The Significance of Fibrous Foods for Kibale Forest Chimpanzees [and Discussion]

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The significance of fibrous foods for Kibale Forest chimpanzees

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SUMMARY

Four categories of plant food dominated the diet of chimpanzees in Kibale Forest, Uganda: non-fig tree fruits, fig tree fruits, herbaceous piths and terrestrial leaves. Fruit abundance varied unpredictably, more among non-figs than figs. Pith intake was correlated negatively with fruit abundance and positively with rainfall, whereas leaf intake was not influenced by fruit abundance. Piths typically have low sugar and protein levels. Compared with fruits and leaves they are consistently high in hemicellulose and cellulose, which are insoluble fibres partly digestible by chimpanzees. Herbaceous piths appear to be a vital resource for African forest apes, offering an alternative energy supply when fruits are scarce.

1. INTRODUCTION

Chimpanzees (*Pan troglodytes*) are primarily frugivores (Ghiglieri 1984; Hladik 1977; Isabirye–Basuta 1990; McGrew *et al*. 1988; Nishida & Uehara 1983; Wrangham 1977). When fruit is rare, chimpanzees, like other frugivores, must migrate to more productive areas (Nishida 1979), reduce energy expenditure (Wrangham 1977), or broaden their diet. Here the nutritional constituents of piths and their pattern of utilization is examined to test the hypothesis that chimpanzees rely on fibrous piths when fruit is scarce.

Like other African apes, chimpanzees eat piths, primarily from herbaceous stems in the ground layer. The number of species eaten varies from two (Mount Assirik, Senegal (McGrew *et al*. 1988)) to 28 (Mahale Mountains, Tanzania (Nishida & Uehara 1983)). Chimpanzees select stems that are typically more than 2 cm thick. They use their teeth to break the tough outer peel and extract the softer central pith. Unlike most other primates and ungulates, African apes have teeth that appear effective at shearing such stems, because of their large size, thin enamel, and long cutting edges (Kay 1981). In addition, the relatively efficient digestion of high-fibre foods in captive chimpanzees, presumably due to their large hindgut and total gut volumes (Milton & Demment 1988), suggests that chimpanzees may have special adaptations for eating piths.

Together with leaves eaten in the ground layer, piths have been reported to provide critical fallback foods in three studies of bonobos (pygmy chimpanzees, *Pan paniscus*) and one of frugivorous gorillas (*Gorilla gorilla*) when fruits were thought to be scarce (Badrian & Malenky 1984; Kano 1983; Kano & Mulavwa 1984; Rogers *et al*. 1988). In habitats with little fruit, terrestrial piths and leaves (TPL) provide the principal components of gorilla diet (Calvert 1985; Goodall 1977; Watts 1984).

In contrast to the importance of terrestrial piths and leaves in sustaining bonobos and gorillas, their significance for wild chimpanzees during periods of fruit shortage is little known. Instead of relying on piths and leaves, present indications are that fruitless chimpanzees resort to a variety of low-quality items (e.g. bark (Nishida 1976)). In the only study relating dietary changes to phenological measures of fruit abundance, Isabirye–Basuta (1990) found that when preferred fruits were scarce, Kibale Forest chimpanzees increased their diet diversity without emphasizing any particular class of food such as leaves. Similarly, comparisons between geographical areas suggest that poor food conditions favour a generalized increase in diet diversity involving stems, barks, underground storage organs and insects (see, for example, McGrew *et al*. 1988; Nishida 1989; Suzuki 1969).

In this paper we investigate the use of terrestrial fibrous foods by unprovisioned chimpanzees in the Kibale Forest. These foods have previously been designated as THV (terrestrial herbaceous vegetation) (Rogers & Williamson 1987; Wrangham 1986). Here we call them TPL (terrestrial piths and leaves) because of the occasional importance of woody species. We ask how TPL intake is related to both fruit abundance and rainfall, and whether TPL, including herbaceous pith, herbaceous leaves and shrub leaves, should be regarded as substitutes for fruits, because of sugar components, as suggested by Badrian *et al*. (1981) and Kano (1983) or as complementary because of their protein value, as proposed by Hladik (1977) and Malenky (1990).

2. STUDY SITE AND METHODS

We observed chimpanzees in the Kibale Forest Reserve, western Uganda (0° 13′–0° 41′ N, 30° 19′–30° 32′ E), from December 1987 to March 1991 (Wrangham *et al*. 1993). The Kanyawara community was the principal study group, comprising about 50 individuals in more than 20 km², (Isabirye–Basuta 1990). Kanyawara has undulating ground and an elevation of ≈ 1500 m. The vegetation is a mosaic of mid-altitude moist forest, secondary forest, tall grassland, swamps and softwood plantations. Supporting data came from the Ngogo community (Ghiglieri 1984) and sympatric Ngogo baboons (*Papio anubis*). Ngogo is 10–15 km S.E. of Kanyawara in similar habitat ≈ 150 m lower, without logged forest or softwood plantations (Butynski 1990). Feeding records were collected by direct observation, by inspection of feeding remains, and by dung analysis. Observations were made by the authors and field assistants (Wrangham *et al.* 1992). Direct observations reported here were by R.W.W.

