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Feeding Ecology of Western Lowland Gorillas in the Nouabalé-Ndoki National Park, Congo

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ABSTRACT. The feeding ecology of western lowland gorillas (*Gorilla gorilla gorilla*) living in the Nouabalé-Ndoki National Park, northern Congo, was surveyed for one full year. This is the first record to make clear the seasonal changes in the feeding habits of gorillas in a whole year, living in the primary lowland forest almost completely undisturbed. Fecal contents, feeding traces, and direct observation were analyzed with reference to a fruit availability survey. Although the gorillas fed largely on fruits in the forest, their basic diet was fibrous parts of plants, including shoots, young leaves, and bark. Terrestrial herbaceous vegetation, such as monocotyledons of the Marantaceae and aquatic herbs having much protein content and minerals, were frequently eaten even in the fruiting season. As these highly nutritious fibrous foods were superabundant all year, the major foods of the Ndoki gorillas seemed to be those plants. However, they selected fruits as their alternative food resources in the fruiting season. Gorillas foraged on many fruit species, while showing strong preferences for some particular species. The swamp forest, including marshy grasslands, was an important and regular habitat for the Ndoki gorillas.

Key Words: Ndoki; Western lowland gorillas; Feeding behavior; Fruits; Swamp.

INTRODUCTION

Recent ecological studies on western lowland gorillas (*Gorilla gorilla gorilla*) have made clear that their feeding habits were different from those of mountain gorillas (*G. g. beringei*) whose major foods are fibrous plants. Western lowland gorillas eat more fruits in the fruiting season and more fibrous plants in the non-fruiting season. In Rio Muni, Equatorial Guinea, dominated by secondary vegetation, gorillas depend largely on fibrous parts of herbaceous plants such as *Aframomum* spp. (JONES & SABATER PI, 1971; SABATER PI, 1977). TUTIN and FERNANDEZ (1985) concluded that western gorillas in Belinga, Gabon, could not be accurately classed as folivores. In Lopé, Gabon, where the Scottish Primate Research Group has conducted research for ten years, gorillas frequently eat fruits in the primary forest although part of it had been selectively logged (WILLIAMSON, 1988; ROGERS et al., 1988; WILLIAMSON et al., 1990; TUTIN, FERNANDEZ, ROGERS, WILLIAMSON, & MCGREW, 1991; TUTIN, WILLIAMSON, ROGERS, & FERNANDEZ, 1991; TUTIN & FERNANDEZ, 1993). Feeding habits of eastern lowland gorillas (*G. g. graueri*) have an intermediate characteristic between mountain gorillas and western lowland gorillas. Some reports pointed out that their important foods were herbs, while they also fed on fruits (YAMAGIWA et al., 1989; YUMOTO et al., 1989; YAMAGIWA et al., 1994).

In the Nouabalé-Ndoki National Park, northeastern Congo, ecological surveys have been continued since 1988. To date, intermittent surveys showed the general features of feeding habits of the Ndoki gorillas were almost the same as those of gorillas in Lopé (NISHIHARA, 1992; MITANI, 1992). However, some differences in habitat exist. While savanna dominates more than 30% of the study area in Lopé (WILLIAMSON et al., 1988), primary tropical

lowland forest, undisturbed for at least 50 years, and large swamp vegetation cover the study area in Ndoki.

The aim of this study was to clarify feeding habits and habitat use of the Ndoki gorillas and the seasonal changes through a consecutive survey for a whole year for the first time. In particular, their fruit diet, which occupies an important part of their feeding habits, was analyzed with reference to a fruit availability survey. In addition, the significance of swamp vegetation for the Ndoki gorillas is discussed.

STUDY AREA AND METHODS

STUDY AREA AND STUDY PERIOD

The Nouabalé-Ndoki Reserve, stretching between northeastern Sangha Province and northwestern Likouala Province, Republic of Congo, is about 3,870 km^2. This area became a National Park in September 1993 (Fig. 1). The study area was about 20 km^2 lying north-

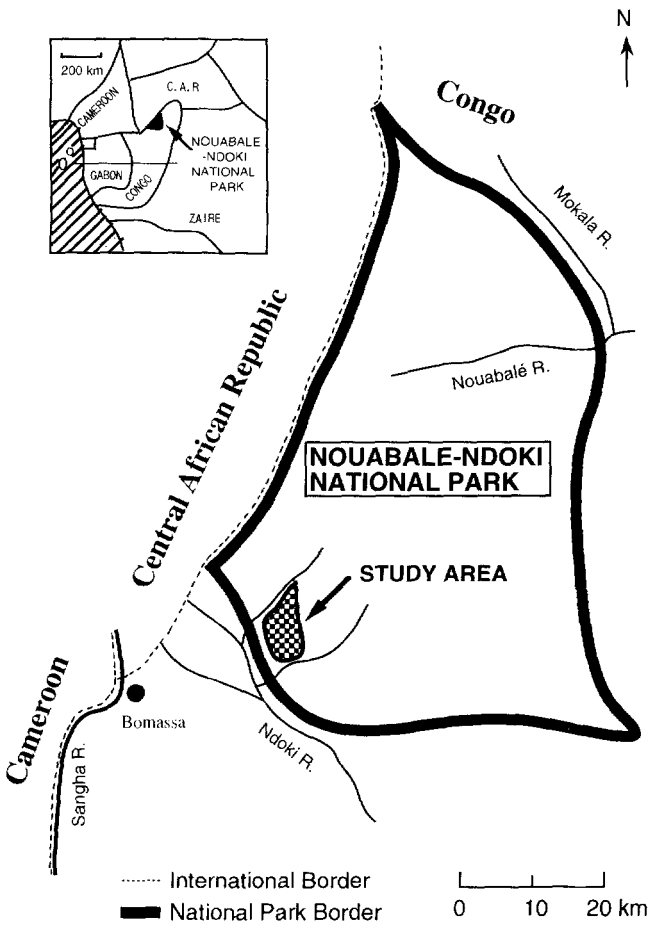

Fig. 1. Nouabalé-Ndoki National Park and study area.

east of the Ndoki River, which flows along the southwestern edge of the National Park. The study base camp was at 2°20′N and 16°19′E. The study period was 287 days over 12 months from December 1991 to November 1992. Eleven species of diurnal primates including gorillas and chimpanzees (*Pan troglodytes troglodytes*) were living sympatrically at high density (MITANI, 1990a, b). The rainfall was 1,430 mm during the study period, and the one year was roughly divided into two seasons: dry season (December – February) and rainy season (March – November) (NISHIHARA & SUZUKI, unpubl. data).

VEGETATION

The study area can be classified into three types of vegetation: Swamp Forest, *Gilbertiodendron* Forest, and Mixed Species Forest (NISHIHARA, 1992). In the Mixed Species Forest, there are some small patches of *Gilbertiodendron* Forest with sparse undergrowth. Here, *Gilbertiodendron* Forest means both the Riverine *Gilbertiodendron* Forest and small patches of *Gilbertiodendron* Forest. Marshy grassland ("Bai" in the vernacular) is distributed patchily in the Swamp Forest, where dominant species are aquatic herbs, such as *Hydrocharis* sp.

