



Nutritional Aspects of Western Lowland Gorilla (*Gorilla gorilla gorilla*) Diet during Seasons of Fruit Scarcity at Bai Hokou, Central African Republic

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*Traditionally, gorillas were classified as folivores, yet 15 years of data on western lowland gorillas (*Gorilla gorilla gorilla*) show their diet to contain large quantities of foliage and fruit, and to vary both seasonally and annually. The consumption of fruit by gorillas at Bai Hokou, Central African Republic, is correlated with rainfall and ripe fruit availability (Remis, 1997a). We investigated the nutritional and chemical content of gorilla foods consumed at Bai Hokou during two seasons of fruit scarcity as measured by phenological observations and compared our findings with the nutrient content of gorilla foods at other African sites. We conclude that during lean times, Bai Hokou gorillas consumed fruits with higher levels of fiber and secondary compounds than those of other populations of western lowland or mountain gorillas. Conversely, leaves consumed by Bai Hokou gorillas were relatively low in fiber and tannins. Bai Hokou gorillas appeared to meet their nutritional needs by eating a combination of fruit and foliage. They ate fruits comparatively high in secondary compounds and fiber when necessary. While gorillas are selective feeders, wherever and whenever preferred foods are scarce, their large body*

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size and digestive anatomy enable them to consume and process a broader repertoire of foods than smaller bodied-apes.

KEY WORDS: fiber; phenolics; feeding ecology; African apes.

INTRODUCTION

Gorillas are the largest living primates and possess colons that contain a large number of cellulose digesting ciliates (Collet *et al.*, 1984). Otherwise, gorillas have a generalized ape morphology that seems adapted for frugivory (Kay, 1975; Chivers and Hladik, 1980; Martin *et al.*, 1985). Gorillas have traditionally been viewed as terrestrial folivores, largely a consequence of their size (Schaller, 1963; Fossey and Harcourt, 1977) and theoretical considerations of the effects of body size on ecology (Schoener, 1971; Demment and van Soest, 1985; Perrin, 1994). They appear to be able to retain low quality foods in the gut in order to maximize absorption of nutrients (Remis, 2000). Our perceptions of gorillas have been reinforced by study of the terrestrial mountain gorilla, whose diet is herbivorous, not very diverse or seasonally variable (Watts, 1996), and whose teeth are adapted for shearing leaves (Groves, 1986; Uchida, 1998). A growing body of field data on western lowland gorillas, however, challenges the notion that gorillas are folivores (Tutin *et al.*, 1991; Remis, 1994, 1997a, b). More than 15 years of fieldwork on western lowland gorillas suggests that diets vary seasonally but their dietary preferences are similar to those of sympatric frugivorous chimpanzees.

Western lowland gorillas consume ripe fleshy fruits whenever available (Williamson *et al.*, 1990). In these periods, their foraging strategies (Tutin *et al.*, 1993a), ranging behavior and grouping patterns may converge with those of frugivorous chimpanzees (Remis, 1997b; Goldsmith, 1996). During months of fleshy fruit availability, western lowland gorilla diet consists of $\geq 50\%$ and $\leq 90\%$ fruit (Tutin *et al.*, 1997; Remis, 1999). Despite the importance of fruit in their diet, diet shifts seasonally at all lowland gorilla sites. Consequently, they might be best referred to as seasonal frugivores (Tutin *et al.*, 1991; Remis, 1997a). During periods of fleshy fruit scarcity, fibrous fruits become staple fallback foods and consumption of herbs, leaves and bark increases (Rogers *et al.*, 1990). Leaf flush frequently occurs during non-fruiting seasons, and gorillas take advantage of high quality young leaves (Tutin and Fernandez, 1993b).

Variation in dietary selectivity and food preferences among primates likely relates to niche separation (Ganzhorn, 1989; Wrangham *et al.*, 1998), which may reflect differences in digestive strategies for metabolizing nutrients and secondary compounds in plants (Freeland and Janzen, 1974; Rhodes

and Cates, 1976; Glander, 1981). Folivorous primates often consume foods that are relatively high in digestion inhibitors, such as lignin and carbon-based secondary plant compounds, e.g., tannins, and also relatively higher in protein (Hladik, 1978; Waterman *et al.*, 1983; Waterman and Kool, 1994; Mowry *et al.*, 1996) compared with foods not eaten.

Gorillas lack the morphological specializations associated with forest-omach fermentation and microbial adaptations to tannins (Oates *et al.*, 1977; Kay and Davies, 1994). However, they have an enlarged hindgut (Chivers and Hladik, 1980), associated with colocecal fermentation (Bauchop, 1978; Parra, 1978; Milton and Demment, 1988). Accordingly, relative to other hominoids, they are probably well equipped to digest fiber and may tolerate tannin-rich foods (Rogers *et al.*, 1992; Cork and Foley, 1992; Simmen *et al.*, 1999).

Despite these features, the dietary choices of gorillas may be more similar to those of other ape frugivores than of folivores. Primate frugivores often choose mature or ripe fruits over immature or unripe fruits or other plant parts (Gautier-Hion *et al.*, 1985); apes exemplify this trend (Wrangham *et al.*, 1998). Frugivores typically act as seed dispersers rather than seed destroyers (Garber and Lambert, 1998). Unripe fruits may be avoided if they have low energy or protein content or higher concentrations of secondary compounds than ripe fruits (Hulme, 1971; McKey, 1979; Janzen, 1983). Many plant species have considerable quantities of condensed tannins in unripe fruit flesh (Swain, 1979), which cause astringency and may interfere with digestion by reducing protein availability in the gut (cf. Mole and Waterman, 1987; Waterman and Mole, 1994). During ripening, fruits usually undergo color change, tannins lose their astringency and palatability increases (Barnell and Barnell, 1945; Harborne, 1988, 1991).

Gorillas are selective eaters, despite their large size and ability to consume a tough, low quality diet (Strait, 1997). They often discard the outer bark of vines, stem layer of herbs and proximal, distal and midrib sections of leaves (Casimir, 1975). Mountain gorillas are primarily herbivorous and choose vegetation that is generally higher in protein content and lower in acid detergent fiber and condensed tannins compared with lowland gorilla foods (Goodall, 1977; Waterman *et al.*, 1983; Rogers *et al.*, 1990; Plumptre, 1995; Popovich *et al.*, 1997). Chemical and nutrient analysis of the diet of the more frugivorous western lowland gorillas at Lope' shows that many fleshy fruits consumed by gorillas are fructose rich, low in crude protein and fat. Some fruits, especially those species used in times of scarcity by both chimpanzees and gorillas, have been described as high in fiber and phenolics (Rogers *et al.*, 1990; Wrangham *et al.*, 1991; Popovich *et al.*, 1997). Relative consumption of tannins is variable; it is not yet clear whether gorillas

consume more tannins than chimpanzees do (Rogers *et al.*, 1990; Tutin and Fernandez, 1993a; Wrangham *et al.* 1998,). To date, we lack an adequate picture of the variability of ape diet between and within sites and species.

The nutritional and chemical analyses of primate foods permit a better understanding of species-specific ecological niches and provide a means to compare closely related taxa. We investigated the chemical content of foods eaten by western lowland gorillas at Bai Hokou, Central African Republic. Analysis of diet during scarcity of preferred fruits permits us to examine how the anatomical specializations of gorillas may impact dietary selectivity and distinguish them from other species. Our specific objectives were 1) chemically to analyze foods eaten by Bai Hokou gorillas during seasons of scarcity, 2) to determine the influence of plant chemistry on Bai Hokou gorilla feeding ecology during scarcity, and 3) to compare the seasonal nutrient and other phytochemical profile of the Bai Hokou gorilla diet to the averages from other gorilla populations. The analyses do not yet represent a complete picture of Bai Hokou gorilla diet, but they will complement existing data to facilitate a better understanding of the seasonal dietary variability and flexibility reported for gorillas across their range.

METHODS

Field Data

Ecological monitoring and studies of gorilla foraging ecology have been conducted at Bai Hokou, Central African Republic since 1984 by Remis (1994, 1997a), Goldsmith (1996) and Carroll (1997). Rainfall averages 1365 mm annually, with a single 3-mo dry season, generally December-March each year. The heaviest rainfall occurs in September-October, usually a period of high fruit availability, with ripe fruit most abundant August-October.

We combined the nutritional analysis of gorilla plant foods collected on gorilla feeding trails and during observations at Bai Hokou by Carroll during late-dry season, March 1989 (leaves and fibrous fruits), with those collected by Remis on a wider variety of fruits consumed by the same gorilla groups during the fruiting or wet season June-August, 1998. This combined data set permits analysis of temporal variations in dietary patterns.

Basic monthly phenological patterns (presence or absence of ripe, unripe or fallen fruit, and new and mature leaves on trees >10 cm diameter at breast height) of 973 marked trees of 152 species along 19 km of cut north-south transects have been recorded at Bai Hokou when researchers were present (Remis, 1997a). The phenological data represent monthly

community-wide fruiting patterns rather than the availability of specific gorilla foods. The data represent the following months: August 1988–May 1989; March 1990–October 1992, August 1993–January 1995, June–December 1995, August 1997, and August 1998. During August 1998, we noted the phenological patterns of only 720 of the 973 marked trees.

