W. Wrangham,<sup>1</sup> N. L. Conklin,<sup>1</sup> G. Etot,<sup>2,3</sup> J. Obua,<sup>2</sup>  
K. D. Hunt,<sup>4</sup> M. D. Hauser,<sup>1</sup> and A. P. Clark<sup>5</sup>

Received December 3, 1990; accepted January 28, 1991

---

*Nine Ugandan figs have consistent differences in nutrient concentration between the pulp and seed fractions. Pulp has more water-soluble carbohydrates, complex carbohydrates, calories, and ash, while the seed fraction has more condensed tannins, lipids, and fiber. Because species differ, nutrient concentration in pulp could not be predicted from analysis of whole figs. Chimpanzees in Kibale Forest relied heavily on figs throughout 29 months, feeding relatively intensely at large trees. Fig size varied between species, between individuals of the same species, and between fruiting cycles of the same tree. Larger figs had higher water concentrations but still led to higher rates of nutrient intake per minute for chimpanzees, monkeys, and hornbills. Chimpanzees ate more than 40 cal/min, excluding calories derived from insoluble fiber, when harvesting large figs.*

---

**KEY WORDS:** figs; chimpanzees; intake rates; nutrient composition; frugivore assemblages.

### INTRODUCTION

The aims of this paper are to describe the nutritional quality of figs that are commonly eaten by Ugandan primates, especially chimpanzees, *Pan troglodytes*, and to determine how nutrient intake rates vary for frugivores between different fig species.

<sup>1</sup>Department of Anthropology, Harvard University, Cambridge, Massachusetts 02138.

<sup>2</sup>Makerere University Biological Field Station, Department of Zoology, Makerere University, P.O. Box 7062, Uganda.

<sup>3</sup>Deceased, July 1990.

<sup>4</sup>Department of Anthropology, Indiana University, Bloomington, Indiana 47405.

<sup>5</sup>Department of Anthropology, University of Michigan, Ann Arbor, Michigan 48109.

Figs. (*Ficus* spp. "fruits") are a common food for many tropical primate populations (Leighton, 1986; Sugardjito *et al.*, 1987) and often provide a reserve food supply during periods of general food scarcity (Terborgh, 1983). Yet their dietary significance is unclear. Only a few of the >750 species of figs (Berg, 1989; Berg and Hijman, 1989) have been analyzed, and current generalizations are contradictory. Fig fruits were considered by Janzen (1979) to have high nutritional value because of their importance to specialized frugivores. In support of this, figs were found by Vellayan (1981) to have higher caloric values than nonfig fruits. Yet the more common claim is that figs have poor nutritional quality and are eaten mainly because of distributional factors, such as huge crop size (Bronstein and Hoffmann, 1987; Lambert, 1989).

Therefore, to assess the nutritional value of figs for chimpanzees, we first describe the nutritional qualities of the particular species of figs that are eaten in Kibale Forest. Comparative data are provided for fruits of *Mimusops bagshawei* S. Moore (Sapotaceae), which was the most common nonfig-tree fruit in the chimpanzee diet during the study period. (*M. bagshawei* fruits are cherry-sized, sweet-tasting drupes.)

Many published data use whole-fruit assays. These are difficult to interpret because fig-eaters typically digest pulp (fig wall) but not the seeds or other reproductive parts (Janzen, 1979). Therefore, we compare assays of pulp, seed fraction, and whole fruit to find out whether data from whole fruits are useful for comparison with pulp-only assays.

Because the ultimate value of food depends partly on how fast it can be ingested, we also examined the relationship between nutritional quality and feeding rate. In view of the likely importance of fruit size for food intake rates, we test the hypothesis that frugivorous primates obtain more nutrition per minute by eating large figs than small figs.

Kibale Forest, Uganda, is typical of many tropical forest sites in having several primates that eat figs from a variety of *Ficus* species (Isabirye-Basuta, 1989; Ghiglieri, 1984; Struhsaker and Leland, 1979). Our focus is on chimpanzees, with additional data on feeding rates among blue monkeys (*Cercopithecus mitis*), redbellied monkeys (*C. ascanius*), gray-cheeked mangabeys (*Cercocebus albigena*), and black-and-white hornbills (*Bycanistes subcylindricus*).