To determine the fruiting patterns of each species, all individual plants, whose fruits fell to the ground, were observed every month (NISHIHARA & SUZUKI, unpubl. data). This fruit census method was conducted on the predetermined line of 10 m in width and 37.05 km in length through the forest (*Gilbertiodendron* Forest: 13.61 km; Mixed Species Forest: 23.44 km). The total number of fruiting plants and fruiting species by month were counted. One year was divided into two seasons: the "fruiting season" from April to September when fruits were abundant (number of fruiting plants >200 or number of fruiting species >50), and the "non-fruiting season" from October to March when fruits were scarce (number of fruiting plants <200 or number of fruiting species <50).

FECAL ANALYSES

Fecal samples were limited to those found soon after direct observation, found on gorilla trails (pathways of gorillas on the ground), found in and around gorilla beds, or confirmed from the smell, form, and quantity. The gorilla dung is normally composed of several rice-ball-like units, and usually their quantity is much larger than that of chimpanzees. Their herbaceous smell is clearly distinguished from chimpanzees'.

The number of fecal samples was 522 (December: 57; January: 57; February: 58; March: 45; April: 58; May: 43; June: 53; July: 51; August: 30; September: 21; October: 40; November: 9). The samples were placed in sieves with 1 mm mesh, washed in running water, and then the contents of each sample were examined for plant parts: fruit (including seed, fruit skin, and pulp), leaf, bark, and other fibrous parts (mainly pith). In fecal samples, most fruits were identified to species level from seeds, skin, or pulp. However, there were some exceptions when more than one species of the same genus have indistinguishable seeds, such as *Dialium* spp., *Landolphia* spp., *Ficus* spp., *Palisota* spp., and *Aframomum* spp. Each of these genera was treated as a "fruit species group." "One identified fruit species" means one "fruit species group." The number of fruit species groups was counted in each sample. We then calculated the number of each fruit species group by month and the average number of each fruit species group per sample. Volume percentage of each fruit species group and other plant part per sample was recorded by 5% intervals; less than 5% was scored as 0%. Average volume percentage of each plant part per sample by month was defined as a "monthly percent score" for each plant part.

ANALYSES OF FEEDING TRACES

Feeding traces of gorillas were limited to those found on their trails, in direct observation sites, or near beds, feces, or with knuckle- or footprints, which were all within 2 days old. Two feeding traces of the same species, the same part eaten, or the same day, if separated from each other by more than 1 m, were treated as independent feeding traces. When the number of individuals was known on trails, the number of feeding traces per distance (km) per individual was calculated in each bimonthly period to measure the observability of feeding traces.

DIRECT OBSERVATION AND CONTACT

One direct observation unit of gorillas was defined as that from the moment of discovery to the moment of last observation. One indirect observation means that the presence of gorillas was confirmed only through vocalization, drumming, feeding sounds, moving sounds, and so on within 30 m of observers. Contacts with gorillas were combined with direct and indirect observation.

Contact frequency per study distance (km) in each vegetation type was calculated bimonthly. Contact frequency, which was assumed to reflect the frequency of utilization of each vegetation, was compared between that in the Swamp Forest and in the Inland Forest.

FOOD LIST

The food list of the gorillas was made through fecal analyses, feeding traces, and direct observation. The list also includes those recorded in the past studies — plant species which have been confirmed by fecal analyses and direct observation, and by feeding traces identified as in this study (NISHIHARA, 1992; KURODA, unpubl. data; YAMAGIWA, unpubl. data; SUZUKI, unpubl. data). Life forms, feeding position (on the ground or in the trees), and food processing were recorded. Fruit species in the gorilla diet and those not in their diet, observed in the fruit census, were compared between the fruiting and non-fruiting seasons. Termites and ants eaten by gorillas were excluded in this list.

Basic nutrients, such as proteins and lipids of *Haumania danckelmaniana* and *Hydrocharis* sp., which gorillas fed on, were analyzed by R. AZATO; and some mineral components of those species by K. KANAYA. Plant species were identified by J. M. MOUTSAMBOTÉ.

RESULTS

COMPOSITION OF DIET

Gorillas ate 182 plant parts of 152 species (Appendix). Among these plants, 126 species (80.9%) were species in which the number of plant parts eaten was 1 per species; 22 species, 2 per species; and 4 species, 3 per species. The most common life forms were trees (49.3%), and the most frequent plants consumed were fruits (63.2%) (Table 1).

Gorillas were directly observed 93 times, for 3,297 min in total. Foraging behavior was observed 56 times (60.2%), moving or resting 37 (39.8%). In foraging behavior, roots of *Hydrocharis* sp. was the item most frequently observed directly (27 times); followed by

Table 1. Life form and parts-eaten of gorilla plant foods.

		Total	Tree	Shrub	Vine	Herb	Unknown
No. species		152	75	4	26	15	32
Percentage		100.0	49.3	2.6	17.1	9.9	21.1
No. items	Fruit	115 (63.2)	55	2	20	7	31
	Seed	18 (9.9)	13	0	5	0	0
	Leaf	29 (15.9)	19	1	6	2	1
	Pith	10 (5.5)	0	0	2	8	0
	Shoot	4 (2.2)	0	0	1	3	0
	Root	2 (1.1)	0	0	0	2	0
	Bark	2 (1.1)	1	1	0	0	0
	Flower	2 (1.1)	2	0	0	0	0
Total		182 (100.0)	90	4	34	22	32

Numbers in parentheses: Percentage. Of 18 dietary seed species, 8 species were eaten only for seeds but 10 species for seeds as well as pulp. As a result, the number of dietary fruit species was 123.

fruits of *Landolphia* spp. (including seeds) (7); young leaves and barks of *Celtis mildbraedii* (6); fruits of *Ficus* spp. (5). Gorillas were indirectly observed 52 times, and therefore the number of contacts with gorillas was 145 in total.

As gorillas swallowed most fruits with their seeds, the monthly percent score of each fruit species group was assumed to reflect the relative quantity consumed of each group. Only 8.9% of seeds of all dietary fruit species was not swallowed as these seeds were too hard and their size was more than 40 mm.

Dietary fruits were categorized as four types, by combination of the length of foraging duration and quantity consumed: "long" duration type (foraging duration was more than half of a year) and "short" duration type (less than half of a year); "large" quantity type (percent score was more than ten in at least one month) and "small" quantity type (less than ten). There was only one "long and large" type of species, *Duboscia macrocarpa*; "short and large" type of species were *Drypetes pellegrinii*, *Kleinedoxa gabonensis*, *Grewia*

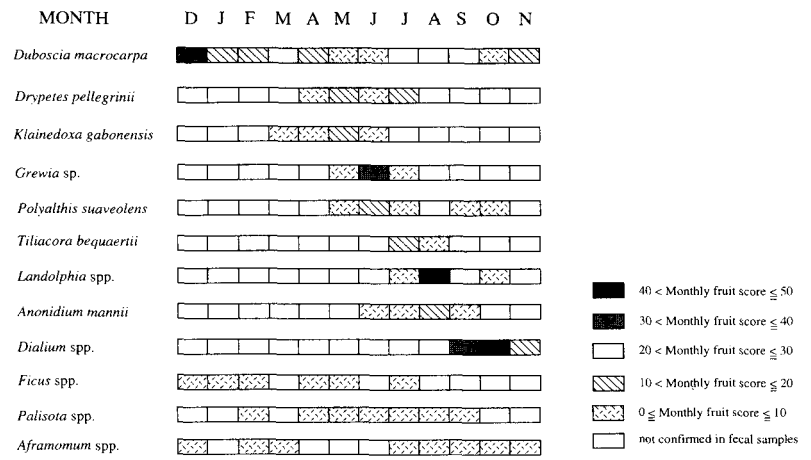

Fig. 2. Monthly change in relative quantity of major fruit species consumed. This also shows that of *Ficus* spp., *Palisota* spp., and *Aframomum* spp. Although monthly fruit score was 0, a small amount of consumption is shown with ▨ in this figure. Months from April to September are the fruiting season.