Monthly fruit abundance was estimated in Kanyawara by recording the phenological state of 227 trees on a 12 km transect every two weeks from December 1987 to March 1990. Species observed were those seen to be important chimpanzee foods from 1983 to 1985 (G. Isabirye–Basuta, personal communication). Non-fig fruit trees were 20 *Celtis africana*, 20 *C. durandii*, 20 *Tabernaemontana* spp. (*T.* (*Conopharyngia*) *holstii* and *T.* (*Gabunia*) *odoratissima*), 9 *Cordia abyssinica*, 7 *Monodora myristica*, 11 *Mimusops bagshawei*, 12 *Pseudospondias microcarpa*, 20 *Teclea nobilis* and 20 *Uvariopsis congensis*. Fig trees were 15 *F. asperifolia* Miq., 5 *F. conraui* Warb., 20 *F. exasperata* Vahl, 9 *F. natalensis* Hochst., 1 *F. sansibarica* Warb., subsp. *macrosperma* (Mildbr. & Burret) C. C. Berg (type 1), 14 *F. s. macrosperma* (type 2) and 4 *F. saussureana* DC. Fig nomenclature follows Berg and Hijman (1989). To obtain fruit availability indices (FA) for each species, we multiplied the percentage of trees with ripe fruit by the density of trees in the study area (found from a stratified sample of 2300 trees) and by the mean basal area of each reproductive stem (also throughout the study area). FA indices were summed across species, and numbers were adjusted to make the largest FA index equal to 100 (i.e. FA (all) in November 1989).

Three fruit abundance indices were calculated by summing across different groups of tree species, i.e. FA (non-fig), FA (fig) and FA (all). Because *F. exasperata* fruits were sometimes not eaten by chimpanzees even when abundant (Isabirye–Basuta 1990), we also calculated FA (all except *F. exasperata*). This measure behaved almost identically to FA (all).

Food samples (only parts eaten by chimpanzees) were air-dried in the field. From this, room-temperature dry matter was calculated. Further analysis was done in the nutritional biochemistry laboratory in the Anthropology Department at Harvard University.

Standard chemical analyses were done to estimate nutritional value. Crude protein was determined using Kjeldahl procedure for total nitrogen, and multiplied by 6.25 (Pierce & Haenisch 1947). The digestion mix contained Na_2SO_4 and $CuSO_4$. The distillate was collected in 4% (by volume) boric acid and titrated with 0.1 N HCl. The detergent system of fibre analysis (Goering & van Soest 1970), as modified by Robertson & van Soest (1980), was used to determine the neutral-detergent fibre, hemicellulose, cellulose and lignin fractions. The lignin determination was done with 72% suphuric acid. Total lipid content was measured using petroleum ether extraction for four days at room temperature (modified from AOAC 1984). Water-soluble carbohydrates were estimated using phenol–sulphuric acid colorimetric assay (Dubois *et al.* 1956), as modified by Strickland & Parsons (1972). Condensed tannin content was measured using the proanathocyanidin test of Bate–Smith (1975) as presented by Mole & Waterman (1987). Dry matter was determined by drying a subsample at 100 °C for 8 h and hot weighing. Total ash was measured by ashing the above subsample at 520 °C for 8 h and then hot weighing at 100 °C (van Soest & Robertson 1991).

Statistical tests are two-tailed except where stated.

3. COMPOSITION OF CHIMPANZEE DIET

The plant diet of Kanyawara chimpanzees fell into three principal categories: tree fruits other than figs (21 species identified to date), fig-tree fruits (10 species), and TPL (14 pith species, 28 leaf species). Additional categories were fruits from shrubs, vines or herbs (15 species), leaves from mature trees (1 species), seeds (1), flowers (1) and bark (1). This list is certainly incomplete as we have found seeds of at least 20 unidentified fruit species in the dung.

We rely principally on dung analysis for comparisons of food intake over time or between populations to overcome sampling biases present in direct observation of food intake: chimpanzees were more easily discovered when eating tree fruits, because they returned repeatedly to productive trees and frequently gave loud calls. By contrast, we often lost contact with chimpanzees when they began to eat TPL, because when doing so they selected their foraging areas unpredictably, tended to be silent, and were rarely visible (the vegetation is often dense and tall).

