

## PHYTOCHEMICAL DETERMINATION FOR LEAF FOOD CHOICE BY WILD CHIMPANZEES IN GUINEA, BOSSOU

HIROYUKI TAKEMOTO<sup>1</sup>

*Primate Research Institute  
Kyoto University  
Inuyama, Aichi 484-8506, Japan*

(Received October 31, 2002; accepted July 17, 2003)

**Abstract**—The feeding selection of leaves by chimpanzees was investigated from the perspective of phytochemistry and leaf availability. Field data were collected for 6 months from 1995 to 1996 and 8 months from 1997 to 1998 in Bossou, Guinea. Time budgets of leaf consumption by chimpanzees were analysed and the abundance of young leaves of each tree species for each month was estimated. Analyses of dried materials, stratified by leaf maturity and edibility, for the relative amounts of crude protein, crude fat, neutral detergent fiber, ash, and condensed tannin were determined. It was found that 1) leaves consumed by chimpanzees had higher levels of ash and lower levels of condensed tannin than leaves that were not eaten; 2) feeding selectivity was correlated with crude protein content; and 3) the availability of young leaves was not correlated with the percentage of feeding time, neither by seasonal changes nor by tree species. Chimpanzees preferred leaves containing higher protein content, but did not consume leaves containing high condensed tannin regardless of protein content. It seems reasonable to consider that a different rule exists for “whether chimpanzees eat it or not” and “whether they prefer it or not” in phytochemical determinants of leaves. Some Moraceae species, which had low levels of condensed tannins, even in mature leaves, were an important food source for the Bossou chimpanzees.

**Key Words**—Chimpanzee, feeding selectivity, leaf consumption, leaf maturity, Moraceae, phytochemistry.

### INTRODUCTION

Chimpanzees are one of the largest mammalian frugivores. According to the law of Kleiber (1961), Jarman (1974), and Bell (1971), a larger animal can eat lower quality foods such as higher fiber herbs and leaves, because energy requirements

<sup>1</sup>To whom correspondence should be addressed. E-mail: takemoto@pri.kyoto-u.ac.jp

are a function of metabolic body weight ( $W^{0.75}$ ). Thus, a larger animal on a lower nutrient diet can extract the same amount of nutrients per unit of body weight as a smaller animal on a higher nutrient diet (Caughley and Sinclair, 1994). Primates also fit this relationship between body size and diet. Species that eat insects tend to be relatively small, whereas those that eat leaves tend to be relatively large (Fleagle, 1999). Larger bodied primates, with their relatively slow metabolic turnover rates, can tolerate the long lag between ingestion and digestion that leaves require, and might also have difficulty finding sufficient quantities of insects on a regular basis (Strier, 2000). In this respect, chimpanzees, which have a relatively large body without having adopted a leafy diet, are a paradoxical mammal.

The diet of chimpanzees consists largely of fruits, and consumption of foliage accounts for only 20–30% of the time spent feeding (Hladik, 1977a; Wrangham, 1977; Yamakoshi, 1998; Newton-Fisher, 1999). In general, leaves are relatively rich in protein, whereas fruits are rich in carbohydrates, but poor in protein (Hladik, 1977a; Milton, 1981; Marks et al., 1988; Rogers et al., 1990; Kool, 1992; Dasilva, 1994; Mowry et al., 1996; Matsumoto-Oda and Hayashi, 1998; Takemoto, 2002). Hladik (1978) pointed out that because fruits yield an average of only 5% protein, then larger primates more than 2 kg should eat leaves because a fruit–insect diet is insufficient for protein. Chimpanzees are fairly large-bodied compared to other primates; therefore, they require a large amount of protein, and leaves are thought to be an important source. Chimpanzees must choose high-quality leaves within a relatively lower time allocation in the diet to meet protein requirements. However, the selection of leaf foods has not been investigated from the perspective of phytochemistry.

Several studies have discussed the reasons for selective feeding on fruits or terrestrial herbaceous vegetation (THV) from the perspective of phytochemistry in chimpanzees. These results showed that chimpanzees preferred food items with high sugar content or caloric intake rate, regardless of protein content (Wrangham et al., 1991, 1993; Reynolds et al., 1998; Matsumoto-Oda and Hayashi, 1999). Tannins significantly reduced the palatability of many unripe fruits for chimpanzees (Wrangham and Waterman, 1983). In contrast, Reynolds et al. (1998) reported that chimpanzees ingested fruit or bark that contained considerable quantities of tannins. Tannins combine with protein, often irreversibly, and inhibit the digestibility of protein. As a result, they are effective as antifeedants (Robbins et al., 1991), although this is not always the case. Tannin-protein precipitation once formed, however, can dissolve, but most animals tend to reject astringent taste foods, such as those containing tannins (Mole and Waterman, 1987). If leaves are an essential food for protein, chimpanzees are likely to avoid those leaves with high tannin content.

Since the primary biochemical processes within a leaf are practically identical in all green plants, the relative amounts of sugars, lipids, polysaccharides, amino acids, and proteins are inevitably similar. Physiological processes (e.g.,

senescence) are more likely than anything else to affect the nutritional status of a plant (Harborne, 1993). Compared to mature leaves, young leaves have a higher protein content and a lower content of fiber or secondary compounds (Coley, 1983). Although chimpanzees prefer young leaves, there are several species whose young leaves they do not consume. These species have been noted in habitat inventories for different groups of chimpanzees (Sugiyama and Koman, 1992; Moor, 1994; Moutsanboté et al., 1994; Tutin et al., 1994; Yumoto et al., 1994). Two sets of analyses, i.e., "within young leaves" and "within mature leaves," will be needed to clarify the chemical differences between food source leaves and nonfood source leaves.

When fruit is in short supply, Bossou chimpanzees allocate less time to feeding (Takemoto, 2002), and their diet does not become more diverse (Yamakoshi, 1998; Takemoto, 2002). These results deviate from the general expectation of primate behavior, proposed by Dunbar (1988), that time spent feeding should increase and feeding items should become more diverse when there is a food shortage. At least, they can digest cellulose more efficiently than predicted by body weight (Milton and Demment, 1988). It is unlikely that a physiological process to digest fiber content, such as shorter retention time or insufficient fermentation in the hind gut, affects chimpanzee feeding behavior. Why do chimpanzees never eat large quantities of leaves when fruit is scarce, even though leaves appear freely available? Answering this question requires not only a phytochemical investigation, but also an estimation of seasonal changes in the availability of food source leaves, especially of young leaves.

According to optimal foraging theory, the time spent on each food item depends upon its availability (Pyke et al., 1977; Post, 1984). Optimal foraging theory has been applied with some success to carnivores, but not to herbivores, whose potential food species display more complex chemical variations, both in nutritional content and in the diverse array of substances they contain that inhibit digestion, some of which are toxic (Rhoades and Cates, 1976; Bryant et al., 1992). Choice, based on a combination of food quality and availability, can make the determination of optimal foraging strategy more difficult (Post, 1984). Accordingly, feeding selectivity indices were used (i.e., the relative use of specific food items compared to their availability) to compare with phytochemistry, which represents food quality.

The purpose of this study was to interpret leaf selection by chimpanzees in terms of leaf chemistry. Specifically, I sought to 1) clarify the phytochemical differences between young leaves from food and nonfood species, and between mature leaves from food and nonfood species, respectively; 2) examine the relationships between phytochemical content and feeding selectivity of leaves from food species; and 3) investigate the influence of young-leaf availability on the amount of time allocated to leaf consumption. On the basis of the results, I discuss phytochemical cues for leaf selection, important foliage species for chimpanzees, and why the time spent feeding on leaves does not increase when fruits are scarce in Bossou.

## METHODS AND MATERIALS

The field survey was conducted in Bossou, Guinea, West Africa. Data were collected from June to November 1996 and November 1997 to June 1998. Annual rainfall in Bossou averaged 2190 mm between 1995 and 1998. The dry season, during which rainfall averaged <100 mm per month, lasted from November to March, while the wet season extended from April to October. Fruit availability in the forest varies throughout the year and peaks between January and April (Yamakoshi, 1998; Takemoto, 2002). Basic observation methods are described in Takemoto (2002). The activity budgets of three individuals (one subadult male [VI] and two adult females [Jr, VI]) were recorded by focal animal sampling (Altman, 1974), following one chimpanzee for an entire day or as long as possible to avoid introducing observation bias associated with grouping patterns or visibility. The total observation time was 379 hr over 121 days. Only observations that lasted for >1 hr in a day were used for the analyses, and no bias of observation time across months nor individuals was found.