Table 2. Major dietary fruits of gorillas.

Species	Family		Dec	Jan	Feb	Mar	Apr*	May*	Jun*	Jul*	Aug*	Sept*	Oct	Nov
Duboscia macrocarpa	Tiliaceae	S	31.9	17.8	11.0	23.9	17.8	3.4	0	0	0	+	14.4	22.1
		N	30	13	15	15	19	25	24	15	4	7	13	22
Dialium spp.	Caesalpiniaceae	S	0	0	0	0	0	0	0	0	0	34.1	46.4	11.7
		N	0	0	0	0	0	0	1	3	8	3	9	0
Landolphia spp.	Apocynaceae	S	0	0	0	0	0	0	0	4.5	45.2	28.8	2.1	0
		N	0	0	0	0	1	0	0	4	5	7	0	0
Grewia sp.	Tiliaceae	S	0	0	0	0	1.1	2.0	38.0	0.1	0	0	0	0
		N	0	0	0	3	10	7	3	0	0	0	0	0
Drypetes pellgrinii	Euphorbiaceae	S	0	0	0	0	0.1	17.3	6.6	16.3	0	0	0	0
		N	0	0	0	0	5	5	1	0	0	0	0	0
Anonidium mannii	Annonaceae	S	0	0	0	0	0	0	+	9.5	12.0	2.6	0	0
		N	0	0	0	0	0	0	0	11	6	0	0	0
Polyalthia suaveolens	Annonaceae	S	0	0	0	0	0	0.2	14.4	8.5	0	+	0.1	0
		N	0	0	1	6	5	2	14	3	4	0	2.	1
Tiliacora bequaertii	Menispermaceae	S	0	0	0	0	0	0	0	18.4	4.3	0	0	0
		N	0	0	0	0	0	0	2	1	1	0	0	0
Klainedoxa gabonensis	Irvingiaceae	S	0	0	0	0.9	3.0	12.7	0.2	0	0	0	0	0
		N	9	15	21	18	31	36	33	0	0	0	3	2
No. all fruiting plants censused by fruit census			69	60	80	122	362	301	684	446	364	206	133	114
No. all fruiting species censused by fruit census			22	25	23	40	71	62	86	65	84	52	33	32

S: Monthly fruit percent score of each fruit species (group); N: number of monthly fruiting plants of each fruit species (group); *months of the fruiting season; +: a small amount of consumption was found in fecal samples although the monthly fruit score was 0.

sp., *Polyalthia suaveolens*, *Tiliacora bequaertii*, *Landolphia* spp., *Anonidium mannii*, and *Dialium* spp.; "long and small" type *Ficus* spp., *Palisota* spp., and *Aframomum* spp.; and others were categorized as "short and small" type (Fig. 2). Nine species groups of fruit of the "long and large" and "short and large" types were regarded as major dietary fruits (Table 2).

Gorillas fed on seeds of at least 18 species, such as *Landolphia* spp., *Haumania danckelmaniana*, and *Diospyros* spp. In fecal samples, these seeds were found to be cracked into small fragment. In particular, seeds of *Landolphia* spp. and *Haumania danckelmaniana* were cracked more often than other species. *Landolphia* spp. was eaten most frequently in July when they were mostly unripe yet, and afterwards decreased until October. All seeds of *Haumania danckelmaniana* were eaten when these fruits were eaten.

Among fibrous foods such as pith and shoots, the number of feeding traces of shoots of *Haumania danckelmaniana* was largest; next the pith of *Palisota* spp. and *Aframomum* spp. The species directly observed eaten most frequently was roots of *Hydrocharis* sp. The number of feeding traces of *Thomandersia laurifolia* was largest for leaves, and eating of *Celtis mildbraedii* was most frequently observed directly for leaves and barks. These fibrous foods were limited to only a small number of species, unlike fruits.

Haumania danckelmaniana, a herbaceous vine resembling a thin bamboo, sometimes grows more than 5 m in height. Gorillas ate the lower part (about 4 – 5 cm) of each node of its shoot. *Hydrocharis* sp. is a dominant species in marshy grassland within the Swamp Forest, and gorillas pulled it out and ate its root and stems near the root. In the case of *Celtis mildbraedii*, gorillas broke twigs with young leaves, about 30 cm long and about 5 mm in diameter, and ate young leaves and its bark. They also ate bark at the base of trunks by scraping with their teeth. They ate leaves of *Thomandersia laurifolia* by breaking off its twigs, about 1 cm in diameter.

Table 3. Nutritional comparison of major terrestrial herbaceous vegetation.

Species	Part-eaten	Fe (ppm)	Na	Protein (%)[1]	Lipid (%)[1]	References
Haumania danckelmaniana	Shoot	95	68	35.5	3.7	This study[2]
Hydrocharis sp.	Leaf	549	361	19.5	3.3	
	Stem	728	256	9.7	1.7	
	Root	7280	1080			
Palisota ambigua	Stem	54	185	10.3	1.7	CALVERT, 1985[3]
Hypselodelphis sp.	Shoot	87	115	13.8	3.2	
Megaphrynium macrostachyum	Shoot	97	40	10.5	2.4	
Aframomum spp.	Stem	92	200	3.8	4.3	
Costus sp.	Stem	77	70	8.9	1.6	
Palisota ambigua	Pith	—[4]		6.37	0.68	ROGERS et al., 1990[3]
Marantochloa cordifolia	Pith	—[4]		5.83	0.81	
Aframomum spp.	Pith	—[4]		7.09	0.78	
Costus afer	Pith	—[4]		3.44	0.90	
Renealmia macrocolea	Pith	—[4]		3.07	1.28	

1) Dry matter percentage; 2) Mineral components (Fe, Na) were analyzed by K. KANAYA and basic nutrients (proteins, lipids) by R. AZATO; 3) Any species shown here was eaten by gorillas; 4) data not available.

According to nutritional analyses, shoots of *Haumania danckelmaniana* contain much more protein than other herbaceous plants (Table 3; CALVERT, 1985; ROGERS et al., 1990). *Hydrocharis* sp. has in roots and stems near roots much more minerals such as iron and sodium than other herbaceous plants, while its protein content was the same as others.

SEASONAL CHANGE IN FEEDING HABITS

Quantity of fruit consumption was small from December to May, but increased rapidly from June to August, and afterwards decreased (Fig. 3). The monthly change in the number of all fruiting plants counted by the fruit census (NISHIHARA & SUZUKI, unpubl. data; see Fig. 3 & Table 2) showed fruit consumption coincided with the number of all fruiting plants (Spearman rank correlation: $N=12$, $r_S=0.713$, $p<0.05$). The quantity of fruit consumption coincided with the number of fruit species groups and with the average number of fruit species groups per fecal sample (Fig. 3: $N=12$, $r_S=0.781$, $p<0.01$; $N=12$, $r_S=0.881$, $p<0.01$). The quantity consumed of each major dietary fruit species group coincided mostly with its number of fruiting plants, except for *Duboscia macrocarpa* (Table 2). Generally, in one to three months after the first period that fruits were not completely mature, gorillas began to eat fruits. Although *Duboscia* produced its fruit all year, the quantity of its fruit consumption coincided with the number of its fruiting plants only in the non-fruiting season. As the fruiting season began, fruits such as *Drypetes pellgrinii*, *Grewia* sp., *Polyalthia suaveolens*, and *Tiliacora bequaertii* were eaten in turn instead of *Duboscia*. In the late fruiting season, fruits of *Landolphia* spp., *Anonidium mannii*, and *Dialium* spp. were eaten in large quantities in a short period (Fig. 2).