## METHODS

### Field

Fieldwork was conducted in the Kibale Forest, Uganda, a 560 km<sup>2</sup> reserve, at Kanyawara (0°34'N, 30°21'E; altitude, 4600–5200 ft). Annual

rainfall is 1500–1800 mm, which supports a multicanopy forest to 50 m. Forest types include unlogged forest, forest lightly or more heavily logged in the late 1960s, pine plantations (1960s), and areas of *Pennisetum purpureum* grassland. Struhsaker (1975), Ghiglieri (1984), and Skorupa (1988) provide fuller descriptions.

R.W.W. and M.D.H. initiated training of a team of field assistants in September 1987, subsequently continued by G.E., J.O., A.P.C., and K.D.H. Field assistants include observers of focal fig trees (J. Bisigara, K. Clement, C. Muruuli, R. Pascal, P. Tuhairwe) and persons who monitor phenology (J. Byaruhanga, E. Tinkasimire, G. Kagaba). G.E. and J.O. conducted observations on focal fig trees from November 1987 to 1989. B. Gault (June–August 1989), P. Novelli (July–December 1989), and C. A. Chapman (November–December 1989) also assisted with the fieldwork.

Data on feeding rates were obtained from 878 days at 33 focal trees by all observers from November 1987 to September 1989. Focal trees had crowns permitting good observation; only large trees were selected. Observations began shortly before or after frugivores had started removing fruits and continued when possible until most fruits had been removed or fallen ( $26.6 \pm 17.0$  observation days per tree; range, 2–56 days). They began around dawn (0700) and continued up to 11 hr per day by one or two observers using binoculars. Observers sometimes concealed themselves in a bird-hide; this showed that the behavior of most frugivores, including those reported on here, was not influenced by seeing people. Exceptions were l'Hoest's monkey (*Cercopithecus lhoesti*), blue duiker (*Cephalophus monticola*), and red duiker (*C. harveyi*), all of which are terrestrial and shy.

The number and species of all birds and mammals present in the tree, and the number that were feeding, were scored every 10 or 15 min. Feeding was defined as actively harvesting or processing food for ingestion. Feeding rates, defined as the number of fruits that an already-feeding individual harvested in 60 sec, were collected opportunistically. When part of the fruit was dropped, only the fraction eaten was scored.

Two transects, 0.5 m wide, were laid out at right angles under the crowns of focal trees. Fallen fruits found on the transects were removed and counted twice daily, at the beginning and end of observations. Five ripe fruits were chosen blind from the collection and their diameters measured.

Because trees were difficult to climb, figs for nutritional analysis were collected from the ground. Care was taken to classify as ripe fruits only those that had not been damaged by insects or vertebrates. The ideal collection was of ripe fruits knocked down inadvertently by socially active animals.

The phenological state of 68 figs, belonging to six species on a 112-km transect, was recorded every 2 weeks. These were 15 *F. asperifolia* Miq., 5 *F. conraui* Warb., 20 *F. exasperata* Vahl., 9 *F. natalensis* Hochst., 1 *F. sansibarica*

Warb., subsp. *macroserma* (Mildbr. & Burret) C. C. Berg (type 1), 14 *F. s. macroserma* (type 2), and 4 *F. saussureana* DC. Fig nomenclature follows Berg and Hijman (1989).

Chimpanzee feces were collected in plastic bags whenever found and were analyzed within 1 week. The presence of fig seeds was scored on a 5-point scale from 0 to 4: In feces scored 4, fig seeds were often the only seeds recognizable.

### Laboratory

Samples collected in Kanyawara from October 1987 to November 1989 were air-dried in the field. Analysis was carried out in the nutritional biochemistry laboratory in the Anthropology Department at Harvard University.

Fig pulp and seeds were separated quantitatively and analyzed separately. The seed fraction included the fruit chaff immediately surrounding the seed; the pulp fraction included the skin. Standard chemical analyses to estimate nutritional value were performed. Crude protein was determined using the Kjeldahl procedure for total nitrogen and multiplied by 6.25 (Pierce and Haenisch, 1947). The digestion mix contained  $\text{Na}_2\text{SO}_4$  and  $\text{CuSO}_4$ . The distillate was collected in 4% boric acid and titrated with 0.1 N HCl. The detergent system of fiber analysis (Goering and Van Soest, 1970), as modified by Robertson and Van Soest (1980), was used to determine the neutral-detergent, or total cell wall, fraction. Total lipid content was measured using petroleum ether extraction for 4 days at room temperature. Water-soluble carbohydrates were estimated using a phenol/sulfuric acid colorimetric assay (Strickland and Parsons, 1972). Condensed tannin content was measured using the proanthocyanidin test of Bate-Smith (1975) as modified by Mole and Waterman (1987). Dry matter was determined by drying a subsample at 100°C for 8 hr and hot weighing. Total ash was measured by ashing the above subsample at 520°C for 8 hr and then hot weighing at 100°C. Complex carbohydrate content was estimated by subtraction, and total calories were calculated based on the energetic value of the above nutrient fractions (National Research Council, 1989).