(*a*) *Non-fig tree fruits*

Fruit eating occupied the majority of feeding time, and during any month the fruit diet was dominated by only one or a few species. During 14 days in 1991, each with at least 5 h of focal observation per day, 59.7% of time was spent feeding: chimpanzees ate arboreal fruits for 71.7% of feeding time ($n = 100.5$ h; $n = 4$ days in February, 4 days in March and 6 days in April). Fruits in this sample came from six species of tree, two of which predominated (*M. bagshawei* 66.0% of fruit-eating time, *Ficus natalensis* 23.2%). These figures appear typical of Kibale chimpanzees (Ghiglieri 1984; Isabirye–Basuta 1990).

Non-fig tree fruits of preferred species were eaten frequently when available. The most important fruit species at Kanyawara was *M. bagshawei* S. Moore, which was eaten in 14 out of 35 months. Its seeds occurred in an average of 22.1% of dungs in all months (range 0–94.1%). Phenological data for *M. bagshawei* fruits show that they were selected as a function of their availability (figure 1). In Kanyawara only five other species produced fruits whose residues were found in at least 50% of dungs in any month (*Cordia abyssinica*, *Monodora myristica*, *Pseudospondias microcarpa*, *Taberna-*

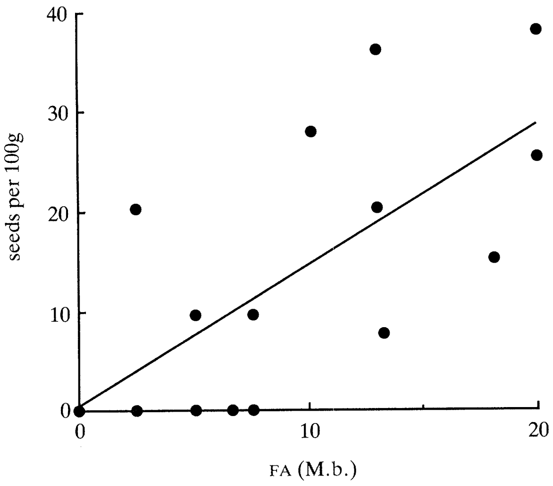

Figure 1. Frequency of eating *Mimusops bagshawei* S. Moore fruits in relation to their availability. 'FA (M.b.)' = fruit availability index of *M. bagshawei* ripe fruits. Each point is one month. 'Seeds per 100 g' = mean number of *M. bagshawei* seeds found per 100 g of chimpanzee dung (wet mass). (The mean mass of a *M. bagshawei* seed is 0.6 g, representing 1.8 g of fruit pulp.) Data are from December 1987 to March 1990. The slope of the linear regression is shown ($r^2 = 0.62$, d.f. = 27, $p < 0.001$).

emontana holstii and *T. odoratissima* (not distinguished in the field), and *Uvariopsis congensis*). The equivalent list for Ngogo was similarly small: *Chrysophyllum albidum*, *M. bagshawei*, *M. myristica*, *U. congensis* and *Warburgia ugandensis*. Each species fruited irregularly (eaten for a mean of 3.5 months per year), and because the number of potentially important tree-fruit species was small there were times when few tree-fruits were available (e.g., in 1989 only figs were present for four months). Fruits from lianas, vines and herbs are generally taken in small amounts.

(*b*) *Fig-tree fruits*

Figs were nearly continuously available (see below) and were eaten throughout the study period (cf. Wrangham *et al.* 1993). Fig seeds (predominantly from fig trees) occurred in 93.7 % of Kanyawara dungs (n = 839) (cf. 94.9 % of Ngogo dungs, n = 416), and were present in dungs in all months (Kanyawara: 35 months, December 1987–October 1990; Ngogo: 32 months, February 1988–October 1990). The abundance of fig seeds in dung was scored on a 0–4 scale (i.e. zero, rare, few, common, abundant). Mean scores were nearly equivalent at Kanyawara (mean = 2.54, n = 839) and Ngogo (mean = 2.68, n = 416).

(*c*) *TPL*

During our February–April 1991 sample, focal chimpanzees spent 17.6 % of their feeding time eating TPL, including occasions when we interpreted their activity from the sounds of breaking stems. The mean duration of 27 TPL-eating sessions was 24.0 min (s.d. 46.7), with 2.8 food types eaten per session (s.d. 2.0).

Stands of herbs whose pith is eaten vary from isolated individuals to high density, monospecific 'fields'. Pith fields occur especially in gaps or at forest edges, are available year round and can cover 0.1 ha† or more. Although pith fields tend to be dominated by a single species, such as *Pennisetum purpureum* or *Acanthus pubescens*, they normally contain a variety of edible items including the piths, young leaves and fruits of several species. Thus, ten or more food items may be selected during a single feeding session.

