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RESEARCH ARTICLES

Western Lowland Gorillas (*Gorilla gorilla gorilla*) as Seasonal Frugivores: Use of Variable Resources

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The gorillas studied at Bai Hokou, Central African Republic, between August 1990 and October 1992 consumed 239 kinds of foods from 138 species of plants and invertebrates, including the fruits of 77 species. Seeds were present in 99% of all fecal samples (n = 859). Although gorillas ate fleshy fruit whenever it was available, herbaceous plants and fibrous fruits were consumed year-round and were important during times of fleshy fruit scarcity. At Bai Hokou and across their range, resources are temporally discontinuous, and western gorilla diet exhibits marked seasonal and interannual variation. Although their large body size lends them dietary flexibility relative to chimpanzees, seasonal fruit-eating shapes the foraging and ranging patterns of western lowland gorillas. Am. J. Primatol. 43:87–109, 1997. © 1997 Wiley-Liss, Inc.

Key words: ***Gorilla gorilla gorilla;* feeding ecology; phenology; fruit availability; Bai Hokou, Central African Republic**

INTRODUCTION

More than 12 years of study in lowland rain forests have demonstrated that fruit-eating and tree-climbing are important aspects of lowland gorilla behavior [e.g., Tutin & Fernandez, 1985; Carroll, 1988, 1996; Fay, 1989; Williamson et al., 1990; Mitani, 1992; Remis, 1994, 1995; Yamagiwa et al., 1994; Nishihara, 1995]. In fact, despite their large size and the widespread correlations between body size and diet [e.g., Clutton-Brock & Harvey, 1977a,b; Salier et al., 1985], western lowland gorillas are quite distinct from the terrestrial and herbivorous mountain gorillas living in montane forests [Tutin and Fernandez, 1993a; Remis, 1994; Nishihara, 1995]. For even the largest of living primates, habitat appears to have a significant influence on dietary patterns.

Prior to work on gorillas at Lopé, Gabon, all studies of gorillas had been conducted in environments marked by a scarcity of fruit and low overall species diversity in disturbed forests [Jones & Sabater-Pi, 1971; Calvert, 1985a,b] or montane forest [Casimir, 1975; Fossey & Harcourt, 1977; Goodall, 1977; Vedder, 1984; Watts, 1984]. Throughout their range, gorillas consume large amounts of herbaceous vegetation [e.g., Schaller, 1963; Watts, 1984]. However, in mature

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lowland forests gorilla diet is more diverse and variable between seasons and years, reflecting a higher diversity and more variable distribution of foods, particularly fruit, than in disturbed or montane forests.

In particular, gorilla diet contains fruit and insects in quantity whenever possible, and strict folivory prevails only when there is no alternative [e.g., Watts, 1984, 1990; Tutin & Fernandez, 1985, 1992; Williamson et al., 1990; Nishihara & Kuroda, 1991; Yamagiwa et al., 1994; Nishihara, 1995].

Western gorillas exhibit substantial dietary overlap with sympatric chimpanzees, and niche separation becomes apparent only in periods of fruit scarcity [Tutin et al., 1991; Remis, personal observation]. At this time, gorillas exploit fruits and other foods relatively high in fiber, condensed tannins, and phenols, while chimpanzees continue to consume fleshy fruits and appear to minimize their fiber and tannin intake [Rogers et al., 1990; Tutin et al., 1991; Kuroda, 1992; Suzuki & Nishihara, 1992; Leighton, 1993; Tutin & Fernandez, 1993a; Wrangham et al., 1993; Remis, 1994; Nishihara, 1995]. As a result of their dietary flexibility, lowland gorillas recently have been argued to be more opportunistic, less selective, and less persistent fruit foragers than chimpanzees [Kuroda et al., 1996; Yamagiwa et al., 1996].

Chimpanzees and western lowland gorillas are similar in craniodental morphology [Shea, 1983a,b, 1985; Uchida, 1992, 1995] and in the morphology and relative surface area of the gut [Chivers & Hladik, 1980]. Nevertheless, gorillas have relatively larger colons with more cellulose-digesting ciliates [File et al., 1976; Collet et al., 1984] and slightly slower gut passage rates than chimpanzees [Milton, 1984]. Additionally, mountain gorillas have more highly crested molar surfaces than lowland gorillas or chimpanzees [Uchida, 1992]. These features, as well as their absolutely large size, presumably allow gorillas to tolerate high levels of fiber, total phenols, and condensed tannins in their foods [Waterman et al., 1983; Wrangham & Waterman, 1983; Calvert, 1985b; Rogers et al., 1990].

This paper documents the diet of the gorillas at Bai Hokou, Central African Republic, between 1990 and 1992 and examines seasonal and interannual fluctuations in food availability and consumption. Sex- or size-related differences in fruit and fiber intake are considered, and gorilla foraging is compared to that of other populations and species of great apes. I will demonstrate that gorillas consume succulent fruit in large quantities whenever possible. When fleshy fruit becomes scarce, gorillas switch to fibrous foods. Despite the dietary flexibility conferred upon them by their large size, it is clear that the foraging and ranging patterns of the Bai Hokou gorillas are shaped by their preference for fruit.

METHODS

Study Site

This study took place at the 40 km^2 Bai Hokou study site, Dzanga-Ndoki National Park, Dzanga-Sangha Reserve, Central African Republic (2°50’N, 16°28’E). Bai Hokou is situated within a semideciduous rain forest with marked seasonal variation in rainfall (463 m in altitude). Rainfall and minimum and maximum temperatures were measured daily in a clearing at base camp at 6:00 AM. Average rainfall in the region is approximately 1,400 mm per year (Slovenia-Bois logging company records taken 30 km away in Bayanga at approximately 410m altitude) (Fig. 3). Typically, fewer than 100 mm of rain falls during the dry season, January–March. Prior to 1982, parts of the study area were selectively logged at low intensity for species not known to be consumed by the gorillas (one to two stems per hectare of *Entandrophragma utile* and *E. cylindricum* were removed). Incidental damage to the forest has been described as minimal but includes the construction of principal roads at intervals of up to 1–2 km, secondary roads at 500 m intervals, and skidder paths at 250 m intervals. Differences between logged and unlogged forest in density (unlogged forest = 516.2 trees per hectare; logged forest = 505.1 trees per hectare) and abundance of species are few [Carroll, 1996, unpublished report].