## RESULTS

### Fig Species and Characteristics

Kanyawara figs vary from a small, abundant shrub (*F. asperifolia* Miq.) to large, low-density trees, most of which begin life as stranglers; *F. exasperata*

Vahl. is an exception (Table I). Fig tree densities are similar to those in a variety of tropical sites (McKey, 1989). From December 1987 to March 1990, individual *F. asperifolia* Miq. fruited irregularly throughout the year. Other species fruited, on average, once every 1–2 years. The trees of some species [*F. exasperata* Vahl.; *F. s. macrosperma* (Mildbr. & Burret) C. C. Berg] tended to fruit during the same 3- to 4-month period but any species could fruit at any time of year.

Fruit weight varied among species over roughly two orders of magnitude, between *F. thoningii* Bl. and *F. s. macrosperma* (Mildbr. & Burret) C. C. Berg (Table I). Within species, *F. natalensis* Hochst. ripe fruit diameters at nine focal trees ranged from  $1.12 \pm 0.08$  cm ( $N = 22$  days) to  $1.43 \pm 0.10$  cm ( $N = 33$  days). Intraspecific variation in fig size was particularly clear for *F. s. macrosperma* (Mildbr. & Burret) C. C. Berg. The mean fruit diameter for eight focal fruiting cycles varied from  $1.74 \pm 0.19$  cm ( $N = 6$  days) to  $4.50 \pm 0.45$  cm ( $N = 11$  days). Variation included differences between successive fruiting cycles for the same tree. Thus, one tree (H16) was observed fruiting three times (Oct.–Dec. 1987, Oct.–Nov. 1988, Nov. 1989). Mean ripe fruit diameter was, respectively,  $4.16 \pm 1.69$  cm ( $N = 14$  days),  $2.43 \pm 0.33$  cm ( $N = 10$  days), and  $4.17 \pm 0.18$  cm ( $N = 12$  days). Because there is clearly much less variation in fruit size within than between fruiting cycles, data on intake rate have been analyzed here using separate fruiting cycles instead of species means.

### Frequency of Fig-Eating

Ripe fig-tree fruits were available in every month from December 1987 to March 1990. During this period fig seeds were present in 95.5% of chimpanzee feces ( $N = 1050$ ), and the monthly mean fig seed abundance score in feces was consistently high (mean,  $2.8 \pm 0.7$ ; minimum, 1.5;  $N = 28$  months). Direct observation showed that fruits of *F. asperifolia* Miq. were eaten rarely ( $\leq 1\%$  of all fig-eating). Therefore, tree figs were an exceptionally important component of the chimpanzee diet.

All fig tree species were eaten intensely by chimpanzees, though individual trees were sometimes untouched. For instance, chimpanzees were estimated to have removed between 0 and 84.3% of the total crop from 10 trees having total crops between 228 and 2052 kg (wet weight) of figs. [Crop size was calculated retrospectively by estimating the total number of fallen figs and the total number of figs removed by each frugivore species. The trees were FEX ( $N = 2$ ) and FN ( $N = 3$ ), FSM(1) ( $N = 1$ ), and FSM(2) ( $N = 4$ ), observed for 307 days. See Table I for abbreviations.] Smaller crops received relatively less attention ( $R^2 = 0.42$ ,