In Kanyawara the herbs whose pith is eaten most often are *Pennisetum purpureum* (elephant grass), *Aframomum mala and Marantochloa leucantha*. Chimpanzees also eat piths from shrubs, especially *Acanthus pubescens*. Piths from at least one of these four species are probably eaten almost daily. Piths are occasionally eaten from the saplings of trees or from the midrib of palm fronds.

TPL leaves eaten by chimpanzees were invariably young, and came from herbs (8 species), shrubs (3 species), vines (3 species), or saplings (14 species). Leaves typically were eaten for less time than pith, but the leaves of *Acalypha ornata* and *Ficus urceolaris* (a shrub) were sometimes the dominant food item.

Rates of pith intake were calculated on five occasions, in bouts lasting from 1 to 23 min. The amount of food eaten was reconstructed by measuring the remains of the peel. Calculated intake rates varied from 5 to 54 g (wet mass) per minute. This is very similar to the range for fruit intake (Wrangham *et al.* 1993). There is no indication in either case that intake rates influence selectivity.

To compare the frequency of TPL feeding between Kanyawara and Ngogo, dungs were scored on a 0–4 scale for abundance of fibrous strands (FBR), and green leaf fragments (GLF). The easily identifiable, long fibrous strands, which we assume came only from eating herbaceous piths, occurred in 93.8 % of Kanyawara dungs (n = 839) and 94.9 % of Ngogo dungs (n = 416). Over 35 months (December 1987 to October 1990) the mean monthly FBR score varied at Kanyawara between 0.9 (approximately 0.5 % of dung wet mass) and 3.8 (*ca.* 10 % of dung wet mass), similar to the range at Ngogo (0.0–3.5). Rates of eating fibrous foods were thus high, and similar between Kanyawara and Ngogo.

GLFs were less common: they occurred in 28.4 % of Kanyawara chimpanzee dungs, as against 18.2 % for Ngogo chimpanzees, and had low mean scores (0.4 at both sites, *ca.* 0.2 % of dung wet mass). The maximum mean score in any month was 1.0 at Kanyawara and 0.8 at Ngogo. FBR and GLF scores were not correlated with each other either at Kanyawara (r = 0.16, n = 35, n.s.) or Ngogo (r = 0.18, n = 21, n.s.). The dung data therefore suggest that intake of pith and leaves varied in different ways.

(*d*) *Tree leaves*

Leaves are generally eaten from immature trees (for example, *Celtis africana* and *C. durandii*). Leaves of mature trees are eaten only rarely (e.g. observed once from February to April 1991), although *Ficus exasperata*

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† 1 ha = 10^4 m^2.

leaves can be eaten regularly at times (Isabirye–Basuta 1990).

(*e*) *Miscellaneous plant items*

Seeds, flowers, wood and bark are eaten. They are never predominant, nor are any items eaten regularly. Seeds are mostly immature winged seeds of *Pterygota mildbraedii*, and flowers are from *Mimulopsis arboreus*, which reproduces on a 7 year cycle. Our occasional observations of eating wood and bark fit no clear pattern.

(*f*) *Animals*

We have no records of predation on insects or other invertebrates, nor have we found invertebrate remains in dung samples from Kanyawara ($n = 839$), or Ngogo ($n = 416$), despite the abundant presence of a variety of potential prey species (e.g. *Dorylus* sp. and *Crematogaster* sp.). Chimpanzees ate honey from *Apis mellifera* nests on several occasions.

Vertebrates are eaten regularly. Chimpanzees were observed eating nine *Colobus badiums*, three *Colobus guereza*, one *Cercocebus albigena* and one *Cercopithecus mitis*. Vertebrate remains were found in 2.9% of dungs both at Kanyawara ($n = 839$) and at Ngogo ($n = 416$). Lower rates of vertebrate remains have been found in dung from the Mahale Mountains, Tanzania and Mount Assirik, Senegal (1.8% of 783, and 1.9% of 5777 respectively), and higher rates in Gombe, Tanzania (5.8% of 1963) (Wrangham & Riss 1990). This suggests that meat eating in Kibale occurs at intermediate rates compared with other chimpanzee populations, and that, as elsewhere, it provides occasional supplements to the diet rather than a daily source of high-quality food.

(*g*) *Geophagy*

Consumption of soil or termite clays was not observed.