We have collected information on gorilla diet of unhabituated and semi-habituated study groups. As at other gorilla study sites, we used a combination of direct observations (1685 1-min interval samples of undisturbed focal subjects feeding), and indirect methods including trail and macroscopic fecal analysis (Remis, 1994, 1997a; Carroll, 1997). In addition, we recorded feeding visits once per animal per feeding patch (usually a tree) on a particular date ($n = 155$). Observational dietary data at Bai Hokou are biased in favor of the 9-mo wet seasons ($n = 143$ feeding visits; 1527 feeding min), with less data collected during the 3-mo dry seasons ($n = 12$ feeding visits; 158 feeding min). During research at Bai Hokou, we collected fecal samples opportunistically and examine them macroscopically to determine the number of fruit species eaten. During fecal analysis, we combined the relative abundance score of monocot herbs (0–4 scale) and other foliage (leaf and bark; 0–4 scale) in each fecal sample to yield a total foliage score (0–8 scale) (Tutin and Fernandez, 1993c; Remis, 1997a). It was not possible to accurately detail the relative proportions of plant species eaten in gorilla diet by either observations or fecal analysis, but we collected samples of all fruits observed or known to be eaten by the gorillas.

During 1989 and 1998, we collected foods partially consumed and discarded by gorillas during observations or on feeding trails in association with gorilla knuckle-prints, nests or dung. We dried leaves and stored them in plastic containers with desiccant and fixed fruit samples in ethanol. In addition, we manually collected representative food samples from 3–5 individual plants per species. We attempted to obtain 50–100 g (wet weight) of material for subsequent chemical assays. We determined water content in the field by weighing samples and air-dried leaves in an open-air kitchen until constant weight was achieved. We weighed fruit samples to the nearest 0.1 g and stored them in 70% ethanol for transport. During the 1998 data collection, we also assessed ripeness of fruits eaten, avoided and discarded during observations and along feeding trails, based on color, odor and softness. Seed-eating plays a very minor role in gorilla fruit consumption; Bai Hokou gorillas consume few seeds that do not emerge intact in their feces. We characterized fruits as fleshy if they had a juicy (succulent) pulp or dry if they had a dry fibrous fruit pulp or dehiscent pod. We further defined important fruits as those most prevalent on a yearly basis in gorilla fecal samples ($> 1\%$ of fecal samples), on feeding trails and during observation over > 5 years of field research (Remis, 1999).

Identification of Bai Hokou gorilla plant foods was conducted by Dr. David Harris, Royal Botanical Gardens, Edinburgh Scotland and Dr. J. Michael Fay, Wildlife Conservation Society, New York, USA. Plant parts that we collected in 1989 and 1998 include ripe and unripe fruits, seeds, leaves, stems and vines. We analyzed the 1998 samples for chemical composition and other phytochemicals shortly following collection. Dierenfeld had analyzed samples collected by Carroll in 1989 (Dierenfeld unpublished data; Popovich *et al.*, 1997), but we further analyzed them for phenolics and alkaloids.

Laboratory Data Analyses

Before nutrient analysis, we evaporated ethanol preservative at room temperature under a laboratory fume hood and collected all residue upon drying to a constant weight. We then ground samples using a laboratory mill, and kept them at room temperature until analysis. We calculated crude protein (CP) content as total nitrogen X 6.25 using a macro-Kjeldahl method with a Cu catalyst (AOAC, 1996). We conducted analyses of plant cell wall constituents—(neutral detergent fiber (NDF), acid detergent fiber (ADF), and sulfuric acid lignin (Ls))—on all plant samples via the methods of Van Soest *et al.* (1991). We evaluated water soluble carbohydrates, predominantly simple sugars (SS), in fruits via a phenol/sulfuric acid colorimetric assay (DuBois *et al.*, 1956) as modified by Strickland and Parsons (1972). We assayed macromineral concentrations (Ca, K, Mg, Na, P) and trace elements (Cu, Cr, Fe, Mn, Zn) by inductively-coupled plasma argon emission spectroscopy (Stahr, 1991).

We prepared fruit pulp and seed samples for secondary compound analysis by evaporating the ethanol preservative and drying fruits in an exhaust oven at $\sim 30^{\circ}\text{C}$, and ground samples with any corresponding residue to a powder (20-mesh screen) in a Wiley mill. Leaf samples had been previously collected, dried and milled (Popovich *et al.*, 1997). Although some loss of extractable phenolics may have occurred since leaf collection, the tannin analysis method is appropriate for comparative purposes (Waterman and Mole, 1994). We prepared extractions for hydrolyzable and condensed tannin assays using 50% methanol (Bate-Smith, 1977, 1981; Hagerman and Butler, 1991). We measured hydrolyzable tannins (HT–ellagitannins) under an N_2 environment using an acetic acid-sodium nitrate procedure (Bate-Smith, 1972, 1977). We estimated condensed tannins (CT) as proanthocyanidins using a butanol-HCl technique (Bate-Smith, 1975, 1981). Our procedures followed Shure and Wilson (1993) and Dudt and Shure (1994).

We used tannic acid and quebracho tannin as standards for hydrolyzable and condensed tannins, respectively (Waterman and Mole, 1994). Hydrolyzable tannins are expressed as mg per dry weight of hexahydroxydiphenylglucose equivalents (mg/g HHDP) and condensed tannins as percentage dry mass quebracho tannin equivalents (%QTE). Condensed tannin values are not expressed as percent dry weight of a given sample. Some condensed tannin values actually exceed 100%, indicating the particular sample is more reactive than an equal amount of quebracho tannin. We measured protein precipitation via a modified version of the radial diffusion (RD) method for determining tannin in plant extracts (Hagerman, 1987). Modifications included using a smaller concentration of BSA protein and staining the agarose gels with Prussian blue reagent. We measured the stained gels on a Macintosh computer using the public domain NIH Image program (developed at the U.S. National Institutes of Health and available on the Internet at <http://rsb.info.nih.gov/nih-image/>). Standards and units for the RD assay are the same as those for the CT assay. A significant positive correlation exists between the CT and RD assays ($R = 0.685$, $p < 0.0001$).

We determined the presence or absence of alkaloids in plant samples using Iodoplatinate and Dragendorffs reagents. We extracted 100 mg of milled sample in 10 ml of 95% ethanol at room temperature for 24–36 hours. We then dried the extract completely, and added equal parts water and petroleum ether. After two distinct layers formed, we spotted several drops of the bottom (aqueous) layer on two pieces of filter paper. We then sprayed one filter paper with Dragendorffs reagent and the other with Iodoplatinate reagent. We recorded the degree of color change (0–3) for each reagent spray, indicating the presence and relative amount of alkaloid in each sample, and we generated a single value from the mean.

Statistical Analysis

We used Mann-Whitney U tests to examine nutrient and other phytochemical differences between medians for each of the following: a) food categories (fruits, leaves), b) ripe versus unripe fruit, c) fruits collected in different years (1989 versus 1998), d) dry versus fleshy fruits, and e) important versus less important fruits. We generated Pearson product-moment correlations between each of the nutrient and other phytochemical measurements for all categories of food. We then investigated the levels of significance for pairs of variables that appeared to be correlated by running a regression analysis (Rosner, 1990). We used DataDesk for Macintosh for all statistical analysis (Data Description, 1997).

RESULTS

Food Availability

Long-term community-wide phenological data reveal two major seasons of high and low ripe fruit availability correlated with seasonal patterns of rainfall at Bai Hokou (Remis, 1997a; Goldsmith, 1996; Carroll, 1997). Leaf flush usually occurs at the end of the dry season. The data reveal considerable yearly variation and the occurrence of good and poor fruit years as well as seasons. Nevertheless, the numbers of species that contain ripe fruit generally peaks during the rainy months of July and August. During the dry season, unripe and fibrous fruits are present, but ripe fleshy fruit is scarce. During 1988–89, however, fewer species on phenology trails produced fruit than in subsequent good fruit months or years (Fig. 1).

Data collection in 1998 also occurred during a poor fruiting season, relative to other years. In August 1998, only 7% of marked species contained fruit, with only 4% having ripe fruit ($n = 720$). [In August of other years: 1988, 6%; 1990, 37%; 1991, 21%; 1992, 36%; 1994, 30%; 1995, 35% and 1997, 72% of species bore fruit] (Fig. 1; Remis, 1997a, 1999). While we were not able to quantify total monthly rainfall during 1997 and 1998, the 1998 dry season was unusually long, the rains and fruiting season markedly late, and fruit productivity poor compared with previous years (Chiopelleta and Kpanou unpub). Moreover, leaf flush typically occurs in the dry season, but in 1998 it occurred in August, when 25% of trees bore young leaves. Thus, overall food availability during the study period resembled late dry season months more than previous peak fruiting seasons. Accordingly, in both 1989 and 1998, we had collected gorilla plant food samples during seasonal or interannual periods of low fruit availability. Figure 1 shows the monthly patterns of variation in fruit availability and rainfall over the 10-year period, June, 1988–August, 1998, with June of each year marked on the x-axis for reference.