Table I. Characteristics of Some Kanyawara Fig Species<sup>a</sup>

	Abbreviation	Crown vol. (m <sup>3</sup> )	Density (stems/ha)	Fruit weight (g)	% pulp (% 60°C DM)
<i>F. asperifolia</i> Miq.	FAS	2	366.7	1.4	56
<i>F. conraui</i> Warb.	FCO	44	<0.3	9.8	46
<i>F. cyanithitipula</i> Warb.	FCY	cf. FCO	<0.1	14.8-21.0	49
<i>F. exasperata</i> Vahl.	FEX	939	0.7-1.1	1.8-2.8	47-50
<i>F. mucoso</i> Ficalho	FM	cf. FSM(1)	<0.1	cf. FB	65
<i>F. natalensis</i> Hochst.	FN	3153	0.2-0.5	0.9-2.3	67-73
<i>F. ovata</i> Vahl.	FOV	cf. FEX	<0.1	cf. FD	
<i>F. sansibarica</i> Warb. <i>macrosperma</i> (Mildbr. & Burret) C. C. Berg (Type 1)	FSM(1)	882	0.0-0.2	25	53
<i>F. s. macrosperma</i> (Type 2)	FSM(2)	2656	0.4-0.5	9.2-54.5	41-63
<i>F. saussureana</i> DC	FSA	7728	0.1-0.3	7.4	48
<i>F. sur</i> Forssk.	FSR	cf. FEX	0.0-0.4	3.4	
<i>F. thoningii</i> Bl.	FT	cf. FSM(1)	<0.1	<1.0	
<i>F. trichopoda</i> Bak.	FTR	cf. FEX	0.0-0.1	cf. FB	
<i>F. vallis-choudae</i> Del.	FVC	cf. FCO	<0.1	cf. FB	
<i>Mimusops bagshawei</i> S. Moore	MMS	684	0.9	3.1	57

<sup>a</sup>Crown volume is the mean for reproductive trees on the phenology transect. Stem densities are from Skorupa (1988), mean of estimates from different habitats, with ranges showing estimates from plot counts vs census route methods; single estimates are from unpublished data (Kanyawara only). Ranges for fruit weights and percentage pulp show means from different trees.

Table II. Nutrient Values for Nine Species of Kibale Forest Figs<sup>a</sup>

	Fig pulp	Fig seeds	<i>P</i>	MMS pulp
Protein	7.9 ± 4.2	8.2 ± 2.7	n.s.	6.3
CT	0.5 ± 0.3	1.8 ± 1.1	<0.01	0.0
Lipid	3.5 ± 1.5	7.1 ± 2.8	<0.05	0.0
Fiber	35.6 ± 10.8	63.7 ± 5.8	<0.01	24.5
WSC	12.6 ± 4.8	5.4 ± 3.3	<0.01	32.7
CCHOs	32.1 ± 6.8	8.9 ± 3.6	<0.01	33.4
Ash	7.7 ± 1.5	4.6 ± 1.7	<0.01	3.1
cal/100 g	242.5 ± 45.7	151.1 ± 23.4	<0.01	289.6

<sup>a</sup> Species sampled are FAS (*N* = 2), FCO (*N* = 1), FCY (*N* = 2), FEX (*N* = 5), FM (*N* = 1), FN (*N* = 3), FSA (*N* = 2), FSM(1) (*N* = 2), FSM(2) (*N* = 8 trees), and MMS (*N* = 1). Means were calculated for each species; cells show means and standard deviations of species means. Values are percentage weight for 60°C dry matter. Significance values test fig pulp vs seed (Wilcoxon; *N* = 9).

df = 9, *P* < 0.05), regardless of species, much as found by Leighton (1993). We have not yet studied differences in chimpanzee preference among fig species.

### Composition of Whole Figs

Nutrient composition was determined for 26 fruiting cycles (23 trees) belonging to nine species. Table II shows that pulp and seed fractions differ consistently in concentrations of all components except protein. In Table III “whole-fig” assays, which assume total digestion of the seed fraction, are compared with “pulp-only” assays, which assume no digestion of the seed fraction.

Whole-fig assays exaggerate the available concentrations of all components except fiber. Fiber appears at high concentrations in estimates of “available” nutrients (pulp-only assays), because we decided to include the seed fraction as fiber since they are ingested, though not digested. Whole-fig assays particularly exaggerate concentrations of tannins (mean percentage change, 272.1%) and lipid (189.7%). The impact is least for WSC (28.2%) and calories (33.6%).

Table III. Percentage Change In Apparent Nutrient Concentration as a Result of Treating the Seed Fraction as Available for Digestion<sup>a</sup>

	FAS	FCO	FCY	FEX	FM	FN	FSA	FSM(1)	FSM(2)	Mean ± SD
Protein	93.2	77.1	150.1	61.4	114.9	42.0	114.0	96.9	61.4	90.1 ± 31.6
CT	205.9	380.1	564.2	237.2	626.5	168.0	18.3	124.0	124.4	272.1 ± 196.4
Lipid	109.6	326.6	209.9	81.6	91.4	102.5	194.8	384.3	207.0	189.7 ± 101.5
Fiber	-43.2	-26.6	-28.7	-30.3	-35.2	-26.1	-26.2	-33.2	-29.5	-31.0 ± -5.2
WSC	52.9	27.6	34.0	34.7	29.3	24.2	21.1	15.2	15.1	28.2 ± 11.0
CCHOs	16.1	11.5	78.4	30.2	15.3	58.0	31.5	31.7	29.8	33.6 ± 20.4
Ash	78.6	37.5	15.6	47.3	31.4	19.4	47.7	40.1	20.2	37.5 ± 18.4
cal/100 g	52.6	52.5	79.5	49.4	33.8	53.6	68.6	58.2	50.8	55.4 ± 12.0