4. BABOON DIET IN COMPARISON TO CHIMPANZEES

Like chimpanzees, baboons concentrated heavily on non-fig fruit trees in approximate proportion to fruit availability. However, during months when both baboon and chimpanzee dungs were collected (December 1989 to March 1991) baboons ate fewer figs than did chimpanzees. The overall percentage of baboon dungs containing fig seeds was low (66.7% at Ngogo, $n = 96$; 76.5% at Kanyawara, $n = 34$); and fig abundance scores were lower (baboons 1.1 ± 0.7, chimpanzees 2.0 ± 0.7, Wilcoxon $z = 2.61$, $p < 0.01$). In contrast, Ngogo baboons had high FBR scores (baboon monthly mean $= 2.34 \pm 0.91$), compared with Ngogo chimpanzees (2.01 ± 1.00) or Kanyawara chimpanzees (2.03 ± 0.75) (Wilcoxon $z = 1.79$, $p = 0.06$).

Ngogo baboon FBR scores were strongly correlated with Ngogo chimpanzee FBR scores ($r = 0.79$, d.f. $= 14$, $p < 0.001$), and only weakly with Kanyawara chimpanzee FBR ($r = 0.43$, d.f. $= 14$, n.s.). This suggests that monthly variation in FBR intake at Ngogo was influenced for chimpanzees and baboons by local environment factors.

5. VARIATION IN DIET WITH FRUIT ABUNDANCE

Fruit production was not correlated between figs and non-figs. Thus although FA indices which included non-figs were closely correlated with each other ($r^2 = 0.82$–0.93, d.f. $= 27$, $p < 0.001$), FA (fig) was correlated poorly with FA (all) ($r^2 = 0.37$, d.f. $= 27$, $p < 0.001$) and not at all with FA (non-fig) ($r^2 = 0.04$). Mean FA values were similar for non-figs (16.7 ± 17.5) and figs (13.5 ± 9.4), but variance among monthly FA values was greater for non-figs than figs (FA (non-figs), range $= 0$–80.8, $cv = 104.7\%$; FA (fig), range $= 1.8$–37.5, $cv = 69.9\%$; $F_{(27,27)} = 3.65$, $p < 0.01$; data log-transformed to ensure normality). Thus large peaks of fruit availability were primarily the result of extensive fruiting by non-figs, whereas figs represented a relatively consistent level of fruit production.

Variation in FA indices over time showed no clear relation to the annual cycle. FA (non-fig) peaked three times, in April 1988, October 1988 and November 1989. FA (fig) peaked in March 1988, September 1988 and February 1989. None of the FA indices was correlated with monthly rainfall ($r^2 = 0.00$–0.18, d.f. $= 27$, n.s.).

To find how the intake of fibrous foods was influenced by fruit availability, we used data from dung samples (these tests are one-tailed). There was no direct correlation between FBR and any FA index involving non-figs ($r^2 = 0.02$–0.09, d.f. $= 27$, p n.s.). However, fibre levels rose when FA (fig) was low ($r^2 = 0.15$, $p < 0.05$). There were no correlations between any FA index and GLF ($r^2 = 0.00$–0.01, d.f. $= 27$, n.s.). From these results only FA (fig) appears important, and the effect is small. Fibre intake levels were correlated across months among Ngogo chimpanzees and Ngogo baboons, suggesting that environmental factors also influence pith eating.

As piths are likely to be more nutritious during periods of growth, the effect of monthly rainfall was examined in pairwise combination with each FA index. In every multiple regression the combination of rainfall and food availability accounted for a significant proportion of variance in FBR scores ($0.01 < p < 0.02$). When the effect of rainfall was removed, the partial correlation of FA indices with FBR was significant and negative ($0.01 < p < 0.05$; $r = 0.39$–0.48). Conversely, the partial correlation of rainfall with FBR was significant and positive ($0.01 < p < 0.05$; $r = 0.56$–0.58) when the effect of rainfall was removed. The best FA predictor in the multiple regression was FA (all) ($r^2 = 0.39$, d.f. $= 2, 25$, $p < 0.01$). FA (non-fig) was the worst ($r^2 = 0.29$, d.f. $= 2, 25$, $p < 0.05$). Chimpanzees therefore increased their relative pith intake during periods when fruit was scarce, responding to both fig and non-fig fruit production. GLF scores, by contrast, showed no correlation with any FA indices.