Study Subjects

Data were collected from at least three groups of gorillas and four lone males. Most observations centered on a single focal group that varied in composition but typically contained 13 weaned individuals, including two silverbacks, two blackbacks, and five adult females. Observational data were collected on undisturbed, semihabituated focal animals [Tutin and Fernandez, 1991], often when the gorillas were unaware of the presence of the observer. Animals that were feeding in the trees would often tolerate our presence. However, because of problems with habituation and low visibility in the dense forest, the data are biased towards arboreal sightings, and it was not always possible to identify individuals. When the gorillas were on the ground, they did not typically allow us to follow them or collect data from distances of less than 30 m. When animals were feeding in trees, the visibility of group members on the ground was low. No discernible sex differences in habituation were noted, but females may have been less visible than males. An effort was made to equalize samples of males and females. Focal males or females were selected randomly from among those visible. Animals were more difficult to locate in the dry season when their movements left little trace in the forest. In particular, small sample sizes in the dry season may affect the data presented here.

Determining Diet

Diet was determined by a combination of direct observations during focal animal samples [Altmann, 1974] and indirect means (i.e., trail remains and fecal analysis) [Moreno-Black, 1978]. Observational samples taken at 5 min intervals were analyzed. Gorilla plant foods were collected using local Aka species names and tentatively assigned to Latin species or genera pending confirmation by Missouri Botanical and Kew Gardens.

Methods used in the collection and analysis of fecal samples follow those described by Tutin and Fernandez [1985, 1993c]. Fresh feces known to be deposited by gorillas were collected at nest sites and opportunistically during contacts with gorillas. Only one sample was collected from each nest site or individual contact. Samples were washed and sieved through a 1 mm mesh screen. The remaining seeds and vegetative fiber were dried and analyzed in the field on a monthly basis. Most fruit seeds passed through the digestive tract intact and were readily identified with reference to a sample collection maintained at camp. Numbers of seeds of each species present were counted, or estimated if the seeds were very small.

Fibrous remains of herbaceous stems and woody vines could be readily distinguished from the undigested remains of leaves of woody plants, although leaf fragments were often difficult to identify. In this analysis, fiber and leaf components (GLF) were scored separately by their abundance (absent, rare, few, common, abundant) on a 0–4 scale [Tutin & Fernandez, 1993c]. These scores were combined to give a total fiber score (0–8). In some cases large fiber and leaf remains of common species could be attributed to a particular taxon. Insects were also identified from undigested chitinous body parts and scored as present or absent.

Availability of Tree Foods and Herbs

During Carroll's 1986–1989 study of the gorillas at Bai Hokou, 19 km of north–south trails were cut along compass bearings at 250 m intervals [Carroll, 1996]. The trails run perpendicular to the drainage system and cut through a variety of habitat types, including logged and unlogged forest. Trees greater than 10 cm dbh that fell within 5 m of the trails were marked with aluminum tags [see also Carroll, 1996]. In addition, a few individuals that were rare but important gorilla food species yet fell more than 5 m from the trails were included [see also Carroll, 1996]. A total of 973 trees of 152 species were monitored monthly for leaf, flower, and fruit production from March 1990–October 1992 [Remis, 1994]. The number of individuals of each species represented varies widely (1–28). Some small or rare gorilla food species are underrepresented or absent on the phenology trails.

Statistical Analyses

Nonparametric methods that minimize reliance on assumptions about the data set are used to analyze observational and fecal data for seasonal and size-related differences in diet. Observational data are compared using G tests of independence of r × c contingency tables corrected by the Williams correction factor [Sokal & Rohlf, 1981]. Seasonal variation in diet as measured by fecal analysis (mean monthly scores of fiber and numbers of fruit species consumed) is analyzed with Kruskal-Wallis one-way analysis of variance by rank tests. Mann-Whitney tests are used to examine differences between male and female fecal samples. Spearman rank tests are used to analyze the relationships among temperature, rainfall, food availability, and diet [Siegal & Castellan, 1988].

RESULTS

Diet

From information collected from a combination of direct observations, trail remains, and fecal analysis, the gorillas at Bai Hokou ate 230 kinds of plant foods from 129 plant species and nine invertebrate species during this study, including fruits of 77 species, leaves of 70 woody species, flowers of four species, and leaves and stems of 14 species of herbs and understory plants. Although herbaceous stems, leaves from understory plants, and fallen fruits were eaten on the ground, observational and trail data indicate that 79% of the plant foods were typically eaten in the trees. Dirt from termite mounds and salines and rocks from stream beds were swallowed.

Observational data. The composition of the gorillas' diet from 826 1 min samples of feeding or foraging by all age and sex classes was as follows: 51% fruit, 26% leaves, 12% bark and cambium or phloem of trees and lianas, and 10% herbs. These data probably underrepresent the importance of herbs, understory plants, fallen fruits, and other terrestrial foods because observational sampling was biased toward arboreal sightings [also see Remis, 1995]. For example, although trail evidence indicates that gorillas probably consumed fallen fruit fairly frequently, they were observed eating fallen fruit only twice during observational samples. Diet differed between seasons (two-tailed G tests of independence on r × c contingency tables: adult females (G (w) = 29.2, $P < .001$, df = 3; adult males G (w) = 49.2, $P < .001$, df = 3) and between males and females in both seasons (wet season G (w) = 7.4, $P < .01$; dry season G (w) = 15.8, $P < .001$) (Table I). [In the wet seasons, females ate more leaves, especially young leaves, than males, who were recorded more frequently eating fruit. In the dry seasons, gorillas ate more bark and inner piths of lianas and less fruit, and males ate more bark than females. Although termites were observed being eaten only once, termite feeding sites were common on most feeding trials and in fecal samples. In addition, males ate more foods terrestrially than females (sex differences in terrestrial feeding records at 5 min intervals (G (w) = 9.0, $P < .005$).

Fecal analysis. A total of 859 fecal samples were collected and analyzed at the field station between August 1990 and October 1992. The numbers of feces examined varied between months (mean = 35, range = 3–102, st. dev. = 28.9) and years (mean = 281, range = 79–505, st. dev. = 213.9). The number of samples collected each month is correlated with the number of days sampled monthly (r = .8454, $P = .000$, n = 27 months), but neither the number of samples nor the number of days sampled per month is correlated with season (number of samples r = .0341, $P = .866$; number of days sampled r = .1408, $P = .484$). Therefore, the monthly differences in sample size are unlikely to have affected the seasonal comparisons reported here.