<sup>a</sup> Nutrient concentrations (% 60°C DM, or cal/100 g) were calculated per whole fruit in two ways. "Pulp-only" concentrations (PO) included only materials in the pulp. "Whole-fig" concentrations (WF) included material in seed fraction as well as pulp. Cells show % (WF - PO)/PO.



Table III shows that there are substantial differences between fig species in the exaggeration by whole-fig assays, a result of interspecific variation in the relative proportion and composition of pulp and seeds. Whole-fig analysis overestimates protein concentration, for example, by between 42.0% (FN) and 150.1% (FCY). This variation means that the concentration of nutrients in pulp cannot be estimated from whole-fig assays. Therefore, for this paper, fig nutrient concentrations are assayed only from pulp separated from the seed fraction.

### Composition of Pulp and Seed

The concentrations of nutrients in pulp show certain important differences between species. For example, protein concentration (% 60°C DM) varied from  $5.5 \pm 0.3$  (FN;  $N = 3$ ) to  $16.6 \pm 4.9$  (FEX;  $N = 5$ ). Nevertheless, clear patterns emerged in the comparison of fig pulp and seed across species (Table II). Compared to seeds, pulp had higher concentrations of water-soluble carbohydrates (WSC), complex carbohydrates (CCHOs), and ash. Accordingly, pulp is a significantly superior source of calories (Table II) and has lower concentrations of condensed tannin (CT), lipid, and fiber. The only nutrient with the same average concentration in pulp and seed is protein.

Table II also indicates that fig pulp is more similar to MMS pulp than to fig seed. Both pulps have low CT, lipid, and fiber vs high WSC, CCHOs, and calories. Fig pulp has a lower calorie concentration than MMS pulp, a result of its lower concentration of sugars. This suggests that fig pulp is almost as good a source of calories as MMS pulp, but relatively lacking in sugars. There is no indication of a difference in any other nutrients.

When calculating caloric value, the digestibility of the CCHOs was assumed to be equivalent to the digestibility of starch. This point needs further investigation because fig CCHOs probably do not contain starch. The most likely CCHO is pectin (P. J. Van Soest, personal communication). Whereas pectin is indigestible to mammalian enzymes, it is highly fermentable and its energy is probably available to chimpanzees due to hindgut fermentation (Bailey *et al.*, 1978; Eastwood *et al.*, 1986). If so, the overall digestibility of the CCHO fraction is indeed roughly equivalent to that of starch.

### Food Intake Rates

To find out the effect of differences in pulp composition on food intake, intake rates were estimated. Within trees, no relationship was found between fig intake rate and day of the fruiting cycle, observer, time of day,

or chimpanzee party size. Therefore, mean values were used for each fruiting cycle (minimum = 5 observations per species).

The mean fig intake rate for chimpanzees (number of figs harvested per minute) varied from 3 to 12. As might be expected, larger figs were harvested more slowly (slope =  $-0.13$ ,  $R^2 = 0.44$ ,  $df = 18$ ,  $P < 0.01$ ). However, Fig. 1 shows that larger figs provided much more food per minute (slope =  $3.21$ ,  $R^2 = 0.91$ ,  $df = 18$ ,  $P < 0.001$ ). The increase in food intake per minute was less marked for smaller frugivores (combined data for blue monkeys, redtail monkeys, gray-cheeked mangabeys, and black-and-white casqued hornbills; slope =  $0.66$ ,  $R^2 = 0.63$ ,  $df = 19$ ,  $P < 0.001$ ), because they harvested larger figs much more slowly. Thus chimpanzees harvested larger figs at relatively high rates compared to monkeys and hornbills.