Monthly percent scores were also assumed to show the relative quantity of leaf, bark, and pith consumed (Fig. 3). The quantity of fibrous foods consumed in total was large from December to May, and decreased from June to August but increased again from September. The consumption of either leaf or pith was small in the fruiting season and large in the non-fruiting season, while bark was mainly consumed only during four months.

Total tracking distance in the analyses of feeding traces of pith and shoots was 9.09 km. Except for *Haumania danckelmaniana*, finding frequency of feeding traces of pith and

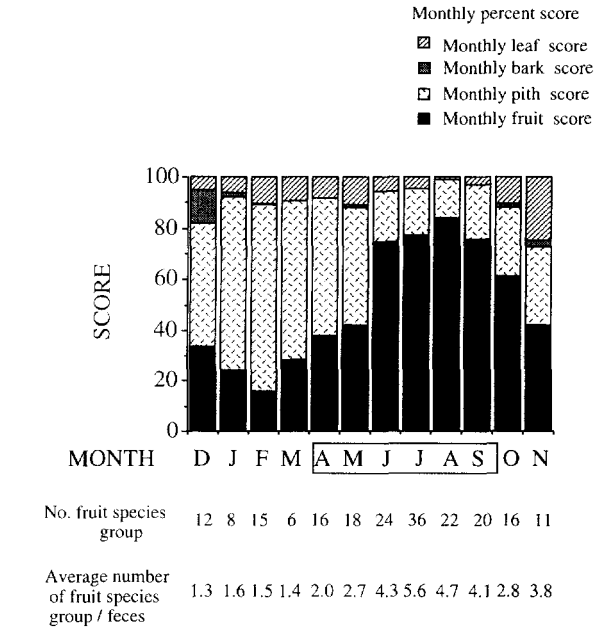

Fig. 3. Monthly change in relative quantity of fruits, pith, bark, and leaf consumed through fecal analyses. Months from April to September are the fruiting season.

shoots, such as *Palisota* spp., *Aframomum* spp., and *Ataenidia* sp., coincided with monthly pith score until August – September (Fig. 4). The finding frequency of feeding traces of

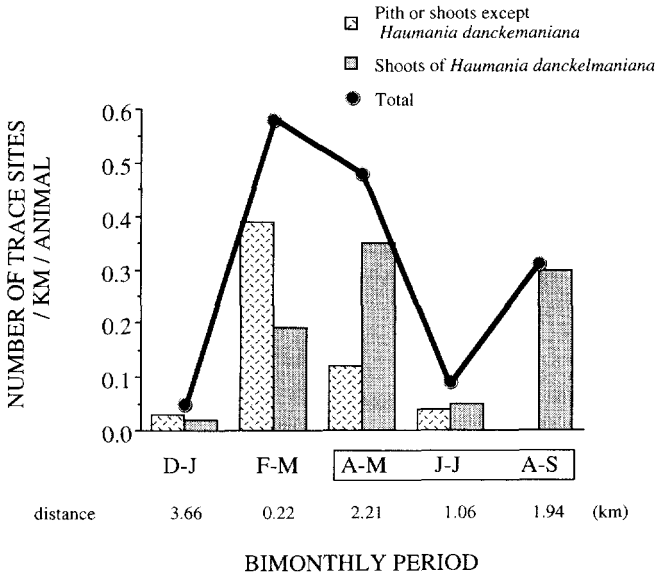

Fig. 4. Bimonthly change in the number of feeding traces per tracking distance per animal. Feeding traces were limited to shoots and pith, and were compared between *Haumania danckelmaniana* and other species. D-J: December and January; F-M: February and March; A-M: April and May; J-J: June and July; A-S: August and September. Months from April to September are the fruiting season.

Table 4. Monthly contact frequency and observation frequency of *Hydrocharis*-eating.

		Total	D-J	F-M	A-M*	J-J*	A-S*	O-N
No. contact	Swamp	59	8	7	5	11	16	12
	Inland	86	19	12	19	14	16	6
	Total	145	27	19	24	25	32	18
No. observation of *Hydrocharis*-eating		27	5	1	3	5	9	4
Study distance (km)	Swamp	673.9	134.4	105.5	111.5	96.0	126.0	100.5
	Inland	2382.5	416.3	347.1	465.3	372.7	407.2	373.9
Contact frequency	Swamp	8.8	6.0	6.6	4.5	11.5	12.7	11.9
(× 100)	Inland	3.6	4.6	3.5	4.1	3.8	3.9	1.6
Observation frequency of *Hydrocharis*-eating (× 100)		4.0	3.7	1.0	2.7	5.2	7.1	4.0

D-J: December and January; F-M: February and March; A-M: April and May; J-J: June and July; A-S: August and September; O-N: October and November. *Months of the fruiting season. Inland: Combined *Gilbertiodendron* Forest and Mixed Species Forest; Contact frequency (in Swamp Forest): number of contact in Swamp Forest/(walking distance on riverine observation route/2); Contact frequency (in Inland Forest): number of contact in Inland Forest/(walking distance on reverine observation route/2 + walking distance on observation routes in Inland Forest); Observation frequency of *Hydrocharis*-eating: number of observation of *Hydrocharis*-eating/(walking distance on riverine observation route/2).

Haumania shoots was higher in April – May, and afterwards decreased, but again increased in August – September. *Hydrocharis*-eating was directly observed in high frequency in August – September (Table 4). *Haumania* shoots and *Hydrocharis* roots were eaten more often even in the fruiting season.

Gorillas ate young leaves and bark of twigs and bases of trunks of *Celtis mildbraedii* in the limited period from the end of rainy season to dry season when its young leaves appeared in large amounts. Leaves of *Thomandelsia laurifolia* were eaten mainly in the dry season.

Vegetation Use

Contact frequency in the Swamp Forest was higher in any period than in the Inland Forest (Table 4). Utilization frequency of the Swamp Forest, based on contact frequency, was higher from June to November. In the Swamp Forest, eating *Hydrocharis* sp. in marshy grasslands was most frequent, and eating other species and moving or resting was infrequent. Observability of all feeding traces in the Mixed Species Forest (17.3/km) was about 1.5 times as high as those in the *Gilbertiodendron* Forest (11.0/km); for *Haumania danckelmaniana* shoots 11.0/km in the Mixed Species Forest, 4.3/km in the *Gilbertiodendron* Forest. Thus, gorillas frequently used the Swamp Forest for eating *Hydrocharis* sp. and the Mixed Species Forest for *Haumania* and other plant species. In contrast with these types of Forests, the *Gilbertiodendron* Forest, which has little undergrowth, seemed to be used as a corridor connecting the Swamp Forest and the Mixed Species Forest.