A subset of fecal samples could be attributed to adult males (n = 279) or females (n = 345) on the basis of size and/or association with nests which contained infants [Schaller, 1963; Tutin & Fernandez, 1993c]. Some fecal samples belonging to female-sized subadult males were likely classed in the female size category. Fruit from both terrestrial and arboreal sources was presented in 99% of fecal samples (n = 859). Insects were present in 73% of samples, primarily *Cubitermes sp.* Fibers of herbaceous plants, especially *Aframomum sp.* and *Haumania sp.* were present in 97% of samples. Leaves of woody species were found in 91% of samples, and woody vines or bark were present in 55% of samples.

Consumption of fruit. In the wet seasons, fruit was present in almost every sample (>99%). In the 1992 dry season, when rainfall was particularly low, remains of fruit occurred in only 60% of samples. The number of fruit species consumed per month varied among months, seasons, and years (5–28) but averaged 13 and was positively correlated with rainfall (Spearman rank r = .56, $P < .01$) and negatively but insignificantly correlated with fiber consumption (Spearman rank r = –.223, m = 25 months) (Fig. 1). In general, the mean number

TABLE I. Diet During Observational Samples: Proportion of Foods Consumed During Feeding Bouts*

Food type	Males, wet season n = 101 (29 visits)	Females, wet season, n = 47 (25 visits)	Males, dry season, n = 11 (4 visits)	Females, dry season n = 19 (8 visits)
Fruit	65	41	0	5
Leaves	20	40	0	58
Herbs	13	13	27	0
Bark/vine	0	0	73	37
Insect	2	0	0	0

*n = number of 5 min observational samples of focal animals (juveniles excluded). Numbers of visits to feeding sites (trees or terrestrial food patches recorded once each) are noted in parentheses. G tests (two-tailed) performed on r × c contingency tables of one minute samples: males vs. females, wet season, G (w) = 7.4, $P < .01$, df = 3; males vs. females, dry season G (w) = 15.8, $P < .001$, df = 3; males, wet vs. dry seasons, G (w) = 49.3, $P < .001$, df = 3; females wet vs. dry season, G (w) = 29.2, $P < .001$, df = 3.

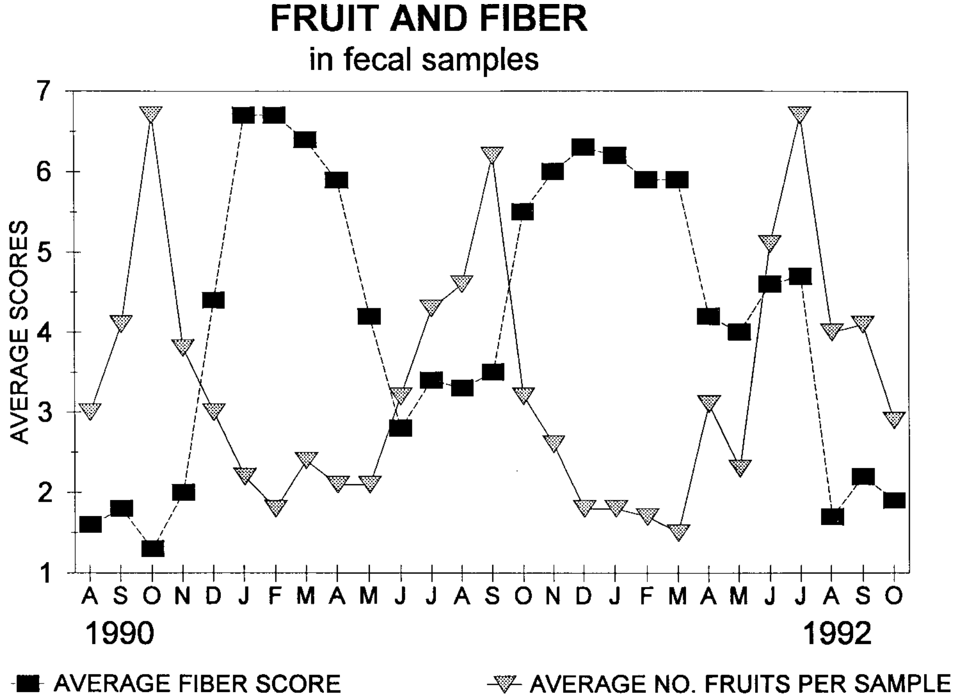

Fig. 1. Abundance of fruit and fiber in fecal samples. Variation in the relative abundance of fiber (mean monthly fiber score) and the numbers of fruits found in each fecal sample (mean monthly numbers of fruit species per sample) are compared over the 27 month study period, 1990–1992.

of fruit species eaten seasonally and per month did not differ significantly between the sexes (Mann-Whitney U = 50,281, $P = .231$, n = 621 samples). On average, 3.2 fruit species were present in each fecal sample (range = 1–12). More species of fruits were eaten (monthly and seasonally per sample) during the wet seasons, and interannual variation was great (mean numbers of fruits eaten per sample by season and year, Kruskal-Wallis analysis of variance U = 115.7, $P = 0.00$) (Table II). The mean monthly number of fruits per sample was inversely correlated with measures of fiber abundance (n = 25 months, Spearman rank r = –.577, $P < .005$) (Fig. 1).

Although consumption of fleshy fruits such as *Anonidium manii, Gambeya africanum,* and *Celtis adolfi-friderici* decreased in the dry seasons, gorillas continued to eat fruits, especially the fibrous *Duboscia macrocarpa* and *Klainedoxa gabonensis.* The diversity of fruits consumed was higher in the poor fruit year, when favored fruit species, such as *Dialium sp.* or *Landolphia sp.,* failed to produce large crops. The number of fruit species per sample varied by sex or size in the poor fruit season of 1991 when females or smaller animals consumed more fruit per sample than males or larger animals (sex difference in the monthly mean number of fruits per sample; Mann-Whitney U = 11,586, $P < .04$, n = 285 samples).