Nutrient intake rates were calculated by converting dry matter concentrations to percentage fresh weight. Intake rate (g/min) of all nutrients increased significantly with fig weight, but at a lower rate than food intake (e.g., chimpanzee slope  $< 0.13$  for all except calories). Nutrient intake rates were lower than expected because larger figs have relatively more water ( $R^2 = 0.72$ ,  $df = 10$ ,  $P < 0.001$ ), so a major effect of eating larger figs was an increase in water intake per minute. Even so, the range of fig weights is so large that it clearly pays to eat larger figs—if intake rate is important. Figure 2 shows that this is true for chimpanzees and for monkeys and black-and-white hornbills. Note that Figs. 1 and 2 include data from MMS, which provided calories at a similar rate to the smallest figs. [Figure 2 does not include calories from fiber. Since chimpanzees have high coefficients of digestion for fiber (Milton and Demment, 1988), the total calories available to the animal are higher than shown in Fig. 2.]

## DISCUSSION

Our analysis shows clear differences between the pulp and the seed component of nine Ugandan figs. The directions of the differences are much as expected, e.g., seeds have more chemical protection and a higher caloric density (more lipid). Because the seed fraction is large, and because species differ in pulp and seed chemistry, the nutrient composition of pulp could not have been estimated without separating the seeds.

How closely pulp nutrient assays reflect the food available to a frugivore depends on the digestibility of what we were separating out as the seed fraction. Our correction factor in Table III assumes that it was totally indigestible. This is undoubtedly an exaggeration, because seed fractions can include digestible nutrients from dead fig-wasps, punctured seeds, and chaff.

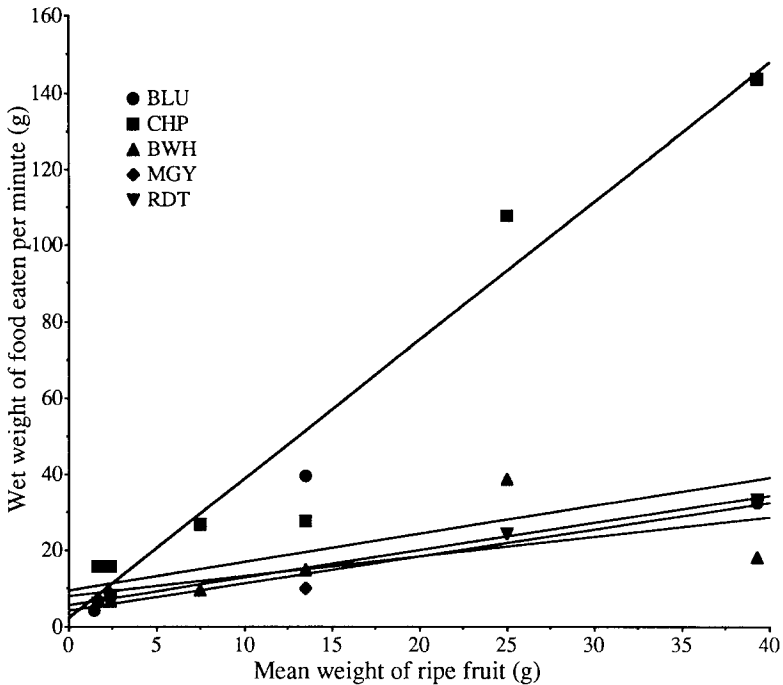


Fig. 1. Feeding rate in relation to fruit size. Food intake rate (wet weight of pulp eaten per minute) is shown as a function of fruit size for six fruit species [*F. conraui* Warb., *F. cyanthistipula* Warb., *F. exasperata* Vahl., *F. natalensis* Hochst., *F. sansibarica* Warb., subsp. *macrosperma* (Mildbr. & Burret) C. C. Berg (type 1), *F. s. macrosperma* (type 2), *F. saussureana* DC, and one nonfig *Mimusops bagshawei*] (see Table I). BLU, *Cercopithecus mitis* ( $n = 392$ ); CHP, *Pan troglodytes* ( $n = 931$ ); BWH, *Bycanistes subcylindricus* ( $n = 649$ ); MGY, *Cercocebus albigena* ( $n = 204$ ); RDT, *Cercopithecus ascanius* ( $n = 493$ ). Lines show slope of linear regression.

Nevertheless, whole-fig analysis is evidently not a good technique for studies of frugivores that defecate a large proportion of seeds unharmed.

Comparison with a classic sugar-rich primate fruit suggests that Kanyawara figs are an energy-rich food with adequate protein. However, some figs (e.g., FB) have rather unpleasant tastes, raising the possibility of metabolic costs of detoxification.

Food intake rate for chimpanzees, monkeys, and hornbills increased with fig size because harvesting rate did not decline sharply with increasing fig size. Although water concentration increased with fruit size, the result was that more nutrients were ingested per minute. Thus, feeding rate thus appears to be a more important influence than nutrient density on the rate of nutrient intake.