DISCUSSION

Fibrous Plants as Basic Foods and Fruit Diet

Fecal analyses in this study showed that gorillas ate more fruits for their foods in the

fruiting season and more fibrous plants in the non-fruiting season. Gorillas in the non-fruiting season often ate fibrous parts of "terrestrial herbaceous vegetation" (THV), such as *Hydrocharis* sp., *Haumania danckelmaniana*, *Palisota* spp., and *Aframomum* spp. as well as young leaves and bark of *Celtis mildbraedii*. On the other hand, even in the fruiting season, they often ate fibrous plants such as *Hydrocharis* and *Haumania*. Because shoots of *Haumania* and roots of *Hydrocharis* might be easily digested, frequent feeding of these herbs did not appear clearly in feces.

Gorillas living in lowland tropical forests feed mainly on fibrous foods in the non-fruiting season (NISHIHARA, 1992; ROGERS et al., 1988; WILLIAMSON, 1988; WILLIAMSON et al., 1990). Those living in regions greatly affected by human disturbances, in the secondary forest zones (YAMAGIWA et al., 1989; YUMOTO et al., 1989; JONES & SABATER PI, 1971; SABATER PI, 1977) and the montane habitats (KAWAI & MIZUHARA, 1959; SCHALLER, 1963; CASIMIR, 1975; GOODALL, 1977; FOSSEY & HARCOURT, 1977; WATTS, 1984), rely on fibrous foods throughout the year. Gorillas in Ndoki are considered to be also fiber eaters through all seasons. Although they largely ate more fibrous foods in the non-fruiting season, they ate *Haumania* shoots and *Hydrocharis* roots with high protein and mineral contents more often in the fruiting season than in the non-fruiting season. In the year with poor crops in the fruiting season, they ate more fibrous foods (NISHIHARA, unpubl. data). As *Hydrocharis* and *Haumania* shoots were abundant even in the fruiting season, possibly the Ndoki gorillas take such THV as basic foods without relying heavily on fruits even in the fruiting season. However, they ate fruits, if available. In other words, they selected fruits as an alternative choice food. As a result, food resources available to gorillas expanded greatly.

Some fruits, such as *Dialium* spp. and *Landolphia* spp. were eaten with strong preference. These two fruit species groups have a sweet-sour taste, and are often eaten by people also. Although *Duboscia* fruits were major dietary fruits in the non-fruiting season, gorillas did not eat them in the fruiting season irrespective of their fruit crops, and instead ate mainly *Dialium* and *Landolphia* fruits. Gorillas preferred fruits of *Dialium* and *Landolphia* much more to *Duboscia* fruits. Fruits of *Anonidium mannii*, which were also eaten by people, might be strongly preferred. One day, gorillas made a long detour to feed on *Anonidium* fruits at two sites, instead of going directly to a nearby Bai marsh.

Consuming the albumen and/or embryo by cracking seeds in the fruiting season is considered to be a feeding behavior for ingesting some nutrients (KURODA, 1992). Generally, seeds is highly nutritious, being particularly rich in proteins and lipids. Protein content per unit weight of seeds equals to that of barks although less than that of young leaves (ROGERS et al., 1990). Seed cracking is a foraging behavior peculiar to western lowland gorillas, unseen in other subspecies. In Lopé, Gabon, 20 species of seeds were observed to be eaten, such as *Dialium* sp., *Diospyros* spp., and *Haumania liebrechtsiana* (WILLIAMSON et al., 1990; TUTIN & FERNANDEZ, 1993). This behavior would be an efficient way for acquiring proteins and lipids, along with calories from pulp.

While sympatric chimpanzees ate more fruits in all seasons (SUZUKI, unpubl. data), gorillas were not as frugivorous as them. This is probably because the digestive function of gorillas have evolved in the way that they could live without fruits. Gut flora and fauna of gorillas could dissolve cellulose from fibrous foods into digestible carbohydrates (COLLET et al., 1984; GAULIN & KONNER, 1977). As larger body size does not allow gorillas easy arboreal locomotion, they do not seem to be as capable of being frugivorous as chimpanzees. Also the gorilla's robust craniodental morphology (SHEA, 1983) is adequate for eating fibrous foods.

Swamp Vegetation as Regular Habitat of Gorillas

The Swamp Forest, including marshy grassland, is an important and regular habitat for gorillas. There gorillas utilized and ate aquatic herbs, particularly *Hydrocharis* sp., in all seasons. They were available in great amounts and provided nutrients, such as minerals and proteins, to gorillas. These herbs are considered to be a valuable nutritional resource, similar to shoots of *Haumania danckelmaniana* with a high protein content and fruits providing high calories. The use of these herbs by chimpanzees was not observed.

Gorillas often forage on swampy plants in all study sites where their utilization of swamp vegetation is reported. Food species reported in other sites are herbs, such as *Cyperus latifolius* (Casimir, 1975 in Kahuzi), *Costus* sp. and *Palisota* spp. (Mwanza et al., 1992), *Marantochloa* spp. (Rogers & Williamson, 1987; Williamson et al., 1988 in Lopé), *Aframomum* spp. (Fay et al., 1989; Fay & Agnagna, 1992 in Likouala, Congo), and swampy plants such as *Pandanus candelabrum* and basal parts of shoots of *Raphia* sp. (Fay et al., 1989; Fay & Agnagna, 1992; Blake et al., in press, in Likouala, Congo).

Similar utilization of aquatic herbs by other primates is observed. In Ndoki, *Colobus guereza* was observed to eat aquatic herbs (unidentified) in marshy grassland (Nishihara, unpubl. data). Oates (1978) reported that *Colobus guereza* ate aquatic herbs, such as *Hydrochtyle ranunculoides*. Chimpanzees of the Mahale Mountains feed on marsh-growing plants such as the pith of *Vossia* and *Phragmites* (Nishida, 1980). Chimpanzees in the Kibale Forest visit swamps at certain times to eat the pith of *Cyperus papyrus* (Wrangham et al., 1993). Bonobos (*Pan paniscus*) in Yalosidi often used swamp vegetation (Kano, 1983), and ate *Hydrocharis* sp. in marshy grasslands in all seasons [although Uehara (1990) reported this as *Ramilsma humile* (KUNCH) BHUTCH, later he found this was a misidentification; Uehara, pers. comm.]. While the Ndoki gorillas ate the root and its connecting stem of *Hydrocharis* sp., bonobos ate the leaf and stem more frequently than the root (Uehara, 1990). Swamp vegetation was likely to be a regular habitat for bonobos in Wamba, foraging on aquatic herbs and shoots of *Sclerosperma mannii* (Kuroda, unpubl. data).

Ecological studies of the great apes to date have not mentioned the importance of swamp vegetation. However, this vegetation has an important value for African apes, and their adaptation to tropical forests should be considered with evaluation of this vegetation. Swamp vegetation would provide a potentially rich resource for African great apes, giving them superabundant, hence stable, and highly nutritious foods. *Hydrocharis* had high mineral contents in leaves, stems, and roots and the same degree of protein content as other THV. Oates (1978) pointed out that herbs in swamp vegetation were important mineral resources. *Pandanus* and *Palmae* shoots are likely to be rich in proteins. Swamp vegetation might be a primary habitat for gorillas, as Fay et al. (1989) suggested.