Gorilla Diet at Bai Hokou

Proportions of fruit, herbs, leaves and bark in western lowland gorilla diet vary in response to rainfall and ripe fruit availability (Remis 1997a; Tutin *et al.*, 1997). When fruit abundance is high at Bai Hokou, consumption of foliage declines, but during periods of low rainfall, when fruits are scarce, consumption of fleshy fruits is reduced. Figure 2 shows seasonal variation

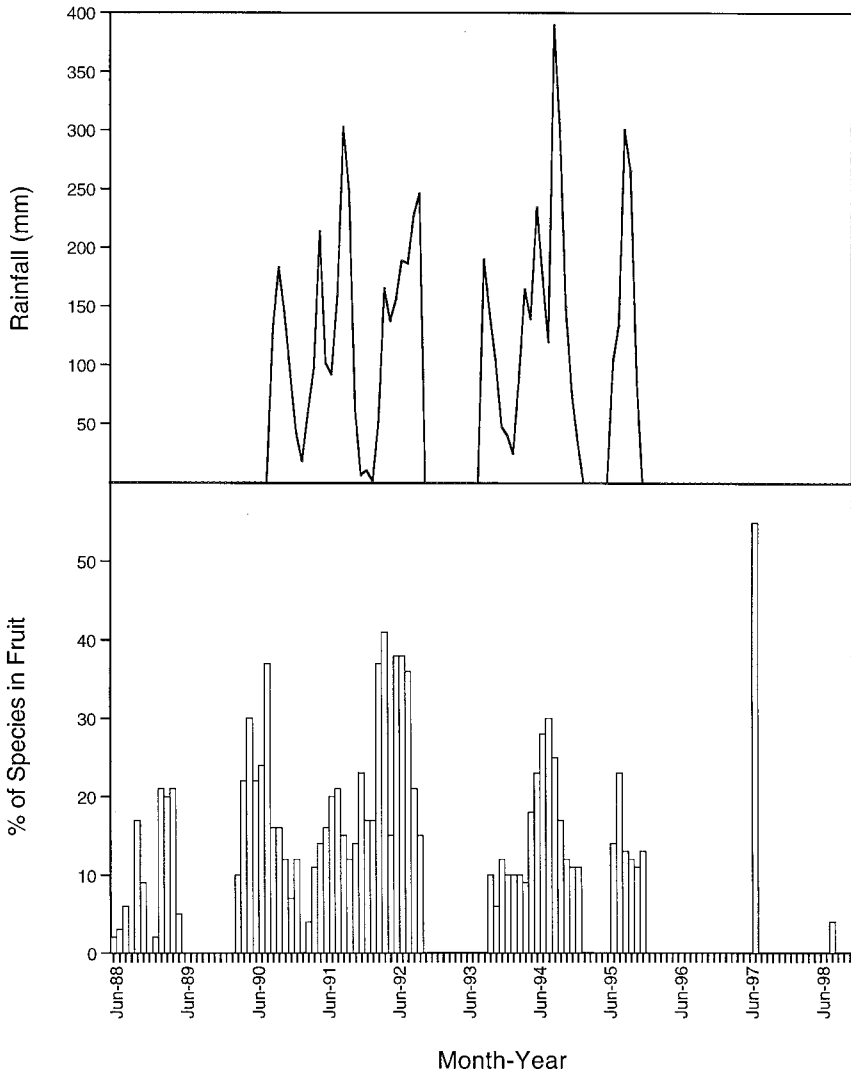


Fig. 1. Phenological patterns of fruit availability at Bai Hokou, 1988–1998. Fruit availability was measured monthly on marked trees at Bai Hokou by one of two observers, Jean Bosco Kpanou or Etienne Ndongbe from August 1988–May 1989 (Carroll, 1997), March 1990–January 1991, March 1991–October 1992 (Remis, 1994), October 1993–January 1995 (Goldsmith, 1996), June 1995–December 1995, August 1997, August 1998 (Remis, 1999 and unpublished). Data are reported here as number of tree species containing ripe fruit in each month ($n = 152$ species, total of 973 individuals). In August 1998 only 148 species, 720 trees were monitored.

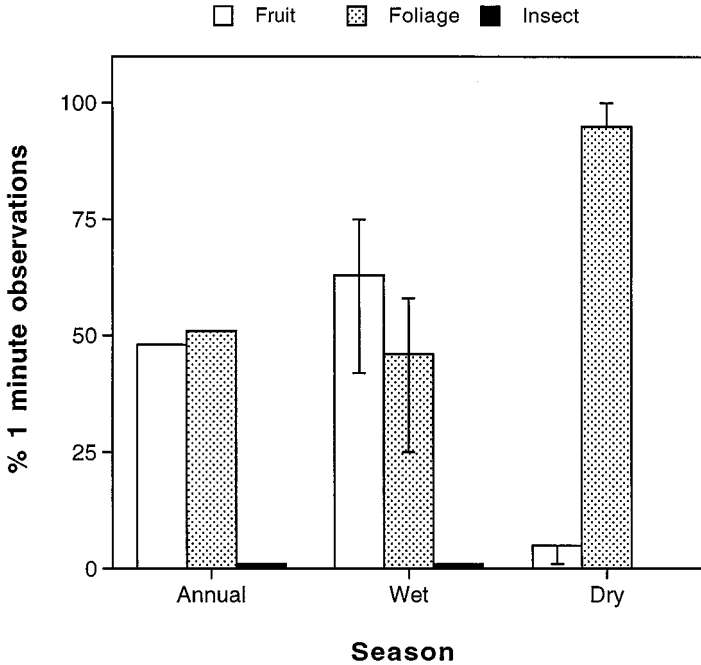


Fig. 2. Gorilla feeding observations by Remis at Bai Hokou (combined data from 4 wet seasons, 2 dry seasons (1685 one-minute observations, 155 feeding visits, 1990–1995).

in the consumption of fruit and foliage by Bai Hokou gorillas during observations by Remis, averaged over 4 wet seasons (143 feeding visits) and 2 dry seasons (12 feeding visits). The data were collected during focal-animal samples on undisturbed gorillas feeding at Bai Hokou ($n = 1685$ 1-minute intervals). A small sample of gorilla fecal samples ($n = 9$) collected during the 1998 study period showed that while gorillas ate fruit (mean number of fruit species per fecal sample is 3), foliage made up a greater proportion of fecal samples (mean foliage abundance score = 5.9, on a scale of 0–8), than it had in 4 previous good fruit wet seasons (foliage scores averaged 3.7, $n = 905$ samples). In previous dry season fecal samples, foliage scores averaged 5.9 ($n = 199$ samples) (Remis, 1997a; Remis, 1999). More extensive fecal analysis and trail data from other field seasons support observations and indications of dietary switching from fruit to leaves during periods of low ripe fruit availability (Remis, 1997a; Goldsmith, 1996; Carroll, 1997).

Nutritional and Phytochemical Content of Gorilla Foods

We analyzed a total of 68 plant samples for the presence of nutrients and other phytochemicals. At least 20 different plant families and 35 species are represented, though some samples are currently known only by their local BaAka names. Overall, Bai Hokou gorilla foods analyzed from these periods of scarcity are relatively high in mean crude protein (12.68%), fiber (mean NDF = 61.63%, mean ADF = 46.55%), and lignin (mean Ls = 24.4%). Compared to foods from other gorilla study sites (see Table IV), Bai Hokou foods are also moderately high (all values listed as % dry weight) in soluble sugars (12.31% dry weight), and tannin: mean HT = 3.13 mg/g HHDP, mean CT = 7.58%QTE, mean RD = 2.11% QTE (Appendix A). Minerals were present at the following unweighted mean levels (all values reported on a dry matter basis): Ca = 0.18%, K = 1.21%, Mg = 0.14%, Na = 0.01%, P = 0.13%, Cu = 11.12 mg/kg, Cr = 0.85 mg/kg, Fe = 79.34 mg/kg, Mn = 135.17 mg/kg, Zn = 18.40 mg/kg (Appendix B). Bai Hokou fruits are lower in sugars and higher in fiber than one might expect during a good fruit season (Rogers *et al.*, 1990). Nevertheless, the negative correlation between fiber and SS suggests that the gorillas were choosing relatively sweet, low fiber fruit (NDF/SS, $R = -0.761$, $p = 0.0006$; ADF/SS, $R = -0.623$, $p = 0.01$). Crude protein in leaves, but not fruits, is negatively correlated with fiber (for foliage, CP/NDF $R = -0.406$, $p = 0.05$; CP/ADF $R = -0.516$, $p = 0.005$). Table I shows Pearson correlation values for fruit and foliage.

Secondary plant compounds and individual mineral constituents are not consistently correlated with any other nutrient component of the foods evaluated. Fruits used as food resources are low in Ca, Mg, P, Na and Fe compared to nutrient recommendations for nonhuman primates (NRC, 1978). While the Ca:P ratio is within suggested ranges (1:1 to 2:1), none of the fruits contained adequate Ca (0.55%). Even selective feeding could not meet requirements for Ca. Native fruits, similar to domestic fruits, are high in potassium compared with all other macrominerals.