The 24 most prominent fruit species in fecal samples (those which occurred in more than 1% of fecal samples during the entire study period) varied in dietary importance within and between years (Table III). The fibrous fruit of *Duboscia macrocarpa* was present in 73% of samples. When present at all, it was often found in almost all samples each month. *Duboscia* is a common middle

TABLE II. Seasonal and Sex Differences in Diet as Measured by Fecal Analysis, 1990–1992*

	Number of fruit species per sample		Herb score		Leaf score	
Season	Males	Females	Males	Females	Males	Females
Wet '90						
Males, n = 28	3.9	3.7	1.5	1.3	1.3	.1
Females, n = 42	(1–8)	(1–7)	(1–4)	(0–4)	(0–4)	(0–4)
Dry '91						
Males, n = 27	2.1	2.6	3.2	3.3	3.5	3.1
Females, n = 28	(1–5)	(1–5)	(0–4)	(0–4)	(0–4	(0–4)
Wet '91						
Males, n = 146	3.2	3.6	2.7	2.4	2.5	2.2
Females, n = 139	(1–9)	(1–9)	(1–4)	(0–4)	(0–4)	(0–4)
Dry '92						
Males, n = 38	1.8	1.7	3.6	3.5	2.7	2.6
Females, n = 53	(1–4)	(1–3)	(2–4)	(1–4)	(0–4)	(0–4)
Wet '92						
Males, n = 39	3.8	3.2	2.1	2	1.6	1.6
Females, n = 81	(1–8)	(1–7)	(0–4)	(0–4)	(0–3)	(0–4)

*Mean scores and range (in parentheses) are reported for 624 adult-sized fecal samples

TABLE III. Changing Representation of Fruits in Gorilla Diet: Percent Occurrence of Important Fruits in Fecal Samples*

Species	Growth form	Wet '90 (79)	Dry '91 (76)	Wet '91 (427)	Dry '92 (124)	Wet '92 (152)
Duboscia macrocarpa	T	56	95	78	94	38
Aframomum sp.	H	56	22	19	2	18
Vitex sp.	T	29	0	25	0	1
Haumania danckelmaniana	H	51	0	17	0	14
Tetrapleura teraptera	T	39	0	16	0	0
Zhana golungensis	T	0	0	19	2	21
Celtis sp.	T	0	0	13	0	28
Gambeya lacourtiana	T	0	0	17	1	11
Polyalthia suaveoleons	T	20	0	12	0	15
Xylopia sp.	T	1	14	15	1	1
Klainedoxa gabonensis	T	1	1	2	6	39
Anonidium manii	T	24	1	10	0	3
Ficus sp.	T	3	19	6	3	13
Tabernaemontana sp.	T	0	0	15	0	2
Treculia africana	T	0	0	6	0	24
Pterocarpus soyauxii	T	4	0	10	0	9
Myrianthus arboreus	T	0	0	10	0	5
Landolphia sp.	T	1	0	0	0	27
Desplatsia deweverei	T	10	11	3	3	2
Synsepalum stipulatum	T	0	0	5	0	7
Hexalobus sp.	T	20	1	2	0	0
Donella ubanguiensis	T	0	0	2	0	9
XX Lamba (Aka name)	T	0	0	5	0	0
Gambeya cf, boukokoensis	T	0	0	3	0	1

*Species represented are the top 24 gorilla fruit species, each present in >1% of all fecal samples (n = 859). They are listed in rank order of importance over the entire study period. Growth form: H, herb; T, tree. The number of fecal samples is given in parenthesis.

canopy tree species, generally available and consumed by the gorillas year-round. It is as much a staple of the diet as herbaceous stems of *Aframomum sp.* and *Haumania sp.* However, consumption of *Duboscia* drops off when favored fleshy fruits, such as the water-vines *Landolphia sp.,* are abundant.

Consumption of fiber and other foods. Herbaceous stems, especially *Aframomum* and *Haumania,* were the most commonly recorded food items in fecal samples (97%). The amount of fiber and leaves in the diet, represented by the total fiber score (stem/herb score + leaf score) varied monthly, seasonally, and between years (seasonal and yearly variation, Kruskal-Wallis statistic = 231.3, $P = .00$, n = 615 samples) (Fig. 1). Nonfruit foods were more abundant in fecal samples during the drier months (especially January–March) and much less abundant during the wettest months (mean total fiber scores for wet seasons: 1990 = 2.5, 1991 = 4.7, 1992 = 3.5; for dry seasons: 1991 = 6.5, 1992 = 6.1; range = 0–7). Consumption of fleshy fruits decreased in the dry season, but gorillas continued to exploit arboreal foods. In the dry seasons, the diversity of nonfruit foods increased. Leaves were more abundant in fecal samples in the dry seasons (seasonal differences in the mean seasonal leaf scores; Kruskal-Wallis U = 171.2, $P = .00$, df = 4, n = 618 samples) (Table II), and a higher proportion contained bark of lianas and trees. During the dry season, gorillas frequently consumed the juicy inner piths of liana species that people use as sources of drinking water. Herbs and leaves were more abundant in the fecal samples of adult males than those of females or smaller animals (Mann-Whitney test on herb score U = 41,741.5, *P* < .01, and leaf (woody) score U = 37,238.5, *P* = .000, n = 618 samples) (Table II). A sex difference in fiber consumption was evident, with males consuming more fibrous foods, particularly leaves, than females (Fig. 2) (Mann Whitney (wet seasons combined) U = 20,902, *P* = .00, n = 470 samples; dry seasons Mann Whitney U = 2,958.5, *P* < .15, n = 145 samples). In the dry season of 1992, rain was particularly scarce, and many trees failed to flush. During this period, leaf consumption and sex- or size-related differences in leaf consumption were reduced (Mann Whitney U = 934, ns, n = 91 samples). Size-related differences in herb consumption were highest during the poor fruit wet season in 1991 (Mann-Whitney U = 8,316, *P* < .01, n = 283 samples).

Invertebrates, particularly *Cubitermes sp.,* were consumed in all months. Monthly variation in consumption of invertebrates was limited and was not correlated with rainfall (Spearman rank r = .171, n = 25 months) or shifts in plant food representation in the diet (e.g., fiber consumption r = .274, mean number of fruit species per fecal sample r = –045).