*Estimating Availability of Young Leaves.* Transects that measured 1600 m in total length were established during the first half of the study period and 2200 m during the second half. The trees surveyed in these transects were used to estimate the availability of young leaves. Young-leaf availability was represented as a percentage of young leaves to total leaves in the maximum volume of a tree. All trees in the transects were assigned a relative leaf abundance score between 0 and 3 twice monthly, and the relative abundance of young leaves among all the leaves on a tree was also scored between 0 and 3. Leaves were considered young from bud emergence until they had fully expanded and acquired adult coloring and toughness, following the definition of Coley (1983). The abundance of young leaves in the transects was described by

$$YLA = \left[ \sum (B_k \times L_k \times Y_{Lk}) / \sum (B_k \times 3 \times 3) \right] \times 100,$$

where YLA represents young-leaf availability (%),  $B_k$  is the basal area of tree k ( $\text{cm}^2$ ),  $L_k$  is the leaf score of tree k (0–3), and  $Y_{Lk}$  is the score for the relative abundance of young leaves on tree k (0–3). When feeding selectivity was calculated, young-leaf availability of species i in a given month (YLAfi) compared with all food species (YLAf) was described by

$$YLAfi = \left[ \sum (B_{ij} \times L_{ij} \times Y_{Lij}) / \sum \sum (B_{ij} \times L_{ij} \times Y_{Lij}) \right] \times 100$$

where YLAfi is the availability of tree species i (%),  $B_{ij}$  is the basal area of tree j of species i ( $\text{cm}^2$ ),  $L_{ij}$  is the leaf score of tree j of species i (0–3), and  $Y_{Lij}$  is the relative abundance of young leaves on tree j of species i (0–3). The monthly averages of YLAfi represent the availability of species i throughout the study period.

Plant species' designations follow Adam (1971–83), and descriptions of plant life forms follow Letouzey (1982–83) and Keay (1989).

*Relative Use of Each Tree Species.* All observations of leaf consumption were recorded, including consumption of mature leaves, although the chimpanzees fed almost exclusively on young leaves. Feeding on petioles was excluded from the analyses (e.g., *Elaeis guineensis*, piths of THV, or Pteridophyta), because petioles and leaf blades may have different nutritive values (Struhsaker, 1975). If the chimpanzees consumed both the leaves and piths of a species (e.g., *Gonglonema latifolia*, *Musanga cecropioides*, and *Myrianthus spp.*), cases in which the chimpanzees ate only the petiole were excluded. June and November were excluded when monthly correlations were calculated (i.e.,  $N = 10$ ).

*Estimation of Feeding Selectivity.* All tree species recorded along the transects were divided into two categories (i.e., food and nonfood species) based on the observed diets of chimpanzees during the study periods. The percentage of time spent feeding on each species was calculated, and this percentage was considered to be the relative use of the species,  $i$  ( $ri$ ); however, feeding of less than 1 min on any item was excluded because it was too short a time to estimate the selectivity index. The availability of young leaves of species  $i$  ( $pi$ ) was calculated as the average of the monthly availability of species  $i$  ( $YLAfi$ ).

Selectivity for each tree species was estimated using Ivlev's selectivity index (Ivlev, 1955) and Johnson's rank (Johnson, 1980). Ivlev's selectivity index ( $Ei$ ), given by  $(ri - pi)/(ri + pi)$ , ranges from  $-1$  to  $+1$ . An  $Ei$  of 0 indicates random feeding, an  $Ei$  of 0–1 indicates preferred items, and an  $Ei$  of  $-1$  to 0 indicates food items that are avoided. Johnson's rank uses the differences between availability rank ( $pi$ ) and usage rank ( $ri$ ) in a given diet (e.g.,  $ri - pi$ ). Increasing use relative to availability (i.e., higher selectivity) results in increasing the negative value, because a higher use rank results in a smaller value for  $ri$  and a lower availability rank results in a larger value for  $pi$ .

*Chemical Analysis.* Leaves of trees on which chimpanzees foraged were collected, regardless of whether they were found along the transects. If the leaves were young, the mature leaf of that species was also collected after growing. In addition, young and mature leaves from transect species with a higher relative dominance ratio (SDR, Table 1) were collected, regardless of their edibility to chimpanzees. Nonfood young leaves were gathered when they were about half-expanded.

Collected materials were immediately placed in sealed plastic bags to prevent desiccation and taken to the field station. At the station, samples were weighed, wrapped in paper bags, and dried, using either a metal oven heated by kerosene stoves (Hladik, 1977b) or by solar drying during the dry season. Water content was estimated after weighing the dried samples.

Nutrient content was analyzed in the Primate Research Institute of Kyoto University. Samples were redried to a constant weight in a vacuum oven at 50°C. Phytochemical contents of dried and milled samples were determined for crude

TABLE 1. STRUCTURES OF PLANT FAMILY IN TRANSECT

Family name	No. of species	BA (%)	density (/ha)	SDR <sup>a</sup>
Sterculiaceae	6	22.82	137.5	17.34
Moraceae	12	9.58	165.0	11.91
Mimosaceae	9	13.46	82.5	10.29
Sapotaceae	4	13.63	33.0	8.24
Anacardiaceae	4	10.84	62.7	8.13
Caesalpinaceae	5	2.61	111.1	6.10
Meliaceae	6	3.87	67.1	4.83
Euphorbiaceae	10	3.48	70.4	4.77
Apocynaceae	8	3.55	44.0	3.67
Papilionaceae	5	1.09	59.4	3.11
Rubiaceae	7	1.35	56.1	3.09
Bignoniaceae	2	0.99	39.6	2.20
Sapindaceae	3	0.76	38.5	2.04
Combretaceae	2	2.61	7.7	1.64
Agavaceae	1	1.14	23.1	1.57
Arecaceae	1	2.09	5.5	1.28
Annonaceae	2	0.32	19.8	1.01
Hypericaceae	1	0.28	18.7	0.95
Bombacaceae	1	1.02	9.9	0.94
Simaroubaceae	3	0.52	14.3	0.88
Myristicaceae	1	0.53	9.9	0.69
Lauraceae	2	0.76	4.4	0.57
Unknown	—	0.13	11.0	0.54
Bursaceae	1	0.47	6.6	0.52
Ulmaceae	1	0.37	5.5	0.42
Rhizophoraceae	1	0.17	7.7	0.42
Verbenaceae	2	0.55	3.3	0.42
Solanaceae	1	0.09	6.6	0.33
Icacinaceae	1	0.09	6.6	0.33
Rutaceae	2	0.15	5.5	0.31
Samidaceae	1	0.13	5.5	0.30
Lecythicaceae	2	0.11	5.5	0.29
Octoknemaceae	1	0.30	2.2	0.25
Flacourtiaceae	1	0.04	3.3	0.16
Loganiaceae	2	0.02	2.2	0.11
Hippocrateaceae	1	0.02	2.2	0.10
Violaceae	1	0.02	2.2	0.10
Rhamnaceae	1	0.02	1.1	0.06
Myrtaceae	1	0.01	1.1	0.05
Tiliaceae	1	0.01	1.1	0.05
Total	116	100.00	1159.4	100.00

<sup>a</sup> SDR: summed dominance ratio (average on BA and density).

protein (CP), crude fat (CFA), neutral detergent fiber (NDF), ash (ASH), and condensed tannin (CT), on the basis of dry matter weight. Crude protein was determined using the Kjeldahl procedure for total nitrogen and multiplying by 6.25. Crude fat was measured as diethyl-ether extract using the Soxhlet method. Ash was determined by ashing at 550°C. Neutral detergent fiber was estimated following the methods of Van Soest (1994). Condensed tannin was extracted with 70% aqueous acetone (Hagerman, 1988), and determined by the buthanol-HCL method (Porter et al., 1986a,b; Porter, 1989).

Phytochemical contents of food and nonfood species were compared among young leaves and among mature leaves by using two-tailed Mann–Whitney *U* test. Spearman’s rank correlation was used to evaluate the relationship between phytochemical composition of the leaves and feeding selectivity.

RESULTS

*Forest Structure and Seasonal Changes in Availability of Young Leaves.* In total, 116 tree species were found in the transects (not including unknown species). Members of the Sterculiaceae family had the highest summed dominance ratio (SDR; Table 1) and the largest total basal area, whereas species belonging to the Moraceae had the greatest density and numbers.