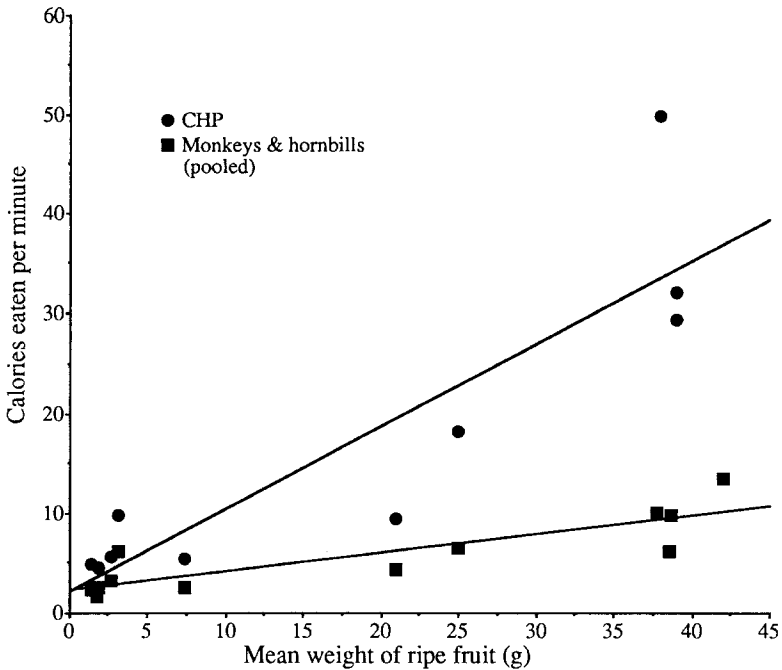


Fig. 2. Caloric intake rate in relation to fruit size. Data are as for Fig. 1, with pulp intake rate converted to caloric values (excluding fermentable fiber). Feeding rates for frugivorous monkeys and hornbills were pooled since slopes were similar (Fig. 1).

Malenky (1990) found a similar result for bonobos (*Pan paniscus*), though with a lower slope. The difference in slopes may be due to a difference in the fruit samples: The bonobo foods covered a larger range of fruit size (0.1 to >500 g) and types (including nonfigs). However, even in the analysis with the same foods, the rate of increase in food intake rate with fig size was steeper for chimpanzees than for monkeys and hornbills (Figs. 1 and 2). The more chimpanzees can harvest, the more they can eat, while smaller frugivores may be limited by how fast they can prepare figs for swallowing. Larger processing surfaces (e.g., teeth) may allow chimpanzees to take better advantage of large fruits than monkeys and hornbills can.

The significance of the large differences in nutrient intake rate with fruit is obscure. Preference might be expected for trees with large figs (e.g., more frequent feeding at species with larger figs when total available crop weight is the same). However, we have seen nothing obvious, and current

data suggest that crop size (i.e., total weight of fruit or pulp on tree) is much more important (Leighton, 1992). Possibly our instantaneous measure of food intake does not represent the pattern over longer intervals. For example, animals might eat larger figs in bursts of activity for a few minutes, with regular rest periods between. Or species differences in the digestibility of fiber may be important. However, the magnitude of the effect suggests that it is real and has important effects on frugivore feeding strategies. Larger figs should allow more energy to be gathered per unit time and, therefore, should promote social activity, long-distance travel, or other activities normally constrained by time and energy.

### ACKNOWLEDGMENTS

We thank the Government of Uganda, especially the National Research Council and Forestry Department, for permission to work in the Kibale Forest Reserve. Facilities were provided by Makerere University Biological Field Station. The Department of Zoology, Makerere University, assisted at all times. Grateful acknowledgement for funding is due to the National Science Foundation (BNS-8704458), National Geographic Society (3603-87), and Leakey Foundation. Assistance in the field was provided by J. Basigara, K. Clement, C. Muruuli, P. Tuhairwe, R. Marumba, C. Opio, J. Byaruhanga, E. Tinkasimire, G. Kagaba, B. Gault, and P. Novelli. G. Isabirye-Basuta provided valuable assistance throughout the study. P. Ipuet and T. Katende aided in plant identification.