Impact of gorilla foraging on their resources. Gorilla foraging has been said to increase the density and quality of their herbaceous resources [Bullock, 1981; Watts, 1987]. It can also diminish the crowns of trees [Williamson et al., 1990], modifying tree structure [e.g., Oppenheimer and Lang, 1969] and making future terminal branch foods more accessible from the bole of the tree [Remis, 1995]. The weight of silverbacks swaying in small saplings often destroys them by pulling the crowns (*Diospyros sp.* at Lopé, *Tabernaemontana sp., Duboscia,*

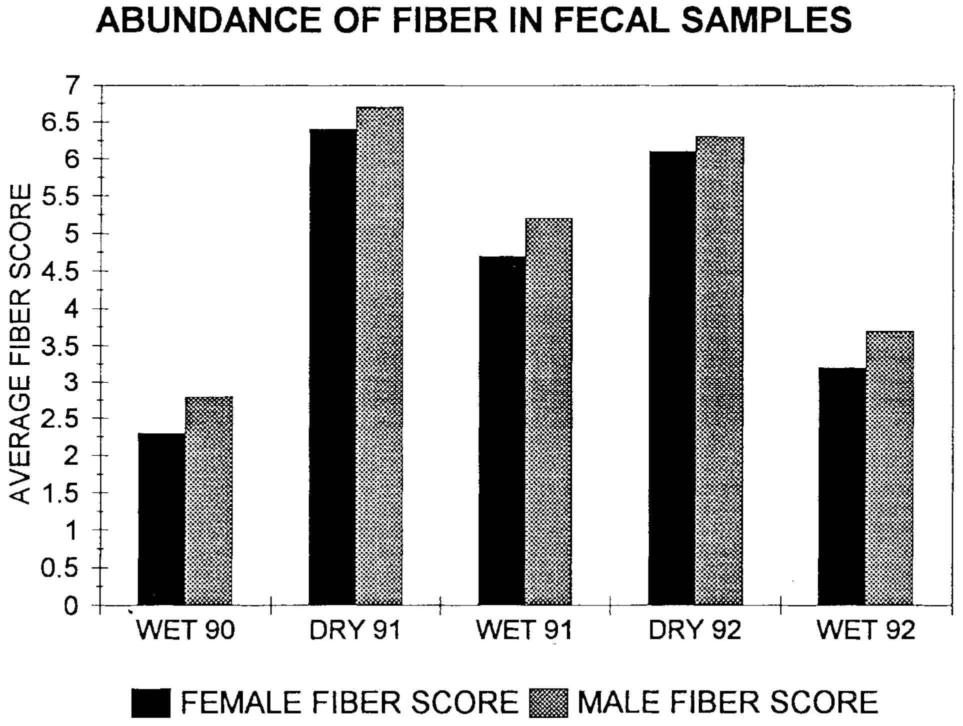

Fig. 2. Seasonal abundance of fiber in fecal samples. This figure depicts seasonal variation in sex differences in the total fiber scores (herb scores and leaf scores combined) for fecal samples, 1990–1992.

and *Akpa* at Bai Hokou) to the ground. When the animal descends, the trees collapse as they snap at the base. On one short stretch of feeding trail a group of gorillas left 15 *Tabernaemontana sp.* trees (10–20 cm dbh) like kindling in their wake [Remis, 1994].

Larger trees often have many of their branches broken off and stripped of bark and/or leaves. Gorillas "pruned" as much as 40% of *Dialium sp.* and *Celtis sp.* crowns while reaching for numerous small terminal branch fruits. Sites of previous gorilla "gardening" were easily detectable throughout the forest, as there were gaps in the crowns of large trees, marked by stubs of branches broken at forks or dangling by a few fibers. Is this, in reality, resource husbandry or resource destruction? Foraging by monkeys on leaf buds has been linked to the subsequent deaths of favored trees or even local extinctions of species [Struhsaker, 1975; Hasegawa, personal communication]. The long-term effects of gorilla actions on tree productivity are not known, although trees heavily damaged during the study did not fruit in subsequent years.

Seasonality of Resources

Bai Hokou received 1,401 mm of rain in 1991 and 1,374 mm of rain from January through October 1992. This is similar to the mean for 10 years at Bayanga. Mean monthly maximum temperature varied between 26°C and 31°C. The mean monthly minimum temperature varied between 18°C and 21°C. The climate is characterized by a dry season, with rainfall typically less than 100 mm over the 3 month dry season from January–March (Fig. 3) and hot days and cool nights. The length and intensity of the dry season vary among years. For example, the 1992 dry season began early, and little rain fell (12/01/91–2/28/92 = 17 mm). In contrast, in the dry season of 1991, mean maximum and minimum temperatures did not diverge as much as usual. Temperatures may have not fallen to their lowest point (at or below 19°C) for a long enough point to trigger flower initiation [Corlett, 1990; Tutin & Fernandez, 1993b; Tutin et al., 1997].

Peaks in new leaf production coincided with the onset of the first rains in March, but fewer trees flushed after the particularly long dry season in 1992 (monthly proportion of trees with new leaves ranged from 1–36%; March 1991 = 36%, March 1992 = 3%). Leaf flush was correlated with maximum mean monthly temperature (Spearman rank n = 25, r = .412, $P < .05$) but not with mean monthly minimum temperature (Spearman rank r = –.157). When trees were not in maximum flush, typically over 90% contained mature leaves.

Flowering peaked in the late dry season, showing a negative correlation with rainfall (r = –.496, $P < .001$). The proportion of individuals bearing flowers in any 1 month during this study ranged from 1–12%, and the proportion of species bearing flowers ranged from 1–33%. In 1991, at peak flowering in March, only 6% of individual trees (18% of species) were flowering, contrasting with 11% (27% of species) in 1990 and 9% (33% of species) in 1992. In this study, flowering was correlated with mean maximum temperature (Spearman rank r = .677, n = 25, $P < .01$) but not with mean minimum temperature (Spearman rank r = .07).