Figure 1 shows seasonal changes in young-leaf availability (YLA) in the transects. YLA increased during the dry season, beginning in November, peaked in

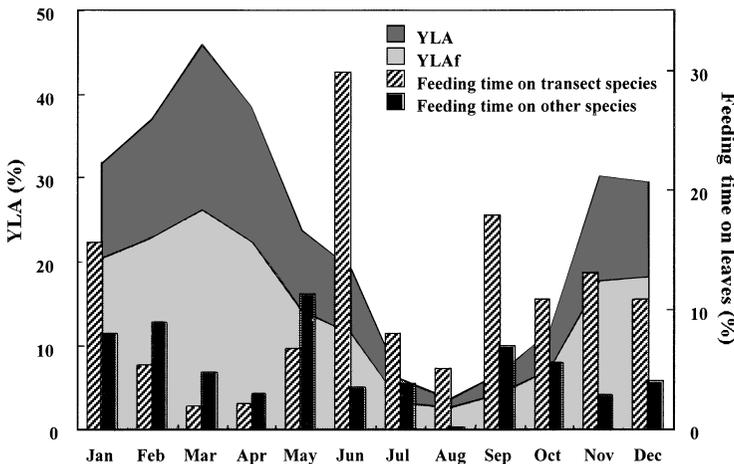


FIG. 1. Seasonal change in young leaf availability (YLA), feeding species (YLAf), and feeding time on leaves divided by transect species (species found in the transect) and other species. The average values of two different years are shown for June and November.

March, and then declined. The lowest index values were from June to October, during the wet season. Leaves from food species (YLAf) showed the same seasonal changes as YLA. Young leaf availability had strong correlation with fruit availability in the forest (FAI), which was shown in Takemoto (2002) ( $r_s = 0.90$ ,  $N = 10$ ,  $P < 0.007$ ).

*Food Species and Young-Leaf Availability.* Chimpanzees were observed to consume the leaves of 52 plant species during the study period (Table 2), and spent the most time feeding on *Baphia sp.*, *Ficus exasperata*, *Antiaris africana*, *Chlorophora excelsa*, and *Bosquia angorensis*. Many species of Moraceae and Papilionaceae were consumed, and the two families constituted 80% of total leaf consumption time (Moraceae: 60%, Papilionaceae: 20%; Table 3).

When food species were separated by plant life form, the leaves of high trees were where the greatest amount of time was spent feeding, whereas epiphytes were fed on the least (Table 4). This result is thought to be concordant with the biomass of the leaves. The chimpanzees ate only one species of epiphyte leaves, *Nephropsis biserrata* (Pteridophyta), which grows on oil palms. They consumed this plant intensively in rice fields between February and March, during the late dry season.

Chimpanzees consumed the mature leaves of five species: *Baphia sp.*, *Bosquia angolensis*, *Ficus exasperata*, *Polycephalium capitatum*, and *Ficus thonngii*. They ate mature leaves of *Polycephalium capitatum* as frequently as young leaves, while the mature leaves of the other four species were consumed much less often than the young leaves.

Figure 1 also shows the monthly percentages of time spent feeding on leaves. The mean proportion of time spent feeding on leaves was 15.9% of the total feeding time. Seasonal changes in time spent feeding on leaves were not correlated with YLA or YLAf (YLA:  $r_s = -0.15$ ,  $N = 10$ ,  $P > 0.05$ ; YLAf:  $r_s = -0.27$ ,  $N = 10$ ,  $P > 0.05$ ). Time spent feeding on the leaves of transect species (species recorded in the transect) also was not correlated with YLA or YLAf (YLA:  $r_s = -0.38$ ,  $N = 10$ ,  $P > 0.05$ ; YLAf:  $r_s = -0.46$ ,  $N = 10$ ,  $P > 0.05$ ). The time spent feeding on the leaves of species that were not recorded on transects did not increase when young leaves were scarce in the transects.

*Feeding Selectivity.* Of the 52 tree species consumed by chimpanzees, 18 were found on the transects. These 18 species were considered food species. Figure 2 shows seasonal changes in the young-leaf availability of these. The area occupied by a species in this graph indicates the relative young-leaf availability of species  $i$  (annual average for YLAf $_i = p_i$ ; see Methods and Materials).

Availability ( $p_i$ ), usage ( $r_i$ ), and selectivity ( $E_i$  and Johnson's rank) for each food species are shown in Table 5. Availability and usage were not correlated ( $r_s = -0.26$ ,  $N = 18$ ,  $P > 0.05$ ). The highest selectivity was found in *Baphia sp.* Eight species (six species of Moraceae, *Baphia sp.*, and *Ceiba pentandra*) were considered "preferred" using Johnson's rank estimator.

TABLE 2. RELATIVE USE OF LEAF FOOD SPECIES BY CHIMPANZEES

Species	Family	Relative use (%)	Life form
<i>Baphia</i> sp. <sup>a</sup>	Papilionaceae	11.29	Small tree
<i>Ficus exasperata</i> <sup>a</sup>	Moraceae	10.73	Small tree
<i>Antiaris africana</i> <sup>a</sup>	Moraceae	9.51	High tree
<i>Chlorophora excersa</i> <sup>a</sup>	Moraceae	8.62	High tree
<i>Bosquia angolensis</i> <sup>a</sup>	Moraceae	6.54	Medium-sized tree
<i>Ficus variifolia</i> <sup>a</sup>	Moraceae	6.41	High tree
<i>Ficus mucosa</i> <sup>a</sup>	Moraceae	6.04	Medium-sized tree
<i>Leptoderris fasciculata</i>	Papilionaceae	5.96	Woody liana
<i>Ficus umberrata</i> <sup>a</sup>	Moraceae	3.56	Medium-sized tree
<i>Musoneuron cecropioides</i> <sup>a</sup>	Moraceae	3.34	Medium-sized tree
<i>Celtis mildbraudii</i> <sup>a</sup>	Ulmaceae	2.88	High tree
<i>Ficus thoningii</i>	Moraceae	2.45	Medium-sized tree
<i>Ceiba pentandra</i>	Bombacaceae	2.18	High tree
<i>Smilax klaussiana</i>	Smilacaceae	2.15	Woody liana
<i>Myrianthus arboreus</i> <sup>a</sup>	Moraceae	1.69	Medium-sized tree
<i>Mesoneuron bentamianum</i>	Caesalpiniaceae	1.59	Woody liana
<i>Polycephalum capitatum</i> <sup>a</sup>	Icacinaceae	1.20	Woody liana
<i>Triplochiton scleroxylon</i> <sup>a</sup>	Sterculiaceae	1.15	High tree
<i>Aningeria altissima</i> <sup>a</sup>	Sapotaceae	1.09	High tree
Unknown (liana)	—	0.97	Woody liana
<i>Dalbergia afzeliana</i>	Papilionaceae	0.93	Woody liana
<i>Gonglonema latifolium</i>	Asclepiadaceae	0.87	Woody liana
<i>Erythrina mildbraedii</i> <sup>a</sup>	Papilionaceae	0.79	Medium-sized tree
<i>Albizia zygia</i> <sup>a</sup>	Mimosaceae	0.68	Medium-sized tree
LUKOSU (liana)	—	0.63	Herbaceous liana
<i>Myrianthus libericus</i>	Moraceae	0.58	Medium-sized tree
<i>Piper guineensis</i>	Piperaceae	0.57	Woody liana
<i>Ipomaea</i> sp.	Convolvulaceae	0.56	Herbaceous liana
<i>Carica papaya</i>	Caricaceae	0.54	Small tree
<i>Craterispermum laurinum</i> <sup>a</sup>	Rubiaceae	0.49	Small tree
<i>Raphiostylis beninensis</i>	Icacinaceae	0.47	Woody liana
<i>Pseudospondias microcarpa</i> <sup>a</sup>	Anacardiaceae	0.43	Medium-sized tree
unknown	—	0.43	Small tree
<i>Glyphaea brevis</i>	Tiliaceae	0.36	Small tree
<i>Ceropegia</i> sp. ( <i>jhonsoni</i> ?)	Asclepiadaceae	0.31	Terrestrial herb
liane (gnegneinson)	—	0.27	Herbaceous liana
<i>Nephrolepis biserrata</i>	Polypodiaceae	0.26	Epiphyte
<i>Illigera pentaphylla</i>	Hernandiaceae	0.23	Woody liana
<i>Tryunpheta heudelotii</i>	Tiliaceae	0.23	Small tree
<i>Voacanga africana</i>	Apocynaceae	0.16	Medium-sized tree
<i>Vigna</i> sp. ( <i>bakolo</i> )	Papilionaceae	0.15	Woody liana
<i>Triumpheta rhonboidea</i>	Tiliaceae	0.14	Small tree
unknown (herb)	—	0.13	Terrestrial herb
<i>Homalium molle</i>	Samidaceae	0.10	Small tree
<i>Monodora tenuifolia</i> <sup>a</sup>	Annonaceae	0.08	Medium-sized tree
<i>Alchornea cordifolia</i>	Euphorbiaceae	0.07	Woody liana
<i>Milletia</i> sp. <sup>a</sup>	Papilionaceae	0.06	Small tree

TABLE 2. CONTINUED

Species	Family	Relative use (%)	Life form
Unknown (tree)	—	0.03	Small tree
<i>Celtis adorfi-frederici</i> <sup>a</sup>	Ulmaceae	0.02	Medium-sized tree
<i>Justicia tennera</i>	Acanthaceae	0.02	Terrestrial herb
<i>Dialium denklagei</i>	Caesalpinaceae	0.01	Small tree
<i>Hibiscus esculentus</i>	Malvaceae	0.00	Terrestrial herb

<sup>a</sup> The species that was used for nutritional analysis.