Nutritional Comparisons between Plant Parts

Foliage vs. Fruits

Foliage—(herbs and leaves of woody species, including vines)—is higher than fruits in ash and crude protein ($p < 0.0001$ for both ash and CP) (Tables II and III). There is no significant difference in the ash ($p = 0.8579$) or crude

Table I. Pearson correlation statistics for nutrient and other phytochemical assays of fruit and foliage

	HT	CT	RD	Ash	NDF	ADF	HC	Ls	CP	SS	Ca	K	Mg	Na	P	Cu	Cr	Fe	Mn	Zn
All Foliage																				
HT	1																			
CT	0.698***	1																		
RD	0.582***	0.854***	1																	
Ash	0.025	-0.26	-0.332	1																
NDF	-0.205	0.053	0.036	-0.134	1															
ADF	-0.159	0.164	0.142	-0.29	0.95***	1														
HC	-0.079	-0.372	-0.344	0.541**	-0.24	-0.53**	1													
Ls	-0.146	0.284	0.315	-0.425	0.724***	0.853***	-0.688**	1												
CP	0.228	-0.206	-0.204	0.681***	-0.406*	-0.516**	0.504*	-0.402	1											
All Fruit																				
HT	1																			
CT	0.199	1																		
RD	0.331	0.814***	1																	
Ash	-0.255	-0.403*	-0.19	1																
NDF	-0.025	-0.251	-0.551**	-0.078	1															
ADF	-0.015	-0.179	-0.417	0.121	0.911***	1														
HC	-0.027	-0.179	-0.255	-0.472**	0.124	-0.295	1													
Ls	-0.225	0.043	-0.244	0.173	0.674***	0.832***	-0.441*	1												
CP	0.108	-0.039	-0.067	0.335	-0.264	-0.238	-0.039	-0.156	1											
SS	0.047	-0.171	0.437	0.022	-0.761**	-0.623**	-0.122	-0.555*	0.021	-0.222	1									
Ca	0.394	-0.118	-0.225	0.044	0.153	0.214	-0.116	0.066	0.329	-0.481	0.226	1								
K	-0.146	-0.251	0.035	0.713***	0.001	0.166	-0.295	0.163	0.179	-0.01	0.442	0.685**	1							
Mg	-0.241	-0.513*	-0.264	0.687***	-0.192	-0.046	-0.252	0.022	0.286	-0.351	-0.2	0.392	0.22	1						
Na	-0.253	-0.051	0.066	0.303	0.133	0.271	-0.252	0.484*	0.493*	0.045	0.048	0.3	0.543**	0.226	1					
P	-0.47*	-0.559*	-0.497*	0.294	-0.009	-0.04	0.053	0.008	0.365	0.166	0.128	0.392	0.359	-0.13	0.395	1				
Cu	0.166	-0.556*	-0.182	0.494*	-0.008	0.01	-0.033	-0.25	0.009	0.253	0.77	-0.431	-0.347	0.212	0.117	-0.071	1			
Cr	-0.021	-0.293	-0.219	-0.157	0.305	0.161	0.369	-0.009	-0.247	-0.318	-0.186	0.215	0.056	0.25	0.033	0.109	-0.059	1		
Fe	-0.099	-0.103	0.237	0.082	0.179	0.161	0.024	0.053	0.191	-0.133	0.419	0.12	0.154	-0.134	0.181	0.036	0.644	-0.263	1	
Mn	-0.108	-0.42	-0.616**	0.031	0.322	0.162	0.271	0.066	0.191	-0.133	0.419	0.12	0.154	-0.134	0.181	0.036	0.644	-0.263	0.644	1
Zn	-0.396	-0.372	-0.266	0.41	0.058	0.03	0.046	0.119	0.203	-0.201	0.017	0.266	0.391	0.157	0.41	0.095	0.383	0.327	0.244	0.327

Abbreviations as in Appendix I and II.

*p = 0.05.

**p = 0.01.

***p = 0.001.

****p = 0.0001.

Table II. Descriptive statistics on the composition of plant parts consumed at Bai Hokou, Central African Republic

All fruit	N	Mean	Range	Unripe fruit	N	Mean	Range
HT	31	3.91	0.24–24.12	HT	7	2.78	0.24–5.79
CT	31	11.96	0.01–95.74	CT	7	22.62	0.01–95.74
RD	27	3.70	0.00–12.17	RD	8	3.96	0.00–9.48
Ash	30	3.82	1.82–7.58	Ash	8	3.28	1.82–6.80
NDF	30	59.27	19.84–94.16	NDF	8	55.82	46.15–68.39
ADF	30	45.30	10.94–83.83	ADF	8	40.52	10.94–56.32
HC	30	13.97	2.84–36.11	HC	8	15.30	2.84–36.11
Ls	30	24.18	3.00–49.18	Ls	8	25.00	3.64–41.92
CP	30	8.72	3.05–15.62	CP	8	9.25	7.11–11.15
SS	16	12.73	1.43–48.92	SS	6	8.80	3.93–13.93
Ca	22	0.18	0.01–0.38	Ca	7	0.18	0.10–0.28
K	22	1.21	0.04–2.97	K	7	1.07	0.44–1.89
Mg	22	0.14	0.02–0.25	Mg	7	0.13	0.02–0.25
Na	22	0.01	0.00–0.02	Na	7	0.01	0.00–0.02
P	22	0.12	0.07–0.18	P	7	0.12	0.07–0.15
Cu	22	11.20	1.74–26.07	Cu	7	8.82	1.74–26.07
Cr	8	0.90	0.25–1.48	Cr	3	0.84	0.52–1.13
Fe	22	80.47	29.33–167.84	Fe	7	90.06	30.98–129.80
Mn	22	135.18	19.54–332.07	Mn	7	118.27	60.15–207.91
Zn	22	18.40	8.44–40.70	Zn	7	19.40	8.65–40.70

Ripe fruit	N	Mean	Range	All foliage	N	Mean	Range
HT	24	4.24	0.44–24.12	HT	23	2.29	0.30–6.79
CT	24	8.84	0.17–49.26	CT	23	3.13	0.11–30.71
RD	19	3.59	0.00–12.17	RD	24	2.83	0.00–34.11
Ash	22	4.01	2.44–7.58	Ash	24	7.50	2.66–14.47
NDF	22	60.52	19.84–94.16	NDF	24	66.25	42.17–83.02
ADF	22	47.04	12.79–83.83	ADF	24	49.49	25.81–70.01
HC	22	13.48	3.65–31.08	HC	24	16.76	9.99–24.46
Ls	22	23.88	3.00–49.18	Ls	24	25.44	6.75–49.84
CP	22	8.53	3.05–15.62	CP	24	17.54	8.11–32.90
SS	11	15.09	1.43–48.92				
Ca	15	0.18	0.01–0.38	Leaves	N	Mean	Range
K	15	1.28	0.04–2.97	HT	15	2.93	0.30–6.79
Mg	15	0.14	0.07–0.24	CT	15	4.52	0.13–30.71
Na	15	0.01	0.00–0.02	RD	16	3.28	0.00–34.11
P	15	0.12	0.07–0.18	Ash	16	7.70	2.66–14.47
Cu	15	12.32	5.39–19.23	NDF	16	63.93	42.17–80.63
Cr	5	0.93	0.25–1.48	ADF	16	47.54	25.81–69.53
Fe	15	76.00	29.33–167.84	HC	16	16.40	10.17–24.46
Mn	15	143.06	19.54–332.07	Ls	16	25.19	6.75–49.84
Zn	15	17.94	8.44–30.41	CP	16	18.86	12.30–32.90

Table II. (Continued)

Stems & vine				Seeds			
	N	Mean	Range		N	Mean	Range
HT	8	1.09	0.66–2.43	HT	6	2.32	0.05–7.62
CT	8	0.53	0.11–1.77	CT	6	2.06	0.12–11.05
RD	8	0.00	0–0	RD	6	0.00	0.00–0.00
Ash	8	7.10	5.42–8.83				
NDF	8	70.90	53.61–83.02				
ADF	8	53.40	37.57–70.01				
HC	8	17.49	9.99–22.61				
Ls	8	25.95	13.93–43.98				
CP	8	14.91	8.11–19.70				
Stems (herb)							
	N	Mean	Range		N	Mean	Range
HT	6	0.93	0.66–1.32				
CT	6	0.59	0.11–1.77				
RD	6	0.00	0.00–0.00				
Ash	6	7.21	5.68–8.83				
NDF	6	67.41	53.61–77.05				
ADF	6	49.22	37.57–67.06				
HC	6	18.19	9.99–22.61				
Ls	6	25.98	13.93–43.98				
CP	6	16.87	11.20–19.70				

Abbreviations and units as in Appendix A.

protein ($p = 0.9412$) content of herbaceous stems and woody leaves. Conversely, fruits contained more soluble sugars ($p < 0.0001$) and condensed tannins ($p = 0.0039$), and a higher protein precipitating ability (as measured by the RD assay, $p = 0.0046$) than in all foliage samples. Fruits and foliage had similar amounts of NDF ($p = 0.104$) and ADF ($p = 0.3638$). As expected, most tannin in the foliage of Bai Hokou gorilla diet comes from tree leaves instead of herbaceous stems; leaves are higher than stem/vines in HT ($p = 0.0131$) and CT ($p = 0.0489$). In fact, there was no measurable amount of tannin in any of the stem/vine samples based on the RD assay. Moreover, none of the foliage samples tested positive for alkaloids (Appendix A).