The proportion of species bearing ripe or unripe fruit ranged from 4–71%. The proportion of individuals bearing fruit was 1–24% (Fig. 4). Fruit production of conspecifics was often highly synchronized. Although particular species did not fruit each year, many did fruit reliably at the same time each year. Fruiting peaked during the middle of the rainy season, in July–September of all years (Spearman rank, number of species fruiting and rainfall r = .465; proportion of individuals fruiting and rainfall r = .514, n = 25, $P < .01$). Fruit production was

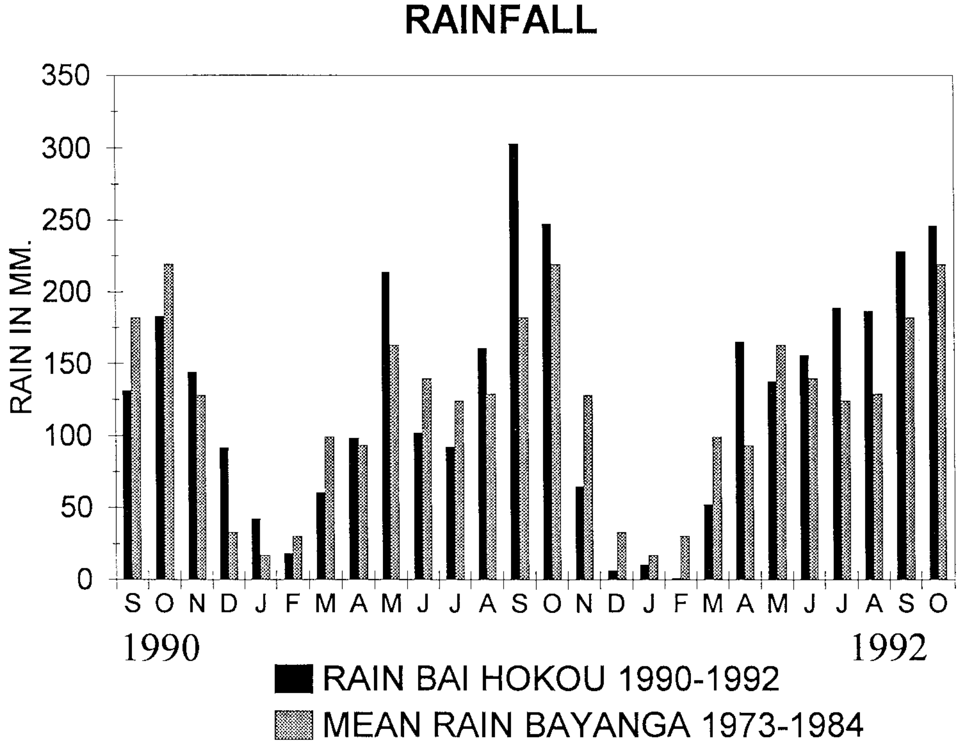

Fig. 3. Rainfall at Bai Hokou, 1990–1992. The monthly rainfall at Bai Hokou, 1990–1992, is compared with the mean monthly rainfall at Bayanga over a 10 year period.

lowest during the dry season, January–March, but intraannual variation was great (fruit production and season, Spearman rank r = .465, n = 25, $P < .01$). For example, fruit production was very low during the wet season of 1991 (Fig. 5).

Variability in availability of important gorilla foods. The availability of fruits eaten by the gorillas varied seasonally among years and through space. Three patterns of fruit species consumption and availability were provisionally identified during this study as measured by the proportion of individual trees fruiting and the proportion of fecal samples containing seeds. What follows are examples of 1) asynchronous fruits, 2) synchronized fruits that may have superannual cycles of production, and 3) fruits that occurred synchronously in each year during the study. *Duboscia macrocarpa* produces a very fibrous fruit and was asynchronous in its production; some fruiting individuals could always be found in the forest (Fig. 6). *Duboscia macrocarpa* was an important fallback food for the gorillas. It was consumed during dry seasons and in all months during the poor fruiting year, 1991. However, when fleshy fruits were abundant during the wet seasons of 1990 and 1992, the gorillas ignored *Duboscia.*

Other foods were more synchronized in their fruiting patterns, although some did not appear to fruit or produce large crops every year. For example, *Dialium sp.* fruit was an important gorilla food in 1988 [Carroll, 1996; personal observation] but occurred in only three fecal samples during this study. *Dialium sp.* are produced on biannual cycles at best [Malenky, 1990; Kano, 1992; Tutin & Fernandez, 1993b; this study], and fruit production is often very localized within the forest (Fig. 7). In 1990 and 1991, very few *Dialium* in the forest produced

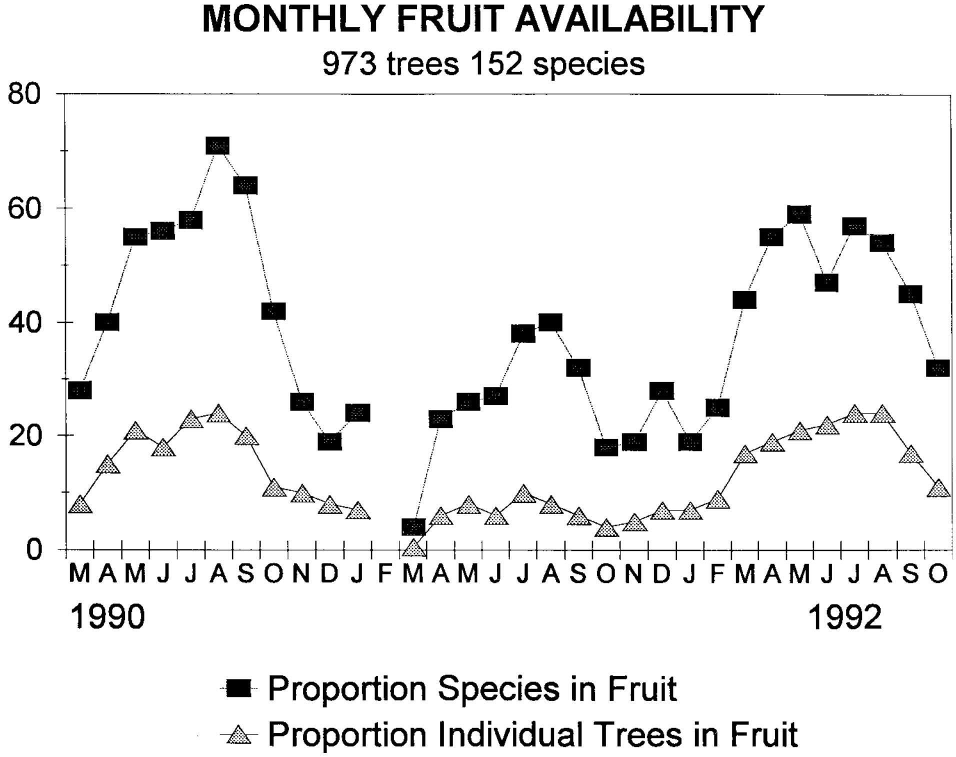

Fig. 4. Monthly fruit availability. Numbers of individuals and species producing fruit, March 1990–October 1992.

abundant crops. In 1992, most of the *Dialium* put out large crops, but consumption may have been delayed by the gorillas' concentration on abundant *Landolphia sp.* liana fruit (another fruit with apparently supraannual fruiting) which ripened just prior to the *Dialium.* At the end of the study period, *Landolphia* fruits were diminishing, and the gorillas were just beginning to eat *Dialium.*

The third pattern observed was tree species that produced fruit synchronously in most years. *Polyalthia suavalens* (Motunga) fruit, was available for a few months in the middle of the wet season each year. When it was available, *Polyalthia* appeared in a large proportion of gorilla fecal samples (Fig. 8). Other species, such as *Pterogata soyauxi* (Embema), *Gambeya lacourtiana* (Mobambu), and *Celtis sp.* (Kakala), fruited each year, but individual trees fruited in alternate years (Fig. 9).