*Phytochemical Differences Between Food Species and Nonfood Species.*

Figure 3 shows the phytochemical differences within leaf categories, stratified by maturity and edibility. Among mature leaves, leaves from food species had a higher

TABLE 3. RELATIVE USE OF LEAVES FOR EACH PLANT FAMILY BY CHIMPANZEES

Family	Relative use	No. of species
Moraceae	59.48	11
Papilionaceae	19.19	6
Ulmaceae	2.90	2
(Unknown)	2.46	(6) <sup>a</sup>
Bombacaceae	2.18	1
Smilacaceae	2.15	1
Icacinaceae	1.67	2
Caesalpinaceae	1.60	2
Asclepiadaceae	1.19	2
Sterculiaceae	1.15	1
Sapotaceae	1.09	1
Tiliaceae	0.73	3
Mimosaceae	0.68	1
Piperaceae	0.57	1
Convolvulceae	0.56	1
Caricaceae	0.54	1
Rubiaceae	0.49	1
Anacardiaceae	0.43	1
Polypodiaceae	0.26	1
Hernandiaceae	0.23	1
Apocynaceae	0.16	1
Samidaceae	0.10	1
Annonaceae	0.08	1
Euphorbiaceae	0.07	1
Acanthaceae	0.02	1
Malvaceae	0.005	1
Total	100.00	52

<sup>a</sup> Parentheses denote unidentified plant species.

TABLE 4. RELATIVE USE OF LEAF FOOD SPECIES BY CHIMPANZEES DIVIDED BY PLANT LIFE FORM

Life form	Relative use	No. of species
High-tree	31.85	7
Medium-sized Tree	26.37	13
Small Tree	24.42	12
Woody Liana	15.18	12
Herbaceous Liana	1.46	3
Terrestrial Herb	0.48	4
Epiphyte	0.26	1
Total	100.00	52

ash content ( $U$  test,  $N_1 = 5$ ,  $N_2 = 32$ ,  $z = -2.36$ ,  $P < 0.019$ ) and a lower condensed tannin content than leaves of nonfood species ( $U$  test,  $N_1 = 4$ ,  $N_2 = 18$ ,  $U = 9$ ,  $P < 0.021$ ). Among young leaves, leaves from food species had a higher ash content than nonfood species ( $U$  test,  $N_1 = 12$ ,  $N_2 = 9$ ,  $U = 11$ ,  $P < 0.002$ ). There was no significant difference between tannin content of young leaves from food species and nonfood species ( $N_1 = 9$ ,  $N_2 = 9$ ,  $U = 24.5$ ,  $P > 0.05$ ). No differences in protein content among mature leaves and young leaves were found (mature leaves:  $N_1 = 4$ ,  $N_2 = 32$ ,  $z = -0.71$ ,  $P > 0.05$ ; young leaves:  $N_1 = 12$ ,  $N_2 = 9$ ,  $U = 47$ ,  $P > 0.05$ ). Tannin was present in inverse proportion to ash across

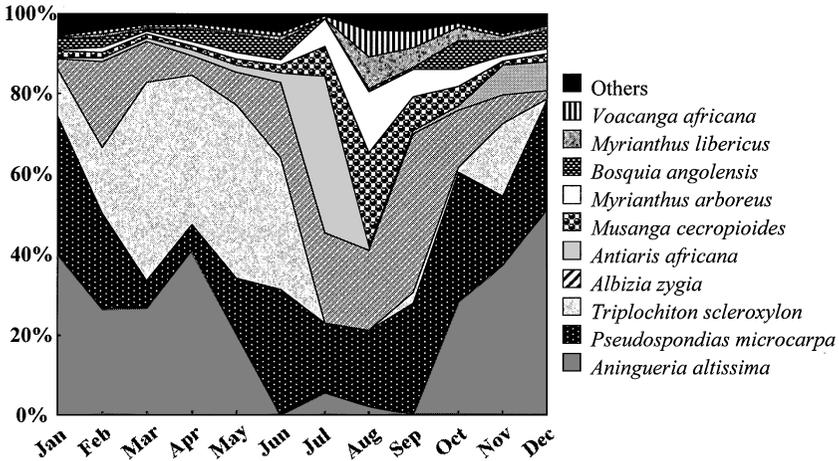


FIG. 2. Relative availabilities for each tree species regarded as chimpanzees' food in the transect. The area for each species shown in the graph represents young leaf availability of the species (pi). Eight species with availability less than 1% are combined and presented as "Others."

TABLE 5. IVEV'S SELECTIVITY INDEX AND JOHNSON'S RANK FOR EACE LEAF FEEDING SPECIES IN TRANSECT

Species	Ivlev's Selectivity Index			Johnson's Rank		
	pi	ri	Ei <sup>a</sup>	pi	ri	Deference <sup>a</sup>
<i>Aningueria altissima</i>	23.35	1.93	-0.85	1	12	11
<i>Pseudospondias microcarpa</i>	21.39	0.75	-0.93	2	16	14
<i>Triplochiton scleroxylon</i>	17.76	2.03	-0.79	3	11	8
<i>Albizia zygia</i>	14.23	1.20	-0.84	4	13	9
<i>Antiaris africana</i>	5.33	10.63	0.33	5	4	-1
<i>Musanga cecropioides</i>	4.64	5.88	0.12	6	7	1
<i>Myrianthus arboreus</i>	3.52	2.42	-0.19	7	10	3
<i>Bosquia angolensis</i>	2.95	10.52	0.56	8	5	-3
<i>Myrianthus libericus</i>	1.82	1.03	-0.28	9	14	5
<i>Voacanga africana</i>	1.54	0.28	-0.70	10	17	7
<i>Craterispermum laurinum</i>	0.89	0.86	-0.02	11	15	4
<i>Ceiba pentandra</i>	0.86	2.91	0.54	12	9	-3
<i>Chlorophora excelsa</i>	0.70	11.35	0.88	13	3	-10
<i>Ficus exasperata</i>	0.59	15.32	0.93	14	2	-12
<i>Baphia</i> sp.	0.15	19.88	0.99	15	1	-14
<i>Ficus mucso</i>	0.13	8.53	0.97	16	6	-10
<i>Homalium</i> sp.	0.10	0.18	0.31	17	18	1
<i>Ficus thonningii</i>	0.06	4.31	0.97	18	8	-10

<sup>a</sup> Italic numbers show preferred species estimated by each indicator.

leaves of which chemical contents were determined, and leaves eaten had less tannin and more ash content (Figure 4). The other phytochemical components showed no differences between leaves from food species and leaves from nonfood species.

*Relation Between Feeding Selectivity and Phytochemistry.* Correlations between Johnson's rank and phytochemical content were investigated (Figure 5). Correlation coefficients with negative values indicate positive correlations between feeding selectivity and each chemical, because Johnson's rank decreases as selectivity increases (see Methods and Materials). Selectivity was positively correlated with crude protein content. Selectivity also had a positive correlation coefficient with condensed tannin content, although sample size was small. All correlations between selectivity and water content, crude fat, ash, and neutral detergent fiber were weak.

## DISCUSSION

No single phytochemical criterion seems to characterize "food sources and nonfood sources" nor "avoided and preferred leaves" within food sources. Chimpanzees preferred leaves with a higher protein content, but no other chemical contents were correlated to selectivity. There were differences in ash and condensed