The validity of summing FA indices from different species depends on the assumption that trees of the

Table 1. *Nutrient composition of major items eaten by chimpanzees*

(*n*, number of species contributing to data; RTDM, % room temperature dry matter; Other columns show % of dry matter for crude protein (CP), lipid (lip), water-soluble carbohydrates (WSC), hemicellulose plus cellulose (H+C), neutral-detergent fibre (NDF) and condensed tannin (CT). Data on 'other ape' foods are extracted from Calvert (1985), Hladik (1977), Malenky (1990), Rogers *et al.* (1990) and Watts (1984), by calculating means across food species within studies; figures show means of study means. Parts analysed are those eaten by apes, i.e. fruit pulp, etc.)

	n	RTDM	ash	CP	lip	WSC	H+C	NDF	CT
Kanyawara fruit	1	36.7	3.1	6.3	0.0	32.7	7.5	40.3	0.0
other ape fruit	23	26.7	3.0	7.7	1.7	38.6	32.2	64.6	6.2
Kanyawara leaf	4	24.8	—	24.1	0.8	3.0	31.5	41.5	1.5
other ape leaf	44	—	—	16.8	2.6	3.9	26.6	46.0	10.9
Kanyawara fig	9	—	7.7	7.9	3.5	12.6	—	35.6	0.5
other ape fig	2	17.9	—	3.5	3.4	32.4	—	—	12.9
Kanyawara pith	8	11.9	13.4	9.3	0.8	9.8	46.9	50.5	0.1
other ape pith	21	17.0	8.1	10.5	1.6	8.4	48.0	56.3	—

same basal area produce equivalent amounts of food. Although this is probably reasonable, we can avoid relying on it by testing the relation between fruit abundance and fibre intake for the most frequently eaten tree-fruit, *M. bagshawei*, which were eaten in approximate proportion to their availability (figure 1). In Kanyawara the longest fruiting season was from August 1989 to February 1990. During this period (including one month before and after the fruiting period) there was a negative correlation between FBR scores and the FA index for *M. bagshawei* ($r^2 = 0.55$, d.f. = 8, $p < 0.05$). The same relation held between FBR and the number of *M. bagshawei* seeds per 100 g of dung, both for Kanyawara ($r^2 = 0.68$, d.f. = 8, $p < 0.01$) and Ngogo ($r^2 = 0.71$, d.f. = 8, $p < 0.01$). This suggests that, both at Kanyawara and at Ngogo, chimpanzees reduced their intake of fibrous stems when more *M. bagshawei* fruit was available. Again, however, GLF scores were not correlated with the index of fruit abundance ($r^2 = 0.11$–0.31, d.f. = 8, n.s.).

6. NUTRIENT COMPOSITION OF MAJOR FOOD TYPES

Fruits eaten by apes and other primates tend to have high concentrations of sugars and low concentrations of protein (table 1), whereas leaves have low sugar and high protein values (Hladik 1977; Rogers *et al.* 1990). We have also previously shown that Kanyawara figs tend to have low protein values in the edible pulp and that they supply digestible calories at rates equivalent to non-fig fruits (Wrangham *et al.* 1993; also see table 1). Our data on fruit and leaves therefore conform to the principle that large-bodied frugivores eat fruits for energy and leaves for protein (e.g. Milton 1980).

As leaves and pith are often eaten together during TPL sessions, it might be thought that they have equivalent nutritional significance, i.e. that piths are also complementary to low-protein fruits. Yet we have shown that fibrous strands from piths were eaten more when fruit are scarce, whereas we have no evidence that leaf intake varied with fruit abundance. Possibly, therefore, piths provide an alternative energy supply to fruits. We therefore ask here whether piths tend to supply sugars, or protein, or other sources of nutrients.

We analysed nine species of herbaceous piths, including all the major genera eaten by chimpanzees in Kanyawara. Table 1 shows that the mean values from our samples are generally similar to the mean values for other species of pith eaten by apes.

First, protein concentrations (Kanyawara, mean 9.3%; other apes' mean, 10.5%) are similar to those in fruits (6.3–7.7%) and lower than those in leaves (16.8–24.1%) (Kanyawara data, Mann–Whitney $n_1 = 6$, $n_2 = 9$, $z = 2.83$, $p < 0.01$). This suggests that protein concentrations do not generally account for ape interest in pith. In support, table 2 shows that protein concentrations vary widely between pith species, from 1.7% (*Cyperus papyrus*) to 26.3% (*Acanthus pubescens*). Pith species eaten frequently include piths with both high protein (*A. pubescens*) and low protein (*P. purpureum*). Thus we find no consistency with regard to protein selection.

Concentrations of water-soluble carbohydrates in pith are greater than in leaves (table 1), although not significantly so (Mann–Whitney $n_1 = 6$, $n_2 = 9$, $z = 0.71$, n.s.). Species values again show substantial variation. For example, *P. purpureum* has almost ten times the sugar concentration of the two species of *Piper*. As with protein, therefore, sugar concentrations do not provide a consistent explanation for the selection of piths.