DISCUSSION

Gorillas at Bai Hokou, like those at Lopé, Gabon, and Nouabalé-Ndoki, Congo, have as diverse a diet as that of chimpanzees and consume at least as many kinds of fruit as chimpanzee populations studied for comparable periods of time [Williamson et al., 1990; Remis, 1994; Nishihara, 1995; Carroll, 1996]. The composition of the diet of gorillas reflects the diversity of foods in their habitats, with the diets of eastern lowland gorillas at low altitudes being intermediate between those of western lowland and higher altitude populations [Yamagiwa et al., 1994] (Tables IV, V).

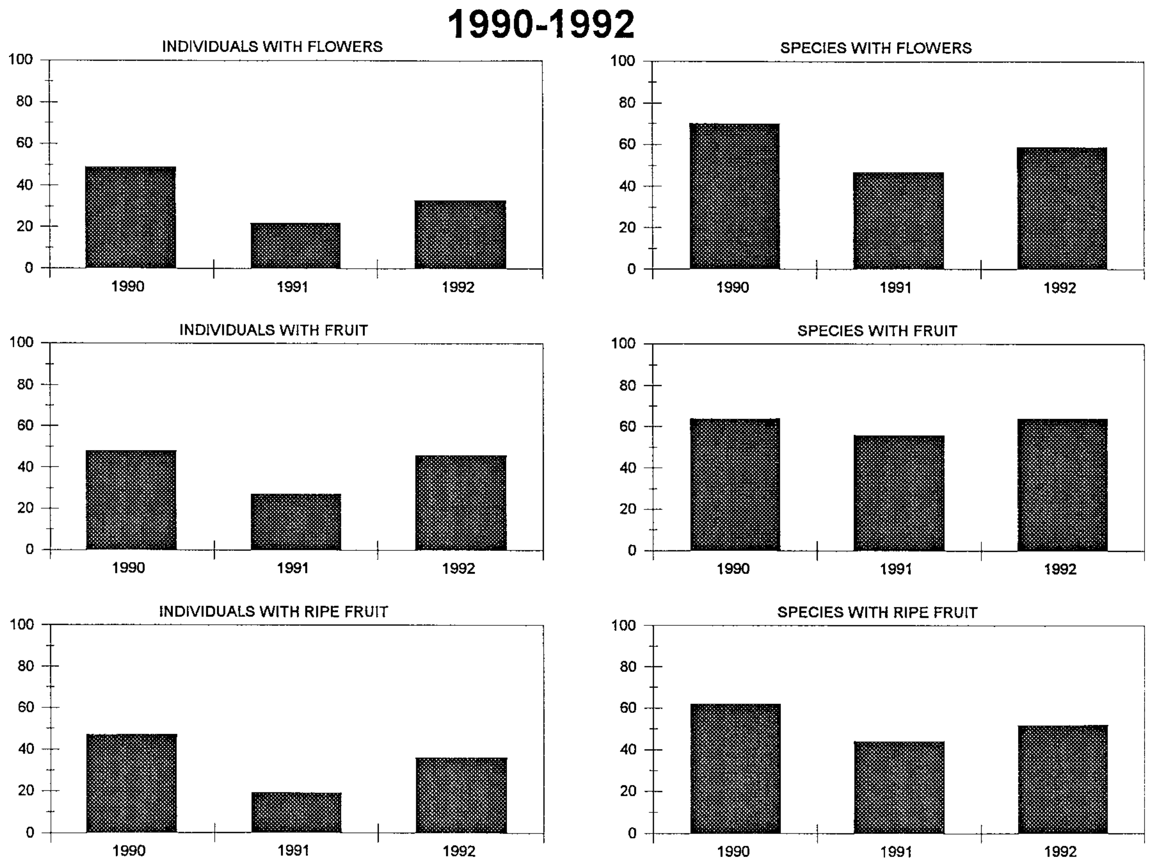

Fig. 5. Interannual variation in fruit production. This figure documents interannual variation in flower, fruit, and ripe fruit production, 1990–1992.