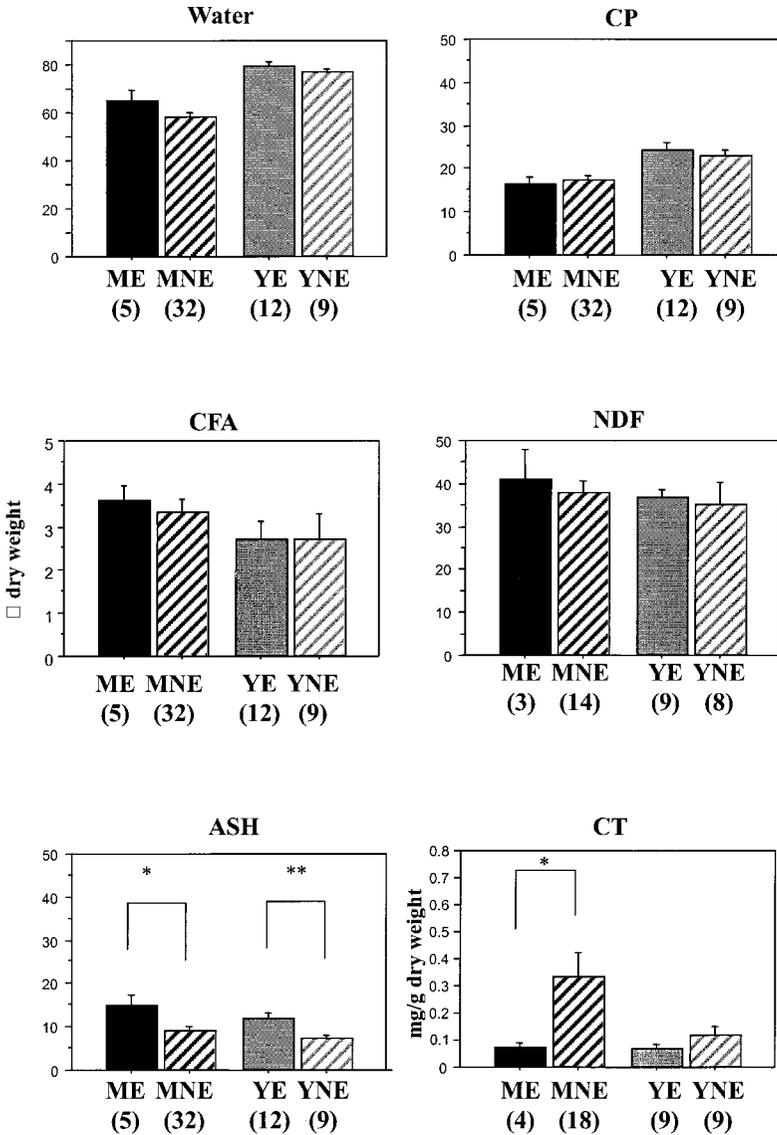


FIG. 3. Mean (+SEM) phytochemical content for food sources versus nonfood sources for chimpanzees stratified by leaf maturity. Condensed tannins (CT) are expressed as milligrams per gram dry weight in sample. Neutral detergent fiber (NDF), ash (ASH), crude fat (CFA), and crude protein (CP) are expressed as % dry weight. ME = mature leaves eaten, MNE = mature leaves not eaten, YE = young leaves eaten, YNE = young leaves not eaten. Numbers inside parentheses represent number of species. \*  $P < 0.05$ , \*\*  $P < 0.01$ .

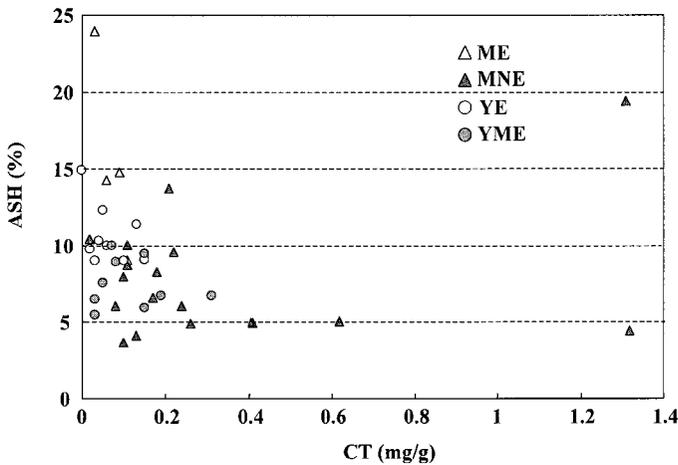


FIG. 4. Relation between ash and condensed tannin (CT) content within each leaf. ME = mature leaves eaten, MNE = mature leaves not eaten, YE = young leaves eaten, YNE = young leaves not eaten.

tannin between food and nonfood sources, but no other differences in chemical content were apparent. Chimpanzees preferred leaves containing higher protein content, but did not consume the leaves containing high condensed tannin regardless of protein content.

The data presented here are derived from observations targeting three individuals. Since each individual may not have the same experience of how to mix diets of different plant species (Provenza et al., 2002), it is difficult to generalize about the Bossou population. According to the long-term study of Sugiyama and Koman (1992) and other previous studies on Bossou chimpanzees (Yamakoshi, 1998), however, the species found to be consumed in large quantity in this study are known to be common food sources for the entire population at Bossou. Additionally, the Bossou population size has been small and stable since the 1970s (around 20 individuals) and female bonds are strong (Sugiyama, 1988; Muroyama and Sugiyama, 1994). No interindividual or interfamily biases in diet choice is expected from the protocol and sample size, as they often feed in close association with each other. Short durations of observation time for leaf eating behavior were eliminated from the analysis to alleviate possible bias from rare behaviors dependent upon individual or observational bias. It can be assumed that the results of this study are reasonably representative of the entire population.

*Phytochemical Determination of Leaf Consumption by Chimpanzees.* Tannins, which deter herbivory, can reduce the digestibility of food, reduce growth, and damage the intestine and kidneys of mammals, sometimes acting as toxins (Mole and Waterman, 1987; Hagerman and Butler, 1991; Robbins et al., 1991; Robbins,

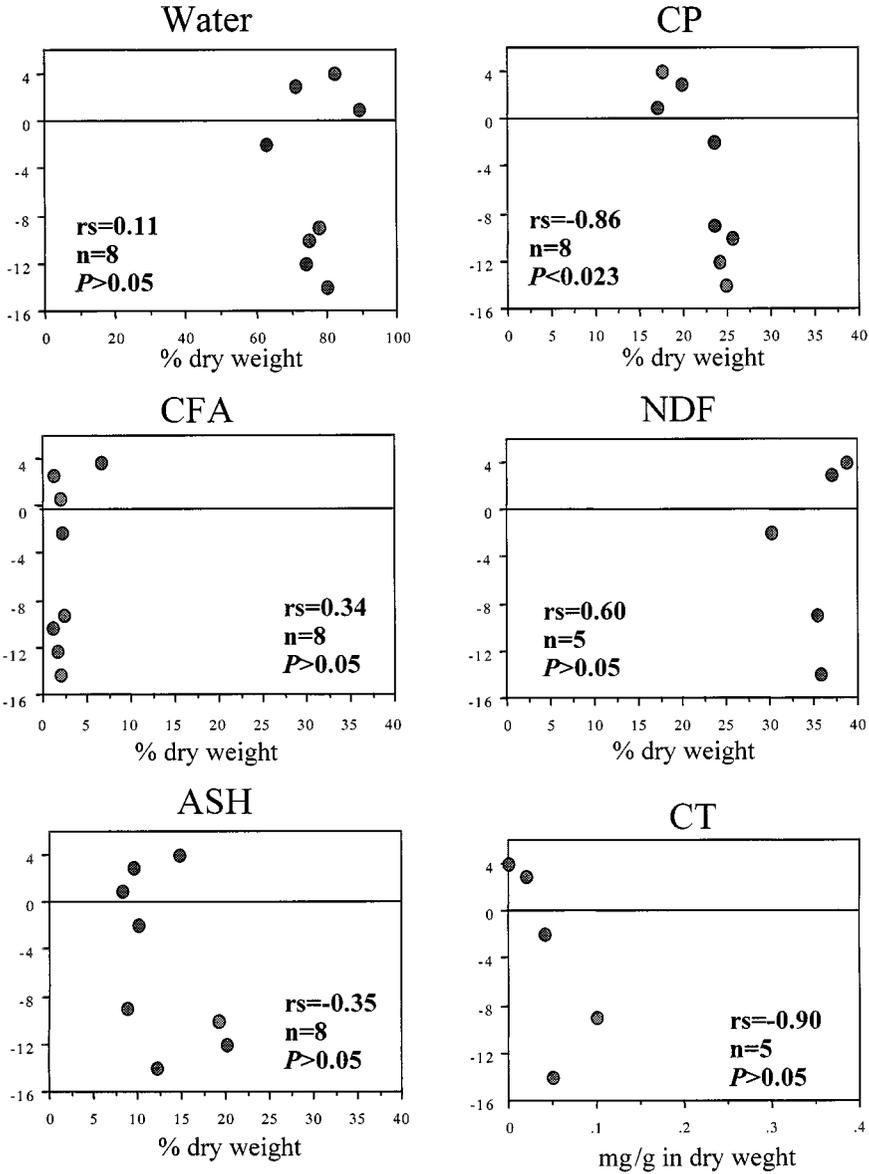


FIG. 5. Relation between each phytochemical content in young leaves eaten and selectivity by Johnson's rank (vertical axis). Refer to Figure 3 for definitions of abbreviations for phytochemical contents. Note the horizontal axis of CT, which represents mg/g.