Although fruits are commonly referred to as high quality foods, Bai Hokou fruits are much more variable interspecifically in putative antifeedants—alkaloids, fiber and tannins—than either herbs or leaves are (Appendix A). There is no evidence that tannins deter gorillas from eating fruit. Further, the fact that gorillas pass undigested seeds through their guts, apparently is not a result of the presence of antifeedants. The few seeds samples are lower in condensed tannins ($p = 0.0219$) and protein precipitating ability ($p = 0.039$) than fruit pulp, (Tables II and III). In tests for the presence of alkaloids, only two fruits, *Tabernatum sp.* and *Ficus sp.*, gave

Table III. Differences in the composition of plant parts consumed by gorillas at Bai Hokou

Assay	Ripe vs. unripe fruit		Fruit(98) vs. fruit(89)		Imp. fruit vs. other fruit		Fleshy vs. dry fruit	
	z-stat	p-value	z-stat	p-value	z-stat	p-value	z-stat	p-value
HT	0.18902	0.8501	0.70014	0.4838	-0.04129	0.4835	-1.3525	0.1762
CT		0.6607		0.2909		0.06		0.7555
RD	0.77249	0.4398	2.4511	0.0142	1.5797	0.0571	0.28611	0.7748
Ash	-1.7591	0.0786	-0.67417	0.5002		0.7144	-1.2752	0.2023
NDF		0.7304		<0.0001		0.3998		0.0426
ADF		0.7304		<0.0001		0.3056		0.0108
HC		0.6293		0.4698		0.9326		0.4809
Ls		0.9086		0.0076		0.2003		0.2261
CP	0.96151	0.3363	2.5667	0.0103	-1.9799	0.0239	2.0106	0.0444
SS		0.2463	1.8998	0.0207		0.0139	ND	ND

Assay	Foliage vs. fruit		Fruit vs. seeds		Leaves vs. stems	
	z-stat	p-value	z-stat	p-value	z-stat	p-value
HT	-1.0147	0.3103	0.94781	0.3432		0.0042
CT	-2.8777	0.0039		0.0219	1.5186	0.0644
RD	-2.8357	0.0046	2.0641	0.039	0.88641	0.1877
Ash	5.1269	<0.0001	ND	ND		0.8579
NDF		0.104	ND	ND		0.5414
ADF		0.3638	ND	ND		0.9714
HC		0.0128	ND	ND		0.2952
Ls		0.7758	ND	ND		0.8579
CP	5.5011	<0.0001	ND	ND	0.07374	0.9412
SS		ND	ND	ND	ND	ND

Abbreviations as in Appendix A and B.

If no ties are present in Mann-Whitney U test, a z-statistic is not calculated.

strong positive results. Most of the tannins in the leaf portion of Bai Hokou gorilla diet are present in only two tree species, *Diospyros sp.* and Egumdu. Further, although mature leaves are commonly characterized as high in both tannin and fiber, compared to fruit, fiber values are not significantly different between the foliage and fruit samples.

Ripe vs. Unripe Fruit

Crude protein and fiber fraction (NDF, ADF) and lignin (Ls) values are not significantly different between ripe and unripe fruit (Table III). Unripe

fruits have slightly higher mean condensed tannin concentrations and protein precipitating ability (RD) than those of ripe fruits, while ripe fruits are generally higher in soluble sugars and ash. However, none of these trends is significant (Tables II and III).

Fleshy vs. Dry Fruit

Dry fruits had dehiscent pods or fibrous, rather than fleshy, pulp. They are higher in fiber (mean Dry NDF = 70.5%, mean Fleshy NDF = 58.22%, $p = 0.0426$ and mean Dry ADF = 55.85%, mean Fleshy ADF = 49.32%, $p = 0.0108$) and lower in crude protein content than fleshy fruits (mean Dry CP = 6.50%, mean Fleshy CP = 9.39%, $p = 0.0444$). Tannin values are not significantly different between dry and fleshy fruits. There were not enough samples analyzed for SS content to allow comparison between dry and fleshy fruits (Table III).

1989 vs. 1998 Fruits

Fruits eaten by gorillas at Bai Hokou in 1998 ($n = 29$), are higher in crude protein (1998 mean CP = 9.49%, 1989 CP = 5.81%, $p = 0.0103$) and have less fiber (1998 mean ADF = 38.98%, 1989 ADF = 70.59%, and 1998 mean NDF = 53.07%, 1989 NDF = 84.05%, $p < 0.0001$) and lignin (1998 mean Ls = 21.22%, 1989 Ls = 36.02%, $p < 0.01$) than the small sample of fruits ($n = 6$) collected at the same site in 1989. Nevertheless, despite their apparently higher nutritional content, 1998 fruits also appear to be higher in tannins (1998 mean RD = 5.05%QTE, 1989 RD = 4.0%QTE, $p = 0.0142$) (Table III).

Important Gorilla Fruits

We analyzed 24 species of fruits from Bai Hokou and divided them into two separate categories: those most important (prevalent) in the gorilla diet during 5 years of field observations, versus all others. Important fruits (IMP) are higher in soluble sugars (mean IMP SS = 23.08%, OTHER SS = 8.03%, $p = 0.0139$) and lower in crude protein content (mean IMP CP = 7.24%, OTHER CP = 9.58%, $p = 0.0239$) than all other fruits. Mean lignin values are also lower for favored fruits, although not significantly

(Table III). Fiber values do not appear to vary between these two classes of fruits. Contrary to expectations, important fruits appear to have higher tannin content than other fruits, although differences do not reach significance (mean IMP RD = 5.37%QTE, OTHER RD = 4.54%QTE) (Table III).

DISCUSSION

Gorillas are seasonal frugivores or mixed frugivores/folivores; their diet shifts along a seasonal and interannual gradient at all low altitude sites, with high variability in dietary proportions of fleshy fruit. Overall, Bai Hokou gorillas consume ≥ 230 plant parts from 129 plant species, including 89 species of fruits (Remis, 1997a). Because we collected plant samples during poor fruit seasons and years, our nutritional study does not assess the full variation present in Bai Hokou gorilla diet. In particular, the fruit samples represent only 46% of the important fruit species used by Bai Hokou gorillas, whereas 67% of the important non-fruit foods are represented in the analysis. Our data represent the nutritional profile of gorillas during seasons of fruit scarcity at Bai Hokou.

Our results suggest that, during periods of fruit scarcity, the Bai Hokou gorillas continue to find and to consume fruits in greater numbers than would be expected from community-wide phenological data, though many of them are quite fibrous and tannin-rich. The Bai Hokou gorillas appear to choose fruit for sugar (energy), with fiber and tannin as secondary concerns, which is similar to chimpanzees in Uganda (Conklin *et al.*, 1998; Reynolds *et al.*, 1998). Conversely, most of the leaves of woody species consumed by Bai Hokou gorillas are low in fiber and tannin.

The soluble sugar carbohydrate (SS) fraction is significantly negatively correlated with all fiber fractions (NDF, ADF, and Ls) in the fruit samples, whereas crude protein and fiber fractions (NDF, ADF) are significantly and negatively correlated in foliage samples. Both sugars and soluble proteins are associated with cell contents, rather than cell wall constituents, so these inverse relationships are to be expected.

Our data lend further evidence that gorillas and other primates selectively consume differing nutrients in different types of foodstuffs. Nevertheless, our limited results suggest that the gorilla preference for fleshy fruits may represent an attempt to limit fiber intake. If selection against high fiber is a consistent finding, concurrent intake of a higher proportion of SS may then result with frugivory, as opposed to higher protein consumption with folivory. Accordingly, fruit and foliage are complementary food sources for gorillas; each provides different sources of energy and other nutrients,

including minerals, though they have been studied in less detail. It seems likely that mixed frugivory/folivory provides the most suitable nutrient balance for gorillas and many other herbivores.

Comparison to Other Gorilla Study Sites

Our study confirms earlier findings that western lowland gorillas in primary and old secondary forests have a more diverse diet than those of gorillas in montane or more disturbed sites (Waterman *et al.*, 1983; Calvert, 1985; Rogers *et al.*, 1990). In fact, diets at Karisoke are distinctive; lower altitude mountain gorillas, western and eastern lowland gorilla diets are all more diverse, and include a variety of fruits and leaves from woody species (Goldsmith, 1999). Among the subspecies, western lowland gorillas appear to consume the most fruit and more secondary compounds (Rogers *et al.*, 1990; Popovich *et al.*, 1997), even when ripe fruit is seasonally scarce. Nevertheless, there is considerable variation in the chemical composition of foods consumed, even in the relatively intact lowland rain forest habitats at Lopé and Bai Hokou.