### REFERENCES

- Bailey, R. W., Chesson, A., and Monro, J. (1978). Plant cell wall fractionation and structural analysis. *Am. J. Clin. Nutr.* 31: s77-s81.
- Bate-Smith, E. C. (1975). Phytochemistry of proanthocyanidins. *Phytochemistry* 14: 1107-1113.
- Berg, C. C. (1989). Classification and distribution of *Ficus*. *Experientia* 45: 605-611.
- Berg, C. C., and Hijman, M. E. E. (1989). *Flora of Tropical East Africa: Moraceae*, A. A. Balkema, Rotterdam.
- Bronstein, J. L., and Hoffmann, K. (1987). Spatial and temporal variation in frugivory at a neotropical fig, *Ficus pertusa*. *Oikos* 49: 261-268.
- Eastwood, M. A., Brydon, W. G., and Anderson, D. M. W. (1986). The effect of the polysaccharids composition and structure of dietary fibers on cecal fermentation and fecal excretion. *Am. J. Clin. Nutr.* 44: 51-55.
- Ghiglieri, M. (1984). *The Chimpanzees of Kibale Forest*, Columbia University Press, New York.
- Goering, H. K., and Van Soest, P. J. (1970). Forage fiber analysis. *Agricultural Handbook No. 379*, ARS, USDA, Washington, D.C.
- Isabirye-Basuta, G. (1989). Feeding ecology of chimpanzees in the Kibale Forest, Uganda. In Heltne, P. G., and Marquadt, L. A. (eds.), *Understanding Chimpanzees*, Harvard University Press, Cambridge, Mass., pp. 116-127.

- Janzen, D. H. (1979). How to be a fig. *Annu. Rev. Ecol. Syst.* 10: 13-51.
- Lambert, F. (1989). Fig-eating by birds in a Malaysian lowland rain forest. *J. Trop. Ecol.* 5: 401-412.
- Leighton, D. R. (1986). Gibbons: Territoriality and monogamy. 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. 135-145.
- Leighton, M. (1993). Modeling dietary selectivity by Bornean orangutans: Evidence for integration of multiple criteria in fruit selection. *Int. J. Primatol.* 14: 257-313.
- Malenky, R. (1990). *Ecological Factors Affecting Food Choice and Social Organization in Pan paniscus*, Ph.D. dissertation, SUNY, Stony Brook, N.Y.
- McKey, D. (1989). Population biology of figs: Applications for conservation. *Experientia* 45: 661-673.
- Milton, K., and Demment, M. W. (1988). Digestion and passage kinetics of chimpanzees fed high and low fiber diets and comparison with human data. *J. Nutr.* 118: 1082-1088.
- Mole, S., and Waterman, P. G. (1987). A critical analysis of techniques for measuring tannins in ecological studies. I. Techniques for chemically defining tannins. *Oecologia* 72: 137-147.
- National Research Council (1989). *Recommended Dietary Allowances*, 10th ed., National Academy Press, Washington, D.C.
- Pierce, W. C., and Haenisch, E. L. (1947). *Quantitative Analysis*, 2nd ed., John Wiley & Sons, Chapman & Hall, London.
- Robertson, J. B., and Van Soest, P. J. (1980). The detergent system of analysis and its application to human foods. In James, W. P. T., and Theander, O. (eds.), *The Analysis of Dietary Fiber in Food*, Marcel Dekker, New York and Basel, pp. 123-158.
- Skorupa, J. P. (1988). *The Effects of Selective Timber Harvesting on Rain Forest Primates in Kibale Forest, Uganda*, Ph.D. dissertation, University of California, Davis.
- Strickland, J. D. H., and Parsons, T. R. (1972). *A Practical Handbook of Seawater Analysis*, Fisheries Board of Canada, Ottawa.
- Struhsaker, T. T., and Leland, L. (1979). Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. In Rosenblatt, J. S., Hinde, R. A., Beer, C., and Busnel, M. C. (eds.), *Advances in the Study of Behavior*, Vol. 9, Academic Press, New York, pp. 159-228.
- Sugardjito, J., te Boekhorst, I. J. A., and van Hooff, J. A. R. A. M. (1987). Ecological constraints on the grouping of wild orangutans (*Pongo pygmaeus*) in the Gunung Leuser National Park, Sumatra, Indonesia. *Int. J. Primatol.* 8: 17-41.
- Terborgh, J. (1983). *Five New World Primates*, Princeton University Press, Princeton, N.J.
- Vellayan, S. (1981). *Chemical Composition and Digestibility of Natural and Domestic Food of the Lar Gibbon (Hylobates lar) in Malaysia*, M.Sc. thesis, University Pertanian Malaysia, Serdang, Selangor.