1993). Many studies have indicated that animals, including primates, tend to reject astringent foods (for primates: Oates et al., 1977, 1980; Mckey and Gartlan, 1981; Wrangham and Waterman, 1981; Kool, 1992). Wrangham and Waterman (1983) suggested that tannins significantly reduced the palatability of many unripe fruits for chimpanzees. In contrast, Reynolds et al. (1998) reported that chimpanzees ingested fruit or bark that contained considerable quantities of tannins. The influence of tannins as feeding deterrents, however, depends on which food types they are contained in (Behmer et al., 2002). Other plant secondary metabolites also affect the food choice of herbivores. In their diet as a whole, chimpanzees have a lower intake of antifeedants, such as tannin or total tannins, than do *Cercopithecines*. Moreover, chimpanzees do not increase their intake of condensed tannin when ripe fruit is scarce (Wrangham et al., 1998). Thus, chimpanzees appear to avoid antifeedants, including tannins.

Tannic acid probably has a greater deterrent effect on feeding of herbivorous insects when the amount of tannic acid increases compared to protein content (Behmer et al., 2002). When tannin infusions were greater, the preference of lambs shifted to higher protein food (Villalba et al., 2002). In field observations, browsing ruminants in the South African savanna rejected leaves with thresholds exceeding 5% condensed tannins, but protein-precipitating polyphenols did not influence palatability (Cooper and Owen-Smith, 1985). Experiments of response to tannin taste for primates also show that there are clear avoidance thresholds (for lemurs: Iaconelli and Simmen, 2002; for Gorillas: Remis and Kerr, 2002).

In food source leaves, chimpanzees showed higher selectivity for leaves with a higher protein content. The influences of other antifeedants (cellulose, silica, other secondary compounds, etc.) must be considered: by avoiding the leaves with high concentrations of tannins, the efficiency of protein absorption is likely to be increased. Although taste, smell, and the visceral system of chimpanzees as a frugivorous mammal are not the same as herbivorous insects and mammals, leaf eating behavior of chimpanzees seems to display phytochemical recognition responses regarding food choices observed in other herbivores. Feeding frequency and the protein or nitrogen content of leaves are positively correlated in leaf-eating monkeys (*Colobus satanas*: Mckey and Gartlan, 1981; *Procolobus badius*: Mowry et al., 1996). Leaves of food species had higher ash contents than did nonfood leaves. Because meat-eating behavior is rare at Bossou (Sugiyama and Koman, 1987), the chimpanzees may be deficient in some minerals. Ash contains many kinds of minerals; however, the mineral requirements of nonhuman primates have not been well studied (Yeager et al., 1997). Since condensed tannin content tended to be inversely proportional to ash content in this study (Figure 4), it is possible that avoiding high levels of condensed tannin would result in the consumption of a high concentration of ash in the leaves of food species.

Young leaves contained more protein and water, and less fiber and tannins, concordant with previous studies (Milton, 1979; Glander, 1981; Kool, 1992;

Mowry, 1996; Reynolds et al., 1998). However, this alone does not explain the selection for leaves, since there were young leaves that were never eaten and mature leaves that were commonly eaten. Young leaves that were never eaten contained as much protein as young leaves that were eaten, whereas mature leaves that were eaten contained lower protein content, similar to mature leaves that were never eaten. Unless such an analysis is stratified by leaf maturity, it will lead to an increase in the number of young leaves in samples of food resources, and will inevitably result in a higher protein content compared with nonfood resources, simply because chimpanzees consume mainly young leaves. Two hypotheses have been proposed to explain dietary generalism among mammalian herbivores: nutrient constraints (Westby, 1974) and detoxification limitations (Freeland and Janzen, 1974). According to the "satiety hypothesis" (Provenza, 1995, 1996), there is a fine line between satiety and aversion, which depends on an animal's morphology, physiology, and nutritional requirements. Odor, taste, and food texture combined with the postingestive effects of nutrients and toxins will determine the palatability of a particular item. Consequently, a complex of phytochemicals, both of nutritional and toxic value, narrows or widens feeding diversity. Besides the highly preferred leaf species (Table 5), chimpanzees consume leaves of as many as 52 other plant species. This may result from the interactions between nutrients and various feeding deterrents, as well as other features such as edible leaf availability.

*Seasonal Changes in Availability of Young Leaves and Time Spent Feeding on Leaves.* There was no relationship between the availability of young leaves and the time spent feeding on leaves. This must be because chimpanzees chose fruits when they were available, although they did consume young leaves of *Antiaris africana* and *Darbergia afzeliana* in large quantities for a short period. In Bossou, fruit in the forest is most abundant from January to April, and least abundant from May to August (Yamakoshi, 1998). Leaves that were consumed in large amounts by chimpanzees were the young leaves of a few species, and availability of these leaves was lower when fruits were scarce. Nearly mature leaves that contain high levels of tannin are difficult to ingest, and chimpanzees appear unable to consume large amounts of mature leaves, even when fruits and young leaves were scarce.

Analyses of the energy budgets of Bossou chimpanzees have shown several points incongruent with optimal foraging theory (Takemoto, 2002). The three focal chimpanzees, when fruits were abundant, increased energy expenditure to maximize energy intake (searched more and fed more). When fruits were scarce, they reduced energy expenditure to compensate for low energy intake (rested more and moved less). According to optimal foraging theory, animals should make an effort to feed more when food is scarce. Because mature leaves and bark contain more antifeedants than do fruits (Wrangham and Waterman, 1981; Calvert, 1985; Reynolds et al., 1998), edible foods for chimpanzees are likely to be scarcer in the fruit scarce season. Antifeedants may prevent chimpanzees from

adopting the strategy of eating more low-quality food in the fruit scarce season. In addition, temperature or climate can affect behavior of chimpanzees (Takemoto, in press). The fruit scarce season at Bossou occurs simultaneously with the rainy season and low temperatures. Colder temperatures increase energy requirements for thermoregulation (Oates, 1987), and the effective temperature may also decline following exposure to rain and wind. The climatic effects of the rainy season probably encourage low activity (such as sleeping in day beds) of chimpanzees to conserve body reserves. Few studies on primates have considered the relationship between seasonal changes in the availability of young leaves and feeding on young leaves. Some young leaves were correlated with feeding frequency, but in general, young leaves showed no relation to feeding time in *Colobus polykomos* (Dasilva, 1994) or Howler monkeys (Glander, 1981). Both of these species preferred fruits or seeds, so the time spent feeding on leaves was influenced by the availability of fruits or seeds. Leaf consumption in chimpanzees may be affected even more by fruit availability, as chimpanzees tend to be more dependent on fruits than the other two species.

*Differences in Selectivity for Each Tree Species and the Importance of Moraceae Species.* The leaves selected by chimpanzees were concentrated in several taxa. Of the 10 species that chimpanzees spent the most time feeding on, 8 belonged to the Moraceae and 2 belonged to the Papilionaceae. Similarly, of the 8 species that had a positive selectivity index among the 18 food species, 6 were from the Moraceae. In some cases, mature Moraceae leaves were consumed, so the selectivity index of Moraceae species may have been overestimated. Mature Moraceae leaves are consumable because they contain a higher ash content, but a lower tannin content, even as they mature. The chimpanzees studied fed on 11 Moraceae species, representing the highest number of feeding species among plant families in Bossou. Consequently, the Moraceae represent the most important family for Bossou chimpanzees.

Moraceae ranked second in summed dominance ratio (SDR), and had a high density and species diversity in the Bossou forest (Table 1). *Ficus exasperata* and *Bosquia angolensis* flushed young leaves constantly throughout the year, although they fluctuated in abundance. The dominance of Moraceae species and their suitability as a protein source, even when fruits are scarce, may result in a favorable nutritional environment for Bossou chimpanzees throughout the year. In addition, most Moraceae fruits are also eaten by the Bossou chimpanzees (Sugiyama and Koman, 1992). *Ficus* fruits are essential foods for chimpanzees in some study sites (Nishida and Uehara, 1983; Wrangham et al., 1996), and *Musanga* fruit is an important food in seasons of fruit scarcity in Bossou (Yamakoshi, 1998). The younger age of first birth, shorter interbirth intervals, and the high infant survival rate of chimpanzees in Bossou (Sugiyama, 1994) may be partly explained by the high density and large biomass of Moraceae food species.

In general, food species or species with a high selectivity index are considered to be pioneer species. According to Swain and Hall (1983), secondary forest species that had a high selectivity index in this study, include *Chlorofora excelsa*, *Ficus mucosa*, *Ceiba pentandra*, and *Musanga cecropioides*. *Albizia zygia*, which had a low selectivity index in this study, was categorized as a primary species. In addition, *Ficus exasperata* was found mostly in forest gaps and was pioneer-like. Coley (1983) indicated that pioneer species lack chemical defenses, such as tannins or total phenols, but develop physical defenses such as hairs on the surface of leaves. Therefore, the leaves of pioneer species may be suitable food sources for chimpanzees, which tended to avoid high tannin concentrations in this study.