Throughout Africa, gorillas consume substantial amounts of relatively high protein herbaceous stems as staples or fallback foods. At Karisoke, however, the vegetation is montane-adapted, fruit is scarce, and gorilla diet is particularly herbaceous (Watts, 1996). Herbaceous stems eaten across mountain and lowland sites are similar in nutrient content and low in condensed tannins, but those eaten at Bai Hokou appear to have more crude protein than those consumed elsewhere. In general, foods consumed by gorillas during seasons of fleshy fruit scarcity at Bai Hokou have more crude protein and fiber than values reported in analyses of average foods consumed by gorillas at other sites (Table IV). High fiber content (ADF) distinguishes the leaf and fruit portion of the diet from the seasonal Bai Hokou data and foods collected at Campo, Cameroon from averages reported from Lopé, Gabon. Although foods consumed by gorillas at all lowland sites have more condensed tannins than foods eaten at Karisoke, leaves consumed at Bai Hokou appear lower in tannins than those analyzed from Lopé or Campo (Calvert, 1985; Rogers *et al.*, 1990).

Plant Chemistry and Food Choice

It is always difficult to interpret the significance of nutritional analyses of plant foods as plants sampled may not adequately capture temporal or spatial variation in plant chemistry (Rogers *et al.*, 1990). Further, we were not

Table IV. Site differences in foods consumed by Western lowland and Mountain Gorillas

Site	Subspecies	CT	NDF	ADF	CP	Ls	n(#)
LEAVES							
Bai Hokou, CAR	<i>G.g.gorilla</i>	4.52	63.93	47.54	18.86	25.19	16
Lope, Gabon ²	<i>G.g.gorilla</i>	14.58	na	28.92	18.37	na	16
Campo, Cameroon ³	<i>G.g.gorilla</i>	7.3	46.1	42.6	16.6	19.4	8
Karisoke, Rwanda ⁴	<i>G.g.beringei</i>	1.1	na	35.5	15.5	na	21
FRUIT							
Bai Hokou, CAR	<i>G.g.gorilla</i>	12.33	58.4	44.42	8.91	23.92	29
Lope, Gabon	<i>G.g.gorilla</i>	8.83	na	23.7	5.22	na	46
Campo, Cameroon	<i>G.g.gorilla</i>	2	64.6	44.8	6.3	26.9	8
Karisoke, Rwanda	<i>G.g.beringei</i>	na	na	na	na	na	na
STEMS (PITH ONLY)							
Bai Hokou, CAR	<i>G.g.gorilla</i>	0.59	67.41	49.22	16.87	25.98	7
Lope, Gabon	<i>G.g.gorilla</i>	1.74	na	48.59	5.08	na	6
Campo, Cameroon	<i>G.g.gorilla</i>	0.5	55.9	44.4	6.7	11.3	11
Karisoke, Rwanda	<i>G.g.beringei</i>	0.72	na	49.3	6.2	na	12

² Rogers *et al.*, 1990.

³ Calvert, 1985.

⁴ Waterman *et al.*, 1983.

Abbreviations and units as in Appendix A and B.

able to determine the relative importance of each food in the diet, though we sampled most foods consumed in the short sample periods. The Bai Hokou data provide a snapshot in time of gorilla diet during scarcity of preferred foods. It is likely that the nutrient and other phytochemical profiles of gorilla diet at Bai Hokou and other sites fluctuate considerably between seasons and over the time interval of any sample.

Our results emphasize the importance of distinguishing between ripe and unripe as well as fleshy and fibrous fruits when considering fruits as high quality. The ripe and unripe Bai Hokou fruits have fiber and secondary compound profiles similar to many leafy and woody foods (Nijboer *et al.*, 1997), though the fruits generally have more soluble sugars and less protein than the foliage.

In general, gorillas across sites, including Bai Hokou, appear to avoid nitrogen-based alkaloids, even when preferred foods are scarce. However, carbon-based tannins are present in some gorilla foods. Although gorillas seem to tolerate moderate levels of tannins, then may well be more prevalent in the fruit than leaf portion of their diets. In fact, the majority of tannins in the Bai Hokou foliage samples came from only two species, including *Diospyros species* (ebony). Fruits of *Diospyros* are important in the gorilla diet, the tannin-rich leaves are not among their preferred foods. *Diospyros* has high levels of phenolics (Waterman, 1986), which gives the wood a characteristic dark color.

Plant secondary compounds have long been thought to have a deleterious effect on herbivores and therefore should be avoided in the diet. Nevertheless, increasing evidence suggests that some plant metabolites, e.g., phenolics, may be a necessary component of a mammalian herbivore diet (Martin *et al.*, 1987; Mole and Waterman, 1987). Spelman *et al.* (1989) found that captive lemurs were extremely susceptible to excess iron deposition—hemosiderosis—in the duodenum, liver, and spleen, which they attributed a diet high in iron and ascorbic acid and low in tannins. We found that the majority of fruits consumed by gorillas at Bai Hokou with Fe content >100 mg/kg, also had high CT levels (Appendix B). Tannins could help to control iron metabolism by binding to excess dietary iron (Roy and Mukherjee, 1979). Berry (1998) found hydrolyzable or condensed tannins or both in many foods consumed by mountain gorillas in Bwindi Impenetrable National Park, Uganda, and suggested that they may help to maintain a healthy population of gut microbes. Specifically, Berry (1998) suggested that phenolics help to control pathogenic microbes, while nonpathogenic, i.e., useful, symbionts can be resistant to the effects of tannins. Finally, many mammals, including primates, secrete proteins in saliva that have a high affinity for tannins (Mehansho *et al.*, 1987; Milton, 1998). These proteins might negate detrimental effects that tannins could have during digestion (Fickel and Joest, 1997).

The Effects of Gorilla Body Size on Dietary Adaptation

The large body size and digestive anatomy of gorillas lends them flexibility to cope with scarcity of preferred foods by selecting and processing large amounts of fiber. Consumption of large quantities of fibrous foods may further facilitate consumption of tannins, as the efficiency of a tannin in reducing protein digestibility is concentration-dependent (Cork and Foley, 1992; Simmen *et al.*, 1999). Captive gorillas retained foods longer in their gastrointestinal tracts (Remis, 2000) than chimpanzees given a similar diet did (Lambert, 1997). Large surface areas of the colon and cecum along with longer gut retention times should allow animals to maximize absorption of nutrients (Chivers and Langer, 1994). Nevertheless, when ripe fruit is abundant, the foliage component declines in western gorilla diet. We need further studies to determine whether a commitment to a high-fiber strategy (Rogers *et al.*, 1992) could affect gorillas' selection of fibrous foods even when fleshy ripe fruit is plentiful.

Although gorillas consume more fruit, even during scarcity, than might be predicted from their body size alone, they also consume more fiber than the more persistently frugivorous chimpanzees do (Remis *et al.*, unpublished;

Kuroda *et al.*, 1996; Conklin-Brittain *et al.*, 1998). The spectrum of variability among the diets of the great apes at various sites complicates efforts to argue for the existence of an ape-level adaptation to frugivory (Andrews, 1981; Temerin and Cant, 1983; Wrangham *et al.*, 1998). Across sites, gorillas appear to be more opportunistic in their frugivory than smaller-bodied hominoids are. The Bai Hokou gorilla fruit sample contains higher amounts of fiber and tannins than those consumed by monkeys and chimpanzees at Kibale, Uganda (Lambert, 1997; Wrangham *et al.*, 1998). Nevertheless, they also contain more fiber and tannins than average gorilla foods from Karisoke, Rwanda or Lopé, Gabon (Waterman *et al.*, 1983; Rogers *et al.*, 1990; Plumptre, 1995). Moreover, in preliminary ongoing species comparisons at Bai Hokou, there is no significant difference in fiber or tannin content of fruits consumed by sympatric gorillas ($n = 31$ fruits), chimpanzees ($n = 7$ fruits) and grey-cheeked mangabeys ($n = 25$ fruits) during the brief 1998 data set on fruit scarcity (Remis *et al.*, unpublished data). Site-specific differences in plant biochemistry occur among sites across the tropics, which likely relate to soil quality, altitude, sunlight and other abiotic factors (Van Soest, 1994). Habitat differences shape the diets of the primates in different locations and reduce our ability to identify specific or demic adaptations. We plan to explore the nutritional aspects of diet in western lowland gorillas during fleshy fruit abundance and to explore seasonal variation in niche overlap and separation with respect to sympatric chimpanzees and cercopithecines.

Finally, little research has specifically focussed on nutrients other than energy or protein in primates. Some interesting speculations on mineral nutrition of free-ranging primates are possible from our data. They provide some rough guidelines for development of suitable substitute diets for captive populations, though captive and wild animals probably differ in gut flora and fauna. For example, plants eaten by Bai Hokou gorillas were relatively low in iron. Excess dietary iron has been related to Cu deficiency (Morris, 1987), recently implicated in heart disease of captive gorilla populations (Meehan pers. comm.). Clearly, the contribution of minerals from dietary foliage needs to be better examined, as green leaves are an important source of Ca and other essential minerals for herbivores.