Wide Food Repertoire and High Density of the Ndoki Gorillas

Gorillas' various feeding habits correspond to differences between habitats, while chimpanzees live largely on fruits in any habitat. Generally, the food repertoire of gorillas living in primary forests was wider than those in montane and secondary vegetation areas (Table 5). The Ndoki gorillas are likely to have the widest food repertoire among gorillas in any habitat. In both Ndoki and Lopé, where feeding habits and habitat resemble each other, gorillas had a wider food repertoire. The number of food species and food items in Lopé was a little larger than that in Ndoki, probably because of its longer study. Study

Table 5. Comparison of life forms and parts-eaten of plant foods of eight gorilla study sites.

Site	Ndoki	Lopé	Belinga	Rio Muni	Itebero-Utu	Masisi	Kahuzi	Virunga
References	1	2	3	4	5	6	7	8
Habitat	Tropical primary	Tropical primary	Tropical primary	Tropical secondary	Tropical primary/ secondary	Montane	Montane/ bamboo	Montane/ bamboo
Tree	75 (49.3)	—	—	42 (45.7)	50 (41.3)	6 (21.4)	18 (23.4)	5 (13.2)
Shrub	4 (2.6)	—	—	11 (12.0)	12 (9.9)	3 (10.7)	8 (10.4)	6 (15.8)
Vine	26 (17.1)	—	—	17 (18.5)	23 (19.0)	4 (14.3)	27 (35.1)	6 (15.8)
Herb	15 (9.9)	—	—	21 (22.8)	20 (16.5)	10 (35.7)	6 (7.8)	16 (42.1)
?	32 (21.1)	—	—	0 (0)	0 (0)	4 (14.3)	0 (0)	0 (0)
Others	0 (0)	—	—	1 (1.1)	16 (13.2)	1 (3.6)	18 (23.4)	5 (13.2)
Total	152	158	89	92	121	28	77	38
Fruit	115 (63.2)	97 (45.5)	72 (69.2)	54 (38.8)	48 (24.7)	16 (51.6)	2 (2.4)	4 (5.3)
Seed	18 (9.9)	20 (9.4)	0 (0)	0 (0)		0 (0)	0 (0)	0 (0)
Leaf	29 (15.9)	56 (26.3)	7 (6.7)	31 (22.3)	79 (40.7)	5 (16.1)	47 (55.3)	19 (25.0)
Pith	10 (5.5)	16 (7.5)	18 (17.3)	17 (12.2)	39 (20.1)	10 (32.3)	10 (11.8)	23 (30.3)
Shoot	4 (2.2)			17 (12.2)		0 (0)		
Root	2 (1.1)	1 (0.5)	2 (1.9)	4 (2.9)	10 (5.2)	0 (0)	0 (0)	10 (13.2)
Bark	2 (1.1)	12 (5.6)	2 (1.9)	14 (10.1)	17 (8.8)	0 (0)	26 (30.6)	10 (13.2)
Flower	2 (1.1)	3 (1.4)	1 (1.0)	1 (0.7)	0 (0)	0 (0)	0 (0)	0 (0)
Others	0 (0)	8 (3.8)	2 (1.9)	1 (0.7)	1 (0.5)	0 (0)	0 (0)	10 (13.2)
Total	182	213	104	139	194	31	85	76
Study period (month)	21	c.a. 120	9	10	13	4	30	17

1: This study; 2: WILLIAMSON et al., 1990; TUTIN & FERNANDEZ, 1993; 3: TUTIN & FERNANDEZ, 1985; 4: SABATER PI, 1977; 5 & 6: YAMAGIWA et al., 1994; 7: CASIMIR, 1975; YAMAGIWA, 1988; 8: WATTS, 1984. Numbers in parentheses: percentage; —: data not available.

duration of Lopé was about ten years; Ndoki two years. If ecological surveys continue for more years there, the Ndoki gorillas' repertoire will probably exceed that of Lopé.

Dietary differences in the same plant species between Ndoki and Lopé were found. Fruits of *Landolphia* spp. and *Anonidium mannii*, which are widespread in lowland tropical forest in Africa, were major foods of the Ndoki gorillas, while in Lopé these plants were rare and not eaten by the gorillas (WILLIAMSON, 1988; WILLIAMSON et al., 1990; TUTIN & FERNANDEZ, 1993). *Celtis mildbraedii*, whose young leaves and bark were eaten frequently in Ndoki, was another similar example. These differences are probably related to differences in vegetation. The Ndoki forest was composed wholly of primary forest, while part of the Lopé vegetation was a drier savanna, also with fewer swamps (WILLIAMSON et al., 1988).

It is suggested that gorillas have a food culture peculiar to each region (KAWAI & MIZUHARA, 1959; CASIMIR, 1975; YAMAGIWA, 1988). The Ndoki gorillas often ate fruits of *Polyalthia suaveolens*, while the Lopé gorillas did not eat its fruits. The Lopé gorillas instead ate fruits of *Uapaca guineensis*, *Duboscia macrocarpa*, etc., although they were fewer than *Polyalthia* in numbers (WILLIAMSON, 1988). Also the Lopé gorillas often ate the young leaves and bark of *Milicia excelsa* (ROGERS et al., 1992) while the Ndoki gorillas ate its leaves rarely, although that species was found in both sites.

The Ndoki gorillas had a wide food repertoire. This is because, corresponding to seasonal change and environmental fluctuation, the gorillas got their food from undisturbed primary forest with rich plant resources, where they had an ability to forage on fruits and utilize swamp vegetation. The Ndoki gorillas used THV as their basic foods all year round. In particular, aquatic herbs in marshy grassland in the Swamp Forest were important

resources for gorillas. In the fruiting season, gorillas could feed on fruits and seeds frequently without remarkable competition with such frugivores as chimpanzees.

Population density of gorillas in Ndoki is estimated to be higher than that in other areas (MITANI, 1990a, b, 1992; NISHIHARA, 1994). It was suggested that variation in THV density could be large to influence the density of apes (WRANGHAM et al., 1993). There are no data available to compare THV density in Ndoki, including aquatic herbs, to that in other study sites. However, THV in Ndoki used by gorillas, particularly aquatic herbs (*Hydrocharis* sp.) and Marantaceae shoots (*Haumania danckelmaniana*), appeared superabundant in a whole year. These THV were high nutritional value. These may have enable gorillas in Ndoki to live at highest density. Additionally, gorillas, in the fruiting season, acquired more calories from fruits and proteins and lipids by eating seeds. This may also contribute to supporting their high density.

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Appendix. Food list of gorillas in the Nouabalé-Ndoki forest#.