Such a preference for certain groups also has been observed in captive chimpanzees. Captive chimpanzees were found to select young leaves or leaf buds of deciduous trees, such as the Ulmaceae or Fagaceae, in a compound that contained planted trees and where chimpanzees could eat any leaves *ad libitum* (Takemoto, 1996). Feeding on particular types of leaves is probably a general feature of chimpanzees, to some extent, based on their digestive system, nutrient requirements, or palate.

The main phytochemical differences between the leaves of pioneer and persistent species, or among taxa, are found not in primary metabolic products, such as protein or fiber content, but rather in secondary metabolites, such as alkaloids or tannins (Howe and Westley, 1988; Harborne, 1993). The evident preference of chimpanzees for the leaves of certain tree species highlights the importance of secondary compounds in their selection of leaves.

*Acknowledgments*—I am grateful to Professors Y. Sugiyama and S. Uehara for their continuing interest and support of my study. Many thanks are due to Professor O. Takenaka for teaching me nutritional analysis, to Professor T. Matsuzawa and Dr G. Yamakoshi for many suggestions and help in the field management, to the members of the Primate Research Institute for their advice throughout this study. I am grateful to Direction National de la Recherche Scientifique et Technique, République de Guinée, for supporting this study; to Dr Morat and his colleagues (Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris) for providing the opportunity to identify plant species, to J. Koman for identifying many of plant species in the field; to G. Goumi, T. Cammara, P. Goumi, and P. Cherif, S. Dagouka, for field assistance; and to Dr M. Myowa-Yamakoshi and Dr A. Uchida for their cooperation in the field. Field research was financed by a grant from the Japanese Ministry of Education, Science, Sports, and Culture (No. 07041135, No. 10041168, No. 10ce2005).

#### REFERENCES

- ADAM, J. G. 1971–83. Flore Descriptive des Monts Nimba. Editions du Muséum, Paris. [In French]
- ALTMAN, J. 1974. Observational study of behavior: Sampling methods *Behavior* 49:227–267.
- BEHMER, S. T., SIMPSON, S. J., and RAUBENHEMER, D. 2002. Herbivore foraging in chemically heterogeneous environments: Nutrients and secondary metabolites. *Ecology* 83:2489–2501.
- BELL, R. H. V. 1971. A grazing ecosystem in the Serengeti. *Sci. Am.* 225:86–93.
- BRYANT, J. P., REICHARDT, P. B., CLAUSEN, T. P., PROVENZA, F. D., and KUROPAT, P. J. 1992. Woody plant–mammal interactions, pp. 344–371, in G. A. Rosenthal and M. R. Berenbaum

- (eds.). *Herbivores: Their Interactions with Secondary Plant Metabolites*, 2nd Edition. Academic Press, San Diego, California.
- CALVERT, J. J. 1985. Food selection by western gorillas (*G. g. gorilla*) in relation to food chemistry. *Oecologia* 65:236–246.
- CAUGHLEY, G. and SINCLAIR, A. R. E. 1994. *Wildlife Ecology and Management*. Blackwell Science, Cambridge.
- COLEY, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* 53:209–233.
- COOPER, S. M. and OWEN-SMITH, N. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. *Oecologia* 67:142–146.
- DASILVA, G. L. 1994. Diet of *Colobus polykomos* on Tiwai Island: Selection of food in relation to its seasonal abundance and nutritional quality. *Int. J. Primatol.* 17:63–84.
- DUNBAR, R. I. 1988. *Primate Social Systems*. Cornell University Press, New York.
- FLEAGLE, J. G. 1999. *Primate Adaptation and Evolution*, 2nd Edition. Academic Press, San Diego, California.
- FREELAND, W. J. and JANZEN, D. H. 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. *Am. Nat.* 108:269–289.
- GLANDER, K. E. 1981. Feeding patterns in mantled howling monkeys, pp. 231–257, in A. C. Kamil and T. D. Sargent (eds.). *Foraging Behavior: Ecological, and Psychological Approaches*. Garland Press, New York.
- HAGERMAN, A. E. 1988. Extraction of tannin from fresh and preserved leaves. *J. Chem. Ecol.* 15:655–680.
- HAGERMAN, A. E. and BUTLER, L. G. 1991. Tannins and lignins, pp. 355–388, in G. A. Rosenthal and M. R. Berenbaum (eds.). *Herbivores: Their Interactions with Secondary Plant Metabolites*, Vol. I, The Chemical Participants, 2nd Edition. Academic Press, San Diego, California.
- HARBORNE, J. B. 1993. *Introduction to Ecological Biochemistry*, 4th Edition. Academic Press, London.
- HLADIK, C. M. 1977a. Chimpanzees of Gabon and chimpanzees of Gombe: Some comparative data on the diet, pp. 483–501, in T. H. Clutton-Brock (ed.). *Primate Ecology*. Academic Press, London.
- HLADIK, C. M. 1977b. Field methods for processing food samples, pp. 595–601, in T. H. Clutton-Brock (ed.). *Primate Ecology*. Academic Press, London.
- HLADIK, C. M. 1978. Adaptive strategies of primates in relation to leaf-eating, pp. 373–395, in C. G. Montgomery (ed.). *The Ecology of Arboreal Folivores*. Smithsonian Institution Press, Washington, DC.
- HOWE, H. F. and WESTLEY, L. C. 1988. *Ecological Relationships of Plants and Animals*. Oxford University Press, New York.
- IACONELLI, S. and SIMMEN, B. 2002. Taste thresholds and suprathreshold responses to tannin-rich plant extracts and quinine in a primate species (*Microcebus murinus*). *J. Chem. Ecol.* 28:2315–2326.
- IVLEV, V. C. 1955. Экспериментальная Экология Питания Рыб. Пищепромиздат, Москва. [Gyorui-no Eiyouseitai-gaku (Experimental Ecology of the feeding of fishes). Trans. in Japanese, 1965] Tatara-Shobo, Tokyo.
- JARMAN, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215–266.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 6:65–71.
- KEAY, R. W. J. 1989. *Trees of Nigeria*. Oxford University Press, New York.
- KLEIBER, M. 1961. *The Fire of Life. An Introduction to Animal Energetics*. Wiley, New York.
- KOOL, K. M. 1992. Food selection by the silver leaf monkey, *Trachypithecus auratus sondaicus*, in relation to plant chemistry. *Oecologia* 90:527–533.

- LETOUZEY, R. 1982–83. Manuel de Botanique Forestière Afrique Tropicale 2<sup>e</sup>. Centre Technique Forestier Tropical, Marne. [In French].
- MARKS, D. L., SWAIN, T., GOLDSTEIN, S., RICHARD, A., and LEITON, M. 1988. Chemical correlates of rhesus monkey food choice: The influence of hydrolyzable tannins. *J. Chem. Ecol.* 14:213–235.
- MATSUMOTO-Oda, A. and HAYASHI, Y. 1999. Nutritional aspects of fruit choice by chimpanzees. *Folia Primatol.* 70:154–162.
- MCKEY, D. and GARTLAN, J. S. 1981. Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biochem. J. Linn. Soc.* 16:115–146.
- MILTON, K. 1979. Factors influencing leaf choice by Howler monkeys: A test of some hypothesis of food selection by generalist herbivores. *Am. Nat.* 114:362–378.
- MILTON, K. 1981. Food choice and digestive strategies of two sympatric primate species. *Am. Nat.* 117:496–505.
- MILTON, K. and DEMMENT, M. W. 1988. Digestion and passage kinetics of chimpanzees fed high and low fiber diets and comparison with human data. *J. Nutr.* 118:1082–1088.
- MOLE, S. and WATERMAN, P. G. 1987. Tannins as antifeedants to mammalian herbivores—Still an open question?, pp. 572–587, in G. R. Waller (ed.). Allelochemicals: Role in Agriculture and Forestry. American Chemical Society Symposium Series No. 330, Washington, DC.
- MOOR, J. 1994. Plants of the Tongwe East Forest Reserve (Ugalla), Tanzania. *Tropics* 3:333–340.
- MUROYAMA, Y. and SUGIYAMA, Y. 1994. Grooming relationships in two species of chimpanzees, pp. 109–128, in R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. G. Heltne (eds.). *Chimpanzee Cultures*. Harvard University Press, Cambridge, AM.
- MOUTSAMBOTÉ, J. M., YUMOTO, T., MITANI, M., NISHIHARA, T., SUZUKI, S., and KURODA, S. 1994. Vegetation and list of plant species identified in the Nouabalé-Ndoki Forest, Congo. *Tropics* 3:277–293.
- MOWRY, C. B., DECKER, B. S., and SHURE, D. J. 1996. The role of phytochemistry in dietary choices of Tana River red colobus monkeys (*Procolobus badius rufomitratus*). *Int. J. Primatol.* 17:63–84.
- NEWTON-FISHER, N. E. 1999. The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *Afr. J. Ecol.* 37:344–354.
- NISHIDA, T. and UEHARA, S. 1983. Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): Long-term record from the Mahale Mountains, Tanzania. *Afr. Study Monogr.* 3:109–130.
- OATES, J. F. 1987. Food distribution and foraging behavior, pp. 197–209, in B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker (eds.). *Primate Societies*. University of Chicago press, Chicago, Illinois.
- OATES, J. F., SWAIN, T., and ZANTOVSKA, J. 1977. Secondary compounds and food selection by colobus monkeys. *Biochem. Syst. Ecol.* 5:317–321.
- OATES, J. F., WATERMAN, P. G., and CHOO, G. M. 1980. Food selection by the south Indian leaf-monkey, *Presbytes johnii*, in relation to leaf chemistry. *Oecologia.* 45:45–56.
- PORTER, L. J. 1989. Tannins, pp. 389–419, in P. M. Dey and J. B. Harborne (eds.). *Methods in Plant Biochemistry*, Vol. 1, Plant Phenolics. Academic Press, London.
- PORTER, L. J., HRSTICH, L. N., and CHAN, B. G. 1986a. The conversion of procyanidins and prodelphinidins to cyanidin and delphinidin. *Phytochemistry* 25:223–230.
- PORTER, L. J., WONG, R. Y., BENSON, M., CHAN, B. G., VISHWANADHAN, V. N., GANDOUR, R. D., and MATTICE, W. L. 1986b. Conformational analysis of flavans: <sup>1</sup>H N.M.R. and molecular mechanical (MM2) studies of the benzopyran ring of 3',4',5,7-tetrahydroxyflavan-3-ols: The crystal and molecular structure of the procyanidin (2R, 3S, 4R)-3',4',5,7-tetramethoxy-4-(2,4,6-trimethoxyphenyl) flavan-3-ol. *J. Chem. Res. (S)*:86–87.
- POST, D. G. 1984. Is optimization the optimal approach to primate foraging? pp. 280–303, in P. S. Rodman and J. G. H. Cant (eds.). *Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismal Biology of Prosimians, Monkeys, and Apes*. Columbia University Press, New York.