Milton & Demment (1988) showed that hemicellulose and cellulose were both partly digested by captive chimpanzees. We therefore examined values of these two fibre fractions to find out whether piths tend to have high concentrations of these fermentable components. Table 1 shows that the mean concentration of hemicellulose and cellulose in pith is indeed high (46.9% in Kanyawara, 48.0% for other ape samples) compared to both fruits (7.5%, 32.2%) and leaves (26.6%, 31.5%). We cannot yet test the difference between fruits and piths with our own data, but Calvert (1985) provided appropriate data from piths eaten by gorillas in Cameroon: piths had higher concentrations of hemicellulose and cellulose than fruits ($n_1 = 7$, $n_2 = 9$, $z = 1.96$, $p = 0.05$). The difference between pith and leaf concentrations was testable in two sets of samples: concentrations of cellulose plus hemicellulose were higher in pith than leaf both in the Kanyawara data ($n_1 = 6$, $n_2 = 9$, $z = 2.00$, $p < 0.05$)

Table 2. *Nutrient composition of herbaceous piths eaten by Kanyawara chimpanzees*

(Abbreviations as in table 1. H, hemicellulose; C, cellulose; NDF, neutral-detergent fibre; lig, lignin.)

	n	CP	WSC	H	C	H+C	NDF	lig
Acanthus pubsecens	3	26.3	14.6	14.2	17.1	31.3	32.6	8.2
Aframomum mildbraedii	2	6.3	5.8	20.1	33.1	53.2	59.7	6.5
A. zambesiacum	3	6.7	5.6	20.9	33.0	53.9	57.9	4.0
Cyperus papyrus	2	1.7	16.4	30.2	29.5	59.7	62.8	3.1
Marantochloa leucantha	3	7.9	15.2	20.2	31.8	52.0	54.5	2.5
Pennisetum purpureum	1	4.4	21.8	19.7	38.6	58.3	63.3	4.9
Piper capensis	1	12.3	2.4	8.8	18.6	27.4	33.7	3.3
P. umbellatum	1	9.6	3.5	12.5	17.9	30.4	30.9	3.5
Renealmia congolana	1	8.8	12.5	21.8	33.4	55.2	59.5	4.3

and in Calvert's (1985) data ($n_1 = 8$, $n_2 = 9$, $z = 2.79$, $p < 0.01$). This difference between piths and leaves was the result of lower lignin levels in piths (Kanyawara, $z = 2.47$, $p < 0.02$; Cameroon, $z = 2.21$, $p < 0.05$). Total fibre (i.e. neutral detergent fibre, NDF), by contrast, did not differ between piths and leaves (Kanyawara, $z = 1.59$, n.s.; Cameroon, $z = 1.34$, n.s.).

7. DISCUSSION

Fibre levels increased as a function of rainfall and decreased in relation to our measures of fruit availability. Furthermore, fibre levels showed a negative correlation with the availability of the most important fruit crop, *M. bagshawei*, during a long fruiting season, and with the number of *M. bagshawei* seeds in the dung both at Kanyawara and Ngogo. We conclude that, in Kibale Forest, chimpanzees tend to respond to tree-fruit shortages by increasing their intake of piths. We found no evidence that leaf intake increased in parallel.

When one considers piths as a single food group, which seems to be how chimpanzees utilize them, our nutritional data support previous conclusions by Calvert (1985) and Rogers *et al.* (1990) that the piths eaten by apes are important sources of energy. However, unlike previous studies we found no evidence that protein concentrations influenced this food group's selection. Nor did we find, in contrast to Rogers *et al.* (1990), that piths provide significant sugar levels: our samples agree instead with Calvert (1985) in having low lignin levels and high NDF. The result is that fermentable fibre is in high concentration. We therefore hypothesize that the importance of piths in the chimpanzee diet tends to result from their providing calories in the form of fermentable fibre.

Previous studies have proposed that terrestrial herbs provide important fallback foods for bonobos and gorillas (Badrian & Malenky 1984; Kano 1983; Kano & Mulavwa 1984; Rogers *et al.* 1988) and mandrills (*Mandrillus sphinx*) (Hoshino 1986). Our results suggest the same is true for Kibale chimpanzees and baboons. However, chimpanzees are not restricted to piths as fallback foods. They exploit a variety of low-quality foods, thereby allowing them access to drier habitats than are known for bonobos or gorillas.

Although we propose that, in general, piths and leaves have different significance, providing energy and protein respectively, this scheme may be too simple. There is some indication that piths of monocotyledons and dicotyledons differ. The only dicotyledons in table 2 are *A. pubescens*, *P. capensis* and *P. umbellatum*, each of which has low levels of hemicellulose and cellulose compared with the monocotyledons. Monocotyledons are predominant in the herbaceous diets of bonobos, forest gorillas, mandrills and chimpanzees, and they appear consistently to provide a critical resource for semi-terrestrial forest primates. Their value as a food source is presumably a result of their basal growth, which leads to a concentration of mobilized nutrients in a relatively compact volume. Thick, tough protective stems may prevent most animals from harvesting piths, leaving them primarily to apes and elephants.