Family	Scientific name	Local name	Life form	Habitat	Part-eaten	Foraging months	Fruiting months	Seed-eating	Foraging position	Methods confirmed
Acanthaceae	*Crossandra guineensis*	gindi	ST	M	LV	+			t	T
	Thomandersia laurifolia	ngoka	ST	M	LV	12-5,9			t	T
	?	ndolu	H	M	LV	4,10			t	T
Anacardiaceae	*Trichoscypha ferruginea*	dembo	ST	M	FR	5,6	6	S	a	F
Annonaceae	*Anonidium mannii*	mbe	MT	M	FR	6-10	7-8	N,S	t	FT
					SD	+	7-8	C		F
	Polyalthia suaveolens	botunga	MT	M	FR	5-7,9-10	2-8,10-11	S	a	FO
	Uvariastrum pierreanum	mpota	ST	M	FR	7-9	12,6-8	S	?	F
					LV	4				T
	Isolona hexaloba	jingo	ST	M	FR	2	3,8,10	S	?	F
	?	bodo	LI	G&M	FR	7	7	S	a	F
Apocynaceae	*Landolphia* sp. 1	pembe	LI	G,M&W	FR	7-8	8	S	a	FT
					SD	7-10	8	C		FO
					LV	5				O
	L. sp. 2	matobe	LI	G,M&W	FR	9	9	S	a	F
	L. sp. 3	mapa	LI	G,M&W	FR	7-8	4,7-8	S	a	FTO
					SD	7-10	4,7-8	C		F
	L. sp. 4	dembo	LI	G,M&W	FR	7-9	8-9	S	a	FO
					SD	7-10	7-10	C		FTO
	L. sp. 5	mongeni	LI	G,M&W	FR	8-9	8-9	S	a	FT
	Pleiocarpa mutica	mosebe	SH	G&M	FR	12,2,9	2,6,8-10	S	t	FT
	Tabernaemontana crassa	tokoloko	ST	M	FR	6-7	4-7	S	t	F
					LV	9				T

(continued)

Appendix. (continued)

Family	Scientific name	Local name	Life form	Habitat	Part-eaten	Foraging months	Fruiting months	Seed-eating	Foraging position	Methods confirmed
	Tabernaemontana penduliflora	dongo	ST	M	FR	9-10	9	S	t	F
					LV	7				T
	Saba comorensis var. florida	masenda	LI	G,M&W	FR	+	*	?	a	F
	Pycnobotria nitida	mtenge	LI	M	PT	1,9			t	T
					LV	1,2				T
Araceae	*Cyrtosperma senegalense*	langango	H	W	RT	11			t	F
Burseraceae	*Santiria trimera*	libaba	TT	M	FR	8	8	S	t	F
Caesalpiniaceae	*Dialium pachyphyllum*	bendongere	TT	M	FR	9-11	6-10	S	a	FT
					SD	+	*	C		F
					LV	4				T
	D. polyanthum	bendongere	TT	M	FR	9-11	6-10	S	a	F
	D. tessmannii	bendongere	TT	M	FR	9-11	6-10	S	a	F
	D. sp.	bendongere	TT	M	FR	9-11	6-10	S	a	F
	Detarium macrocarpa	mbili	TT	M	FR	2	1-11	N	t	F
	Gilbertiodendron dewevrei	bemba	TT	G	SD	8-9	1,6-9	C	t	T
					LV	12,2			a	T
	Tessmannia anomala	phaka	TT	M	FR	2	12-1,6-8	C	?	F
	Isoberlinia doka	fofolo	MT	W	LV	2			a/t	O
Chrysobalanaceae	*Parinari excelsa*	bokanja	TT	G&M	FR	12-2	12-1	N	t	F
Commelinaceae	*Palisota ambigua*	njaya	H	G&M	FR	2,4-9	*	S	t	F
					PT	2,4,9				T
	P. hirsuta	mangabo	H	G&M	FR	2,4-9	6	S	t	F
					PT	12-6,8-9				T
	P. thollonii	mangabo	H	G&M	FR	2,4-9	6	S	t	F
					PT	12-6,8-9				F
Ebenaceae	*Diospyros dendo*	mosisi	ST	G	FR	7-9	6-10	S	a/t	FTO
					SD	7-8	6-10	C		FO
	D. piscatoria	babangu	ST	G	FR	8	6-8	S	a/t	FT
					SD	7-8	6-8	C		F
					LV	+				T
	D. crassiflora	lembe	TT	M	FR	+	5-9	?	t	T
	D. suaveolens	koloka	MT	G&M	FR	8-9	6-9	S	t	FT
					SD	8-9	6-9	C		F
Euphorbiaceae	*Drypetes pellegrinii*	tembo	MT	M	FR	4-7	4-6	S	a	FO
	D. cinnabarina	baso	MT	M	FR	6-7	4-9,11	S	?	F
	D. chevalieri	belenge	ST	G&M	FR	8-9	8-10	S	a	F
	Uapaca guineensis	jambala	MT	W	FR	+	*	S	a	O
	U. sp.	jombo	MT	W	FR	+	*	?	?	F
	Macaranga barteri	mosasala	ST	M	LV	10			a	T
	Manniophyton fulvum	kusa	LI	M	PT	1			t	T
					LV	+				T
Fabaceae	*Angylocalyx pynaertii*	yonga/ likumbi	TT	M	FR	2,4	4	S	t	FO
					LV	2-3				O
	Millettia sanagana	ganda	MT	M	LV	9			?	T
Flacourtiaceae	*Caloncoba welwitschii*	sioko	ST	M	FR	7-8	7-8	S	?	F
	C. glauca	sanza	MT	G&M	FR	5-6	3-6,8-9	S	?	F
Gnetaceae	*Gnetum africanum*	koko	LI	M	LV	4			t	T
Guttiferae	*Mammea africana*	mboto	TT	M	FR	1-2,10	1-5,8-11	N	a/t	FT
	Garcinia kola	mokodongo	ST	M	FR	7	8-9	S	a	F
Hydrocharitaceae	*Hydrocharis* sp.	kongoyasika	H	W	RT	12-2,5-11			t	FTO
Irvingiaceae	*Irvingia gabonensis*	payo	TT	G&M	FR	9	4,8-11	N	t	T
	Klainedoxa gabonensis	bokoko	TT	G&M	FR	3-6	12-6,10-11	N	a/t	FTO
Loganiaceae	*Strychnos* sp.	gede	LI	M	FR	4	8	S	a	F
Marantaceae	*Ataenidia conferta*	boboko	H	M	SH	12-1,3,5,9			t	T
	Haumania danckelmaniana	basele	H	M	SH	12-11			t	FT
					SD	6-11	6-10	C		T
	Hypselodelphys poggeana	kokombe	H	M	SH	+			t	T
	Marantochloa congensis?	bili	H	M	PT	6			t	T
	Megaphrynium macrostachyum	ngongo	H	M	FR	+	*	S	t	FT
					SH	9-10				T
					LV	9				T
	Sarcophrynium prionogonium	gowasa	H	M&W	FR	12	9,10	S	t	F

(continued)

Appendix. (continued)