- PROVENZA, F. D. 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. *J. Range Manage.* 48:2–17.
- PROVENZA, F. D. 1996. Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. *J. Anim. Sci.* 74:2010–2020.
- PROVENZA, F. D., VILLALBA, J. J., and BRYANT, J. P. 2002. Foraging by herbivores: Linking the biochemical diversity of plants to herbivore culture and landscape diversity, pp. 387–421, in J. A. Bissonette and I. Storch (eds.). *Landscape Ecology and Resource Management: Linking Theory with Practice*. Island Press, Washington, DC.
- PYKE, G. H., PULLIAM, H. R., and CHARNOV, E. L. 1977. Optimal foraging: A selective review of theory and tests. *Q. Rev. Biol.* 52:137–154.
- REMIS, M. J. and KERR, M. E. 2002. Taste responses to fructose and tannic acid among gorillas (*Gorilla gorilla gorilla*). *Int. J. Primatol.* 23:251–261.
- REYNOLDS, V., PLUMPTRE, A. J., GREENHAM, J., and HARBORNE, J. 1998. Condensed tannins and sugars in the diet of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Oecologia* 115:331–336.
- RHOADES, D. F. and CATES, R. G. 1976. Toward a general theory of plant antiherbivore chemistry, pp. 168–213, in J. Wallace and R. L. Mansell (eds.). *Biochemical Interactions Between Plants and Insects*. Rec. Adv. Phytochem. vol. 10. Plenum Press, New York.
- ROBBINS, C. T. 1993. *Wildlife Feeding and Nutrition*, 2nd Edition. Academic Press, San Diego, California.
- ROBBINS, C. T., HAGERMAN, A. E., AUSTIN, P. J., MCARTHER, C., and HANLEY, T. A. 1991. Variation in mammalian physiological responses to a condensed tannin and its ecological implications. *J. Mamm.* 72:480–486.
- ROGERS, M. E., MAISELS, F., WILLIAMSON, E. A., FERNANDEZ, M., and TUTIN, C. E. G. 1990. Gorilla diet in the Lopé Reserve, Gabon. *Oecologia* 84:326–339.
- STRIER, K. B. 2000. *Primate Behavioral Ecology*. Allyn and Bacon, Boston, Massachusetts.
- STRUHSAKER, T. T. 1975. *The Red Colobus Monkey*. University Chicago Press, Chicago, Illinois.
- SUGIYAMA, Y. 1988. Grooming interactions among adult chimpanzees at Bossou, Guinea, with special reference to social structure. *Int. J. Primatol.* 9:393–407.
- SUGIYAMA, Y. 1994. Age specific birth rate and lifetime reproductive success of chimpanzees at Bossou Guinea. *Am. J. Primatol.* 32:311–318.
- SUGIYAMA, Y. and KOMAN, J. 1987. A preliminary list of chimpanzees' alimentation at Bossou, Guinea. *Primates* 28:133–147.
- SUGIYAMA, Y. and KOMAN, J. 1992. The flora of Bossou: Its utilization by chimpanzees and humans. *Afr. Study Monogr.* 13:127–169.
- SWAINE, M. D., and HALL, J. B. 1983. Early succession on cleared forest land in Ghana. *J. Ecol.* 71:601–627.
- TAKEMOTO, H. 1996. Selectivity in feeding behaviour of planted trees by captive chimpanzees. *Primate Res.* 12:33–40. [In Japanese with English abstract].
- TAKEMOTO, H. 2002. Feeding ecology of chimpanzees in Bossou, Guinea: Coping with the seasonal fluctuation of food supply and micrometeorology in the tropical forest. PhD Dissertation. Kyoto University, Kyoto, Japan.
- TAKEMOTO, H. in press Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. *Am. J. Phys. Anthropol.*
- TUTIN, C. E. G., WHITE, L. J. T., WILLIAMSON, E. A., FERNANDEZ, M., and MCPHERSON, G. 1994. List of plant species identified in the northern part of the Lopé Reserve, Gabon. *Tropics* 3:249–276.
- VAN SOEST, P. J. 1994. *Nutritional ecology of the ruminant*, 2nd Edition. Cornell University Press, London.

- VILLALBA, J. J., PROVENZA, F. D., and BRYANT, J. P. 2002. Consequences of the interaction between nutrients and plant secondary metabolites on herbivore selectivity: Benefits or detriments for plants? *Oikos* 97:282–292.
- WESTBY, M. 1974. An analysis of diet selection by large generalist herbivores. *Am. Nat.* 108:290–303.
- WRANGHAM, R. W. 1977. Feeding behavior of chimpanzees in Gombe national park, Tanzania, pp. 503–538, in T. H. Clutton-Brock (ed.). *Primate Ecology*. Academic Press, London.
- WRANGHAM, R. W., CHAPMAN, C. A., CLARK-ARCADI, A. P., and ISABIRYE-BASUTA, G. 1996. Social ecology of Kanyawara chimpanzees: Implications for understanding the costs of Great ape groups, pp. 45–57, in W. C. McGrew, L. F. Marchant, and T. Nishida (eds.). *Great Ape Societies*. Cambridge University Press, Cambridge, United Kingdom.
- WRANGHAM, R. W., CHAPMAN, C. A., and HUNT, K. D. 1991. The significance of fibrous foods for Kibale Forest chimpanzees. *Phil. Trans. R. Soc. Lond. B* 334:171–178.
- WRANGHAM, R. W., CONKLIN-BRITAIN, N. L., and HUNT, K. D. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int. J. Primatol.* 19:949–970.
- WRANGHAM, R. W., CONKLIN, N. L., ETOT, G., OBUTA, J., HUNT, K. D., HAUSER, M. D., and CLARK, A. P. 1993. The value of figs to chimpanzees. *Int. J. Primatol.* 14:243–256.
- WRANGHAM, R. W. and WATERMAN, P. G. 1981. Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: With special reference to reproductive strategies and tannin production. *J. Anim. Ecol.* 50:715–731.
- WRANGHAM, R. W. and WATERMAN, P. G. 1983. Condensed tannin in fruits eaten by chimpanzees. *Biotropica* 15:217–222.
- YAMAKOSHI, G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *Am. J. Phys. Anthropol.* 106:283–295.
- YEAGER, C. P., SILVER, S. C., and DIEREFELD, E. S. 1997. Mineral and phytochemical influences on foliage selection by the Proboscis Monkey (*Nasalis larvatus*). *Am. J. Primatol.* 41:117–128.
- YUMOTO, T., YAMAGIWA, J., MWANZA, N., and MARUHASHI, T. 1994. List of plant species identified in Kafuji-Biega National Park, Zaire. *Tropics* 3:295–308.