Gastrointestinal diseases, obesity, and cardiovascular disease reported in captive gorillas (Meehan, 1997) are likely influenced by diet and activity levels. Hence defining nutrient concentrations in native diets can enhance understanding of nutrient interactions in applied feeding programs. High fiber diets, containing relatively moderate protein and soluble sugar concentrations, balanced mineral content, with possibly beneficial effects of dietary tannins, should play important roles in nutritional health of captive and wild gorilla populations.

Appendix A. Nutrient and secondary compound content of foods consumed by gorillas at Bai Hokou, Central African Republic.

Family	Plant Latin	BaAka name	Part	HT	CT	Alkaloid	RD	Ash	NDF	ADF	Ls	CP	HC
Acanthaceae	<i>Whitfieldia elongata</i>	Indolu	I	ND	ND	ND	0.00	14.47	53.84	29.38	9.09	31.50	24.46
Annonaceae	<i>Annonidium mammi</i>	Mobai	Fr	1.17	0.52	ND	ND	5.06	19.84	12.79	3.00	8.53	7.05
Annonaceae	<i>Hexalobus sp.</i>	Pota	Fu	ND	ND	ND	ND	3.39	64.02	46.97	23.17	10.74	17.05
Annonaceae	<i>Polyalthia suaveoleons</i>	Motunga	Fr	24.12	17.63	0	5.08	3.00	62.68	48.45	8.08	12.21	14.23
Annonaceae	<i>Polyalthia suaveoleons</i>	Motunga	se	1.03	0.55	0	0.00	ND	ND	ND	ND	ND	ND
Apocynaceae	<i>Landolphia sp.</i>	Bossindja	Fr	2.11	19.18	1	8.33	2.55	56.69	34.76	4.43	4.87	21.93
Apocynaceae	<i>Landolphia sp.</i>	Bossindja	se	0.05	0.26	0	0.00	ND	ND	ND	ND	ND	ND
Apocynaceae	<i>Orthopichonia barteri</i>	Mongenje	l(v)	0.73	0.28	0	0.00	8.09	83.02	70.01	36.28	10.00	13.01
Apocynaceae	<i>Tabernaemontana sp.</i>	Etolokolo (big)	Fr	1.81	9.99	2	4.83	5.13	43.72	33.94	18.96	14.17	9.78
Apocynaceae	<i>Tabernaemontana sp.</i>	Etolokolo	Fr	0.99	0.17	0	ND	7.58	42.27	32.56	11.86	15.62	9.71
Apocynaceae	<i>Tabernaemontana sp.</i>	Etolokolo (big)	se	0.75	11.05	0	0.00	ND	ND	ND	ND	ND	ND
Bursaceae	<i>Sanitra trimera</i>	Baba	Fr	6.06	0.43	0	0.00	ND	ND	ND	ND	ND	ND
Bursaceae	<i>Sanitra trimera</i>	Baba	se	7.62	0.24	0	ND	ND	ND	ND	ND	ND	ND
Caesalpinaeae	<i>Dialium zenkeri</i>	Mokombe	Fr	ND	ND	ND	ND	2.44	52.60	21.52	10.78	8.95	31.08
Ebenaceae	<i>Diospyros bipindensis</i>	Embandja	I	6.79	30.71	0	34.05	3.47	67.24	57.07	42.35	12.30	10.17
	<i>Gürke</i>												
Ebenaceae	<i>Diospyros iturenensis</i>	Babango	Fr	ND	ND	ND	ND	2.86	76.15	50.75	31.14	5.93	25.40
	<i>or bipindensis</i>												
Euphorbiaceae	<i>Drypetes gilgiana or diopa</i>	Timbu	Fr	3.51	32.43	0	5.13	3.83	61.14	49.83	33.93	10.98	11.31
Euphorbiaceae	<i>Drypetes gilgiana or diopa</i>	Timbu	Fr	1.07	0.24	0	0.00	3.33	48.89	33.39	15.17	8.92	15.50
Euphorbiaceae	<i>Drypetes gilgiana or diopa</i>	Timbu	Fr	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Euphorbiaceae	<i>Drypetes gilgiana or diopa</i>	Timbu	Fr	0.99	1.15	0	0.00	3.59	44.78	32.57	16.07	10.37	12.21
Euphorbiaceae	<i>Drypetes gilgiana or diopa</i>	Timbu	se	1.14	0.12	0	0.00	ND	ND	ND	ND	ND	ND
Euphorbiaceae	<i>Drypetes sp.</i>	Mosarakosarak	I	2.42	0.50	0	0.00	7.33	77.06	55.59	23.31	17.00	21.47
Euphorbiaceae	<i>Drypetes gossweileri?</i>	Ngama	Fu	1.83	0.72	0	0.00	3.07	47.05	10.94	3.64	9.57	36.11

Gnetaceae	<i>Gnetum africanum</i>	Koko	I(v)	5.53	1.89	0	0.00	8.71	52.07	36.75	12.43	19.80	15.32
Gnetaceae	<i>Gnetum africanum</i>	Koko	I(v)	2.43	0.46	0	0.00	5.42	79.69	61.91	15.42	8.11	17.78
Irvingiaceae	<i>Irvingia excelsa</i>	Payo	Fr	6.77	3.28	0	0.00	3.65	82.59	68.26	29.20	5.47	14.33
Irvingiaceae	<i>Irvingia excelsa</i>	Payo	Fr	22.01	5.24	ND	ND	ND	ND	ND	ND	ND	ND
Irvingiaceae	<i>Irvingia excelsa</i>	Payo	Fr	5.88	2.16	ND	ND	ND	ND	ND	ND	ND	ND
Irvingiaceae	<i>Klainedoxa gabonensis</i>	Bokoko	Fr	2.35	0.72	0	0.00	2.71	84.41	70.76	31.85	3.05	13.65
Lauraceae	<i>Beilschmiedia obscura</i>	Ngala	I	0.96	0.92	0	0.00	6.10	80.63	69.53	49.84	14.80	11.10
Meliaceae	<i>Entrandrophragma cylindricum</i>	Boyo	I	5.69	0.53	0	0.00	9.58	49.61	30.21	11.60	27.60	19.40
Meliaceae	<i>Lovoa sp.</i>	Gima	I	1.25	0.58	1	0.00	7.66	76.51	61.01	38.41	22.70	15.50
Mimosaceae	<i>Maranthus glabra</i>	Mokandja	Fr	0.44	0.46	0	0.00	2.59	94.16	83.83	48.92	4.54	10.33
Mimosaceae	<i>chrysobalanaceae</i>												
Mimosaceae	<i>Tetraplaura teraptera</i>	Ekombolo	Fr	2.41	0.88	0	0.00	5.38	82.40	61.93	26.31	7.97	20.47
Moraceae	<i>Chlorophora excelsa</i>	Mobanguï	Fu	0.24	0.01	0	0.00	ND	ND	ND	ND	ND	ND
Moraceae	<i>Ficus sp.</i>	Gumu	Fr	1.14	0.71	2	0.00	5.47	76.55	67.81	42.01	7.77	8.74
Moraceae	<i>Ficus sp.</i>	Gumu	Fr	2.06	13.02	ND	2.83	3.70	49.95	40.25	22.70	5.19	9.70
Moraceae	<i>Treculia africana</i>	Efusa or Pusa	Fr	1.81	0.47	0	0.00	6.10	73.27	69.22	49.18	12.29	4.05
Moraceae	<i>Treculia africana</i>	Efusa or Pusa	se	3.34	0.12	0	0.00	2.34	21.66	13.47	6.00	14.61	8.19
Olacaceae	<i>Strombosia pustulata tetranda</i>	Embongo	Fr	1.09	3.14	0	0.00	3.27	71.04	55.40	31.38	14.63	15.64
Olacaceae	<i>Strombosia pustulata tetranda</i>	Embongo	Fu	2.65	22.42	0	5.98	3.07	54.68	42.66	31.08	7.11	12.02
Papilionaceae	<i>Lonchocarpus sp.</i>	Molindu (Molin)	I	0.85	0.67	0	0.00	4.41	70.38	57.59	38.03	14.50	12.79
Papilionaceae	<i>Pterocarpus soyauxii</i>	Embema	Fu	2.15	0.51	0	2.26	3.27	68.39	50.58	16.39	10.04	17.81
Sapindaceae	<i>Zhana cf. Gultungensis</i>	Iwungu	Fr	2.80	32.01	0	10.62	4.67	46.90	39.54	25.65	7.61	7.36
Sapotaceae	<i>Manilkara letouzeyi</i>	Monginza	Fu	5.79	35.44	0	6.33	2.26	53.47	39.76	28.63	11.15	13.71
Sapotaceae	<i>Manilkara letouzeyi</i>	Monginza	Fu	5.32	95.74	0	9.48	1.82	53.62	41.99	31.05	9.48	11.63
Sapotaceae	<i>Manilkara letouzeyi</i>	Monginza	Fu	ND	ND	0	0.00	2.54	46.15	34.90	24.14	7.97	11.25
Sapotaceae	<i>Manilkara letouzeyi</i>	Monginza	se	ND	ND	0	0.00	ND	ND	ND	ND	ND	ND