Among hominoids thin-enamelled teeth are restricted to the African apes, the only species that rely heavily on terrestrial piths. Orangutans (*Pongo pygmaeus*), by contrast, have thick-enamelled teeth and only occasionally eat piths (Kay 1981; Leighton 1993), although they spend as much time eating leaves as do chimpanzees (Rodman 1977). This suggests that the divergence of African apes and hominoids, which was probably also a division into thin-enamelled and thick-enamelled groups, marked a divergence into pith eaters and non-pith eaters. The thick-enamelled Miocene apes can be expected to have had a different vital food resource from the thin-enamelled apes of today, with consequent differences in many ecological and social variables.

Given the ubiquity and abundance of terrestrial herbs in contemporary African forests, together with their apparent importance for apes and baboons, it is curious that pith eating is so much less important in other continents and, apparently, in other eras (i.e. in the Miocene). The issue is of interest partly because the occurrence of an essential food resource in the ground layer may have influenced the evolution of terrestriality. As a stimulus to further investigation, we speculate that African rain-forests may have higher biomass densities of edible herbaceous piths than other continents. If so, the causes of such differences may help explain the origins of the modern African apes.

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Discussion

K. Milton (*Department of Anthropology, University of California, Berkeley, U.S.A.*). I suggest that considerable pith may not be swallowed, as with bats and spider monkeys eating fig fruit. Thus chimpanzees may take in more soluble carbohydrates that might be apparent, whilst sparing their digestive tracts from having to process much of the fibrous matter.

N. L. Conklin. So far it is not known what percentage of pith is wadged as opposed to swallowed. Habituating the chimps to letting us follow them on the ground has been a very recent accomplishment. Wadging is definitely something the authors plan to investigate more thoroughly now that they are getting better terrestrial observations.

E. Rogers (*Scottish Primate Research Group and Institute of Cell, Animal and Population Biology, University of Edinburgh, U.K.*). Single measures of sugar content in piths may not give the whole story. There are probably variations between individuals, and in different seasons, so it may be misleading to assume piths remain low in sugar content throughout the year. Species with higher sugar concentrations (20% dry mass in their pith, which have been found in Kibale and Lope, suggest that apes may obtain water-soluble sugars from pith some of the time.

A. Whiten (*Scottish Primate Research Group, University of St. Andrews, U.K.*). The authors seem to be attempting to find a single factor which is 'the' explanation of why a particular food type like pith is eaten. There should be caution about assuming such single factors; might it not be that different piths are eaten for different nutritional reasons, and that in some or all cases, the explanation has to do with more than one component? In the case of two pith species at least (*Acanthus pubescens* and *Piper umbellatum*, see table 2), protein levels are quite high and these are the ones with relatively low hemicellulose and cellulose levels; maybe it is the combined contribution of these which makes these piths valuable?

N. L. Conklin. I agree that the pith picture may be more complicated than presented here. The reason the authors chose to look at all piths as one group is because of an aspect of pith eating that was not mentioned in the paper. It appears that on most afternoons, chimps will leave the fruiting tree they have been feeding in, come down to the ground and eat pith for a few minutes to half an hour. So far there are not enough data to show patterns to the pith species chosen for consumption each day and how that relates to what else has been eaten that day.

The two high protein piths are actually the least frequently eaten as far as we can tell so far. Pennisetum is one of the most frequently eaten, as well as readily available. Aframomum and Marantochloa are also frequently eaten and common. It seems that when they eat pith, they feed on one species per session. The two high protein piths are less common in the environment but the authors have not looked at selectivity among piths yet. Richard Wrangham hopes to find a Ugandan masters student to pursue the pith question further.

R. A. Barton (*University of Sheffield, U.K.*). The authors mentioned that baboons are also known to eat some of these fibrous foods exploited by the great apes. Baboons are, of course, much smaller than apes, and hence presumably less capable of digesting high-fibre foods. Is there any evidence that the baboons are in some way more constrained than the apes in their use of fibrous foods as a fall-back? If so, does this mean that the habitat is something of a marginal one for baboons, which might be indicated by low population density and long day journeys relative to group size, or do they have some other way of surviving hard times?

N. L. Conklin. The forest baboons in Kibale have been very little studied. As far as we can tell they are very migratory and the habitat seems to be a marginal one for them but their home range is not known. They do wadge fibrous foods, which is one way to get out the soluble nutrients without having to ingest and pass the fibre, but then chimps wadge pith and fruit also. From information obtained at other sites it is known that baboons will eat plant material higher in secondary plant compounds than do chimps, but during times of food shortage in Kibale the baboons tend to disappear from the study site and it is not known where they go or what they do.