Family	Scientific name	Local name	Life form	Habitat	Part-eaten	Foraging months	Fruiting months	Seed-eating	Foraging position	Methods confirmed
Meliaceae	?	liba	MT	W	FL	2			a	T
	Trichilia heudelotii	toko	TT	M	FL	4			a	T
Menispermaceae	*Triclisia dictyophylla*	molindo	LI	G&M	FR	6-7,10	6-10	S	a	FT
	T. patens	mobangi	LI	G&M	FR	2-4	1,4-5,11	S	a	FT
	T. sp.	molombi	LI	G&M	FR	6-7,10	5	S	a	F
	Dioscoreophyllum cumminsii var. *cumminsii*	mbi	LI	M	FR	12	*	S	t	F
	Tiliacora beguaertii	dombo	LI	G&M	FR	7-8	6-8	S	a	FT
					SD	7-8	6-8	C		F
Mimosaceae	*Tetrapleura tetraptera*	jaga	TT	M	SD	7	*	C	t	FO
Moraceae	*Ficus exasperata*	jolo	LI	G&M	FR	+	*	S	?	O
	F. recurvata	jolo	LI	G&M	FR	1,4	1	S	a/t	O
	F. sp. 2	jolo	LI	M	FR	4	4	S	a/t	O
	F. sp. 3	jolo	LI	M	FR	4	4	S	a	O
	F. sp. 4	jolo	LI	M	FR	5	*	S	t	O
	F. sp. 5	jolo	LI	M	LV	+			t	O
	F. spp.	jolo	LI	M	FR	12-2, 4-5,7	*	S	?	F
	Milicia excelsa (=*Chlorophora excelsa*)	bangi	TT	M	LV	+			a	O
	Treculia africana	fusa	MT	M	FR	4-7	3-7	S	a/t	FT
	Musanga cecropioides	kombo	TT	G&M	FR	+	*	?	?	T
	Myrianthus arboreus	ngata	MT	M	FR	5-8,11	*	S	?	FT
Myristicaceae	*Pycnanthus angolensis*	ntenge	TT	M	LV	12			a	T
	Staudtia stipitata	malanga	TT	G&M	LV	12			?	T
Olacaceae	*Strombosiopsis tetrandra*	bosiko	MT	M	FR	7	5-9	N	a	T
Passifloraceae	*Barteria negritiana*	pbambo	ST	M	FR	7-10	7	S	a	FT
					LV	7				T
Rubiaceae	*Porterandia cladantha*	likoko	MT	M	LV	6			a	T
Sapindaceae	*Chytranthus atroviolaceus*	tokomboli	ST	G&M	SD	8	*	C	t	T
	C. atroviolaceus?	isekeke	ST	M	FR	4-6	4-6	S	t	F
	Pancovia laurentii	goyo	MT	M	FR	2-4	*	S	a	F
	Pancovia?	goyo motani	ST	M	FR	7-8	*	S	t	F
	Allophylus africanus	mapota	ST	W	FR	7-8	*	S	?	F
Sapotaceae	*Gambeya lacourtiana*	bambu	TT	M	FR	4-8	5-9	S	t	F
	Synsepalum longecuneatum	belo	MT	M	FR	4	4	S	a/t	F
	Manilkara letouzei	mbanga	TT	M	FR	4	2-11	N	t	T
Sterculiaceae	*Cola gabonensis*	ngaingai	ST	G&M	FR	7,10	9	S	t	F
	C. nitida?	ligo	MT	M	SD	+	*	C	t	T
	C. rostrata	bombi	ST	M&W	SD	8	8-9	C	t	T
Tiliaceae	*Duboscia macrocarpa*	nguluma	MT	G&M	FR	12-6, 10-11	12-11	S	t	FTO
	Grewia seretii?	patakoli	ST	W	FR	+	*	S	t	F
Tiliaceae	*G. coriacea*	fifi	SH	G	BK	1			t	T
	G. sp.	liamba moke	MT	G&M	FR	4-7	3-6	S	a	F
Ulmaceae	*Celtis adolf-friderici*	kakala	TT	M	FR	1,10	8,11	S	?	F
	C. mildbraedii	ngombe	TT	G&M	LV	12-1			a	FTO
					BK	12-2,4-5				FTO
	C. tessmannii	toko	TT	M	FR	8	3-7	S	?	F
					SD	8	3-7	C		F
Verbenaceae	*Vitex doniana*	folo	MT	M	FR	9-11	7-11	S	t	F
Violaceae	*Rinorea cerasiflora*	mendi/ kombe	SH	G&M	FR	5	3-4,6-7	S	t	F
Vitaceae	*Cissus dinklagei*	bongo/ basapha	LI	G&M	FR	6-10	12-11	S	a	FT
Zingiberaceae	*Aframomum* sp.	tondolo	H	M	FR	12,2-3, 7-11	9	S	t	F
		njii			PT	1-2, 4-7,10				T

(continued)

Appendix. (continued)

Family	Scientific name	Local name	Life form	Habitat	Part-eaten	Foraging months	Fruiting months	Seed-eating	Foraging position	Methods confirmed
	Aframomum citratum	tondolo ya swa	H	W	FR	12,2-3, 7-11	*	S	t	F
		njii ya swa			PT	1-2, 4-7,10				T
	Costus afer	gangalange	H	W	PT	1			t	T
?	?	baso2	MT	M	FR	1-2	*	S	?	F
?	?	bobobo	LI	M&W	LV	1,3			a	T
?	?	bondo	MT	G	FR	12-1	*	S	a	FT
?	?	gama	TT	M	SD	5	5	C	?	F
?	?	ieri	MT	M	FR	6	*	N	t	T
?	?	liamba moke mai	MT	W	FR	8	*	S	?	F
?	?	mbangi	MT	M	FR	5-6	6-7	N	t	FT
?	?	mondonge	MT	M	FR	7	7	S	?	F
?	?	mosasako	SH	M	LV	12			t	T
?	?	timi	?	M	LV	2			?	T
?	?	zila	TT	G&M	LV	1			a	T
FERN	?	lilele	H	G&M	PT	+			a	O
?	?	G1	?	?	FR	12	*	S	?	F
?	?	G2	?	?	FR	12	*	S	?	F
?	?	G3	?	?	FR	3	*	S	?	F
?	?	G4	?	?	FR	4	*	S	?	F
?	?	G5	?	?	FR	4,6	*	S	?	F
?	?	G6	?	?	FR	5	*	S	?	F
?	?	G7	?	?	FR	5,6	*	S	?	F
?	?	G8	?	?	FR	6	*	S	?	F
?	?	G9	?	?	FR	6	*	S	?	F
?	?	G10	?	?	FR	6	*	S	?	F
?	?	G11	?	?	FR	6	*	S	?	F
?	?	G12	?	?	FR	6	*	S	?	F
?	?	G13	?	?	FR	7	*	S	?	F
?	?	G14	?	?	FR	7	*	S	?	F
?	?	G15	?	?	FR	7	*	S	?	F
?	?	G16	?	?	FR	7	*	S	?	F
?	?	G17	?	?	FR	7	*	S	?	F
?	?	G18	?	?	FR	7	*	S	?	F
?	?	G19	?	?	FR	7	*	S	?	F
?	?	G20	?	?	FR	7	*	S	?	F
?	?	G21	?	?	FR	8	*	S	?	F
?	?	G22	?	?	FR	8	*	S	?	F
?	?	G23	?	?	FR	9	*	S	?	F
?	?	G24	?	?	FR	9	*	S	?	F
?	?	G25	?	?	FR	9	*	S	?	F
?	?	G26	?	?	FR	9	*	S	?	F
?	?	G27	?	?	FR	10,11	*	S	?	F
?	?	G28	?	?	FR	11	*	S	?	F
?	?	G29	?	?	FR	+	*	S	?	F
?	?	G30	?	?	FR	+	*	S	?	F
?	?	G31	?	?	FR	7	*	S	?	F

#All plant species presented here were identified by J.-M. MOUTSAMBOTÉ. Life form: ST: Small tree; MT: medium tree; LI: liana (vine); SH: shrub; H: herb; TT: tall tree. Habitat: M: Mixed species forest; G: *Gilbertiodendron dewevrei* forest; W: swamp forest. Part-eaten: LV: Leaves; FR: fruit (pulp); SD: seed; PT: pith; RT: root; BK: bark; SH: shoot; FL: flower. Foraging months: +: Foraging period is beyond this study period. Fruiting months: *: Not confirmed. Seed-eating: S: Swallowing seeds; C: cracking seeds; N: not-swallowing seeds. Foraging position: t: Terrestrial foraging; a: arboreal foraging. Methods confirmed: T: Feeding traces; F: fecal samples; O: direct observation.

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