(Continued)

Appendix A. (Continued)

Family	Plant Latin	BaAka name	Part	HT	CT	Alkaloid	RD	Ash	NDF	ADF	Ls	CP	HC
Tiliaceae	<i>Desplatia deweverei</i>	Liamba	Fu	1.44	3.52	0	3.68	6.80	59.16	56.32	41.92	7.91	2.84
Tiliaceae	<i>Duboscia cf. Viridiflora</i>	Guruma (big)	Fr	9.01	49.26	1	12.17	3.67	32.36	28.71	16.85	4.97	3.65
Tiliaceae	<i>Duboscia macrocarpa</i>	Guruma	F	0.50	8.94	0	0.00	4.47	84.17	70.96	37.84	6.08	13.21
Tiliaceae	<i>Duboscia macrocarpa</i>	Guruma	Fr	1.05	6.80	0	3.39	ND	ND	ND	ND	ND	ND
Ulmaceae	<i>Celtis mildbraedii</i>	Gombe	I	1.44	0.82	0	0.00	10.05	69.75	56.23	28.72	15.60	13.52
Ulmaceae	<i>Celtis</i> sp.	Gombe	I	1.96	0.53	0	0.00	2.66	57.55	45.29	27.01	12.80	12.26
Ulmaceae	<i>Celtis</i> sp.	Gombe	I	1.35	0.41	0	0.00	10.70	74.99	59.41	26.92	15.90	15.58
Zingiberaceae	<i>Aframomum</i> sp.	Njokoko	Fu	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Zingiberaceae	<i>Aframomum</i> sp.	Njokoko	st	0.78	0.74	0	0.00	6.89	77.05	67.06	43.98	18.40	9.99
Zingiberaceae	<i>Aframomum</i> sp.	Njokoko	st	1.14	1.77	0	0.00	5.68	53.61	41.58	21.91	15.70	12.03
Zingiberaceae	<i>Aframomum</i> sp.	Njokoko	st	0.93	0.21	0	0.00	7.85	75.89	55.18	25.00	16.60	20.71
Zingiberaceae	<i>Aframomum sulcatum</i>	Njombo	st	1.32	0.41	0	0.00	7.06	61.21	39.91	20.03	19.60	21.30
Zingiberaceae	<i>Aframomum sulcatum</i>	Njombo	st	0.75	0.28	0	0.00	6.94	60.08	37.57	13.93	11.20	22.51
Zingiberaceae	<i>Renaltia</i> sp.	Dembelebe	st	0.66	0.11	0	0.00	8.83	76.61	54.00	31.02	19.70	22.61
unknown	unknown	Essekelende	Fr	0.69	3.42	ND	ND	3.23	44.91	27.68	10.10	7.45	17.23
unknown	unknown	Batorro	I	3.68	0.64	0	0.00	10.68	51.93	28.96	6.75	32.90	22.97
unknown	unknown	Mopusupusu	I	3.55	0.87	0	0.00	6.39	77.42	58.50	31.26	18.80	18.92
unknown	unknown	Egumdu	I	6.40	28.17	0	6.20	7.70	71.44	58.13	30.68	14.30	13.31
unknown	unknown	Mogombagumbu	I	0.30	0.13	0	0.00	6.36	42.17	25.81	12.96	17.00	16.36
unknown	unknown	Demelle	I	1.72	0.40	0	0.00	6.88	50.34	31.12	13.69	14.20	19.22

I = leaves; I(v) = vines; st = stems; Fr = ripe fruit; Fu = unripe fruit; se = seeds. Alkaloids scored on a scale of 0 (no reaction) to 3 (strong reaction); hydrolyzable tannins (HT) expressed as mg/g hexahydroxydiphenylglucose; condensed and radical diffusion tannins (CT and RD) as % dry weight quebracho tannin equivalents ash, neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin (Ls), crude protein (CP), and hemicellulose (HC) as % of dry matter.

Appendix B. Mineral Content of Fruits collected at Bai Hokou 1998

Family	Latin Plant	BaAka name	Part	Ca	K	Mg	Na	P	Cu	Cr	Fe	Mn	Zn
Annaceae	<i>Annonidium manni</i>	Mobai	Fr	0.013	0.0441	0.103	0.004	0.123	17.36	<.20	40.83	41.97	11.46
Annaceae	<i>Hexalobium sp.</i>	Pota	Fu	0.147	1.288	0.12	0.001	0.154	26.07	<.20	117.87	79.27	13.09
Annaceae	<i>Polyalthia suaveoleons</i>	Motunga	Fu	0.378	0.968	0.097	0	0.078	18.63	<.20	76.85	167.06	8.89
Apocynaceae	<i>Landolphia sp.</i>	Bossindja	Fr	0.051	0.757	0.09	0.003	0.1	10.16	<.20	167.84	52.42	18.65
Apocynaceae	<i>Tabernaemontana sp.</i>	Etokoloko	Fr	0.129	2.032	0.213	0.012	0.18	11.49	0.43	73.17	75.19	16.19
Apocynaceae	<i>Tabernaemontana sp.</i>	Etokoloko	Fr	0.235	2.968	0.243	0.009	0.125	19.23	<.20	43.9	168.34	23.24
Bursaceae	<i>Santira trimera</i>	Baba	Fr	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Ebenaceae	<i>Diospyros iturenis</i>	Babango	Fr	0.132	0.687	0.066	0.003	0.071	5.39	<.20	29.33	219.24	8.44
Euphorbiaceae	<i>Drypetes gilgiana or diopa</i>	Timbu	Fr	0.263	1.225	0.119	0.01	0.12	14.92	<.20	31.17	225.74	20.77
Euphorbiaceae	<i>Drypetes gilgiana or diopa</i>	Timbu	Fr	0.103	1.152	0.084	0.002	0.199	8.76	1.43	77.88	225.71	20.17
Euphorbiaceae	<i>Drypetes gilgiana or diopa</i>	Timbu	Fr	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Euphorbiaceae	<i>Drypetes gilgiana or diopa</i>	Timbu	Fr	0.152	1.256	0.091	0.003	0.115	8.09	<.20	76.06	179.86	22.82
Euphorbiaceae	<i>Drypetes gossweileri?</i>	Ngama	Fu	0.136	1.142	0.175	0.008	0.148	13.27	<.20	96.11	142.81	32.92
Irvingiaceae	<i>Irvingia excelsa</i>	Payo	Fr	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Moraceae	<i>Chlorophora excelsa</i>	Mobangui	Fu	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Moraceae	<i>Ficus sp.</i>	Gumu	Fr	0.375	0.979	0.182	0.001	0.126	10.53	0.25	79.37	53.54	17.78
Moraceae	<i>Treculia africana</i>	Eftusa	Fr	0.119	2.389	0.184	0.021	0.149	16.93	<.20	106.86	96.31	15.85
Olacaceae	<i>Strombosia pustulata tetranda</i>	Embongo	Fr	0.143	0.041	0.113	0.009	0.163	8.81	1.48	63.06	216.04	30.41
Olacaceae	<i>Strombosia pustulata tetranda</i>	Embongo	Fu	0.191	1.11	0.128	0.018	0.089	2.4	<.20	129.8	120.77	9.24
Papilionaceae	<i>Pterocarpus soyauxii</i>	Embema	Fu	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Sapindaceae	<i>Zhana cf. guttugensis</i>	Iwungu	Fu	0.086	1.689	0.096	0.017	0.086	11.12	<.20	150.34	72.91	25.93
Sapotaceae	<i>Manilkara letouzeyi</i>	Monginza	Fu	0.192	1.053	0.11	0.015	0.154	4.1	1.13	70.96	89.99	21.4
Sapotaceae	<i>Manilkara letouzeyi</i>	Monginza	Fu	0.095	0.557	0.015	0.002	0.073	1.74	0.52	55.07	60.15	9.79
Sapotaceae	<i>Manilkara letouzeyi</i>	Monginza	Fu	0.229	0.435	0.134	0.006	0.087	2.82	<.20	30.98	127	8.65
Thiaceae	<i>Desplatsia deweveri</i>	Liamba	Fu	0.28	1.886	0.245	0.005	0.129	11.35	0.88	129.65	207.91	40.7
Thiaceae	<i>Dubosia cf. viridiflora</i>	Guruma (big)	Fu	0.166	1.336	0.179	0.005	0.092	9.16	1.06	58.44	19.54	14
Thiaceae	<i>Dubosia macrocarpa</i>	Guruma	Fr	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Zingiberaceae	<i>Aframomum sp.</i>	Jokoko	Fu	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
unknown	unknown	Essekelende	Fr	0.343	1.707	0.215	0.004	0.165	14.16	<.20	64.84	332.07	14.5

Plant parts as in Appendix A. Ca, K, Mg, Na, and P expressed as % of dry matter. Cu, Cr, Fe, Mn, and Zn expressed as mg/kg of dry matter.

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