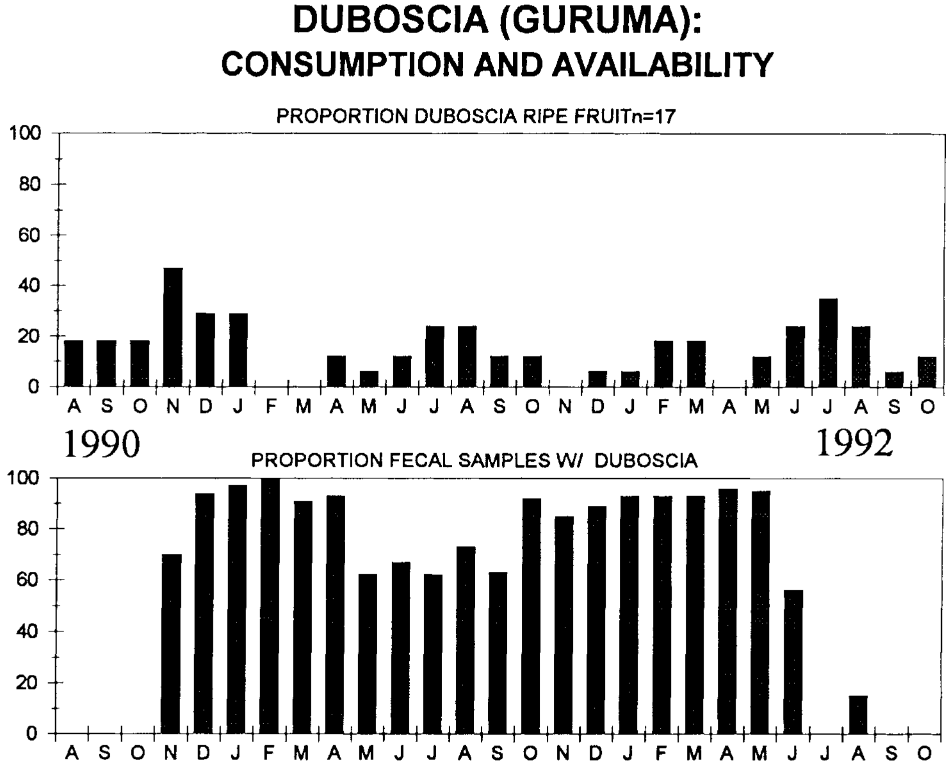

Fig. 6. *Duboscia* availability and consumption. Monthly variation in the proportion of fecal samples to contain *Duboscia* is compared with the proportion of *Duboscia* trees in fruit on phenology trails, 1990–1992.

There is great similarity in broad measures of climate, habitat, and diet between the western lowland gorillas at Bai Hokou, Lopé, and Nouabalé-Ndoki, Congo. Each site receives 1,400–1,500 mm of rainfall annually and is characterized by a single 3 month dry season. Fruit remains were found in 99% of fecal samples at Bai Hokou (n = 863) and 96% of fecal samples at Lopé (n = 4,301 [Tutin et al., 1991]. The mean number of fruits recorded per sample was 3.2 at Bai Hokou and 3.0 at Lopé. Fiber of herbaceous stems, shrubs, and vines and leaves of woody species were consumed year-round but were most abundant in the dry season, when fleshy fruits were scarce. The diet of gorillas at Bai Hokou, Nouabalé-Ndoki, and Lopé diversified in the dry season, when gorillas consumed more species of leaves [Williamson et al., 1990; Nishihara, 1995]. During the dry season at Bai Hokou, the numbers of species of fruits per fecal sample decreased and the kinds of fruit eaten shifted. Invertebrate remains were found in at least 30% of gorilla fecal samples across lowland habitats [Tutin et al., 1991; Nishihara, 1995; Carroll, 1996].

Observational data and fecal analysis show differences in the diets of males and females at Bai Hokou, but the results from these two methods were in conflict. The two data sets sample the feeding regime of the gorillas in different ways, and it is possible that both data sets are saying something real. During this study, males spent more time eating overall [Remis, 1995] and may, in fact, have consumed both more fruit and relatively more fiber than females. Nevertheless, seasonal and between year variation in sex differences are pronounced, and these remain to be fully explored [Remis, in preparation].

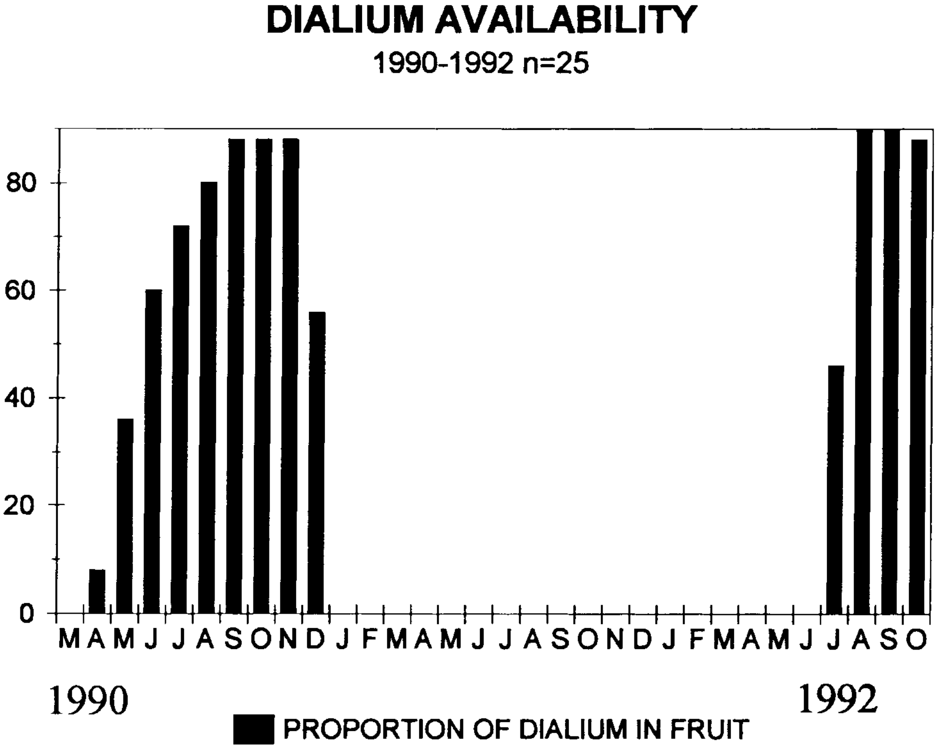

Fig. 7. *Dialium* availability. Monthly variation in the proportion of *Dialium* trees in fruit on phenology trails, 1990–1992. *Dialium* appeared in only three fecal samples during this study period.

Resources at Bai Hokou and Lopé are marked by great intraannual variation. In addition, there is marked variation among years in availability and consumption of wet season foods. In particular, during this study and at Lopé, fruit resources exhibit several patterns of availability; species but not all individuals of each species may fruit synchronously on yearly, biennial, or supraannual cycles [Tutin & Fernandez, 1993b; Remis, 1994]. Gorillas, like other frugivorous primates [Galdikas, 1988; Chapman & Chapman, 1990], adjust their behavior accordingly. Consumption tracks availability, as signaled on phenology trails, of some apparently favored fruits but not others. In fact, certain favored foods are consumed even when their availability was not signaled on phenology trails, while those apparently less favored fruits are sometimes ignored despite their presence.

It has been suggested that flower initiation of some tropical trees is dependent on a critical minimum temperature [Corlett, 1990; Tutin & Fernandez, 1993b], and at Bai Hokou as at Lopé, poor fruit years, small fruit crops, and failures of certain species to fruit were associated with high mean minimum temperatures during the dry season [Remis, 1994; Tutin & Fernandez, 1993b]. At both Bai Hokou and Lopé, during periods of fruit scarcity in the dry season and in poor fruit years, gorillas, like orangutans and chimpanzees, fed heavily on fallback foods: leaves and bark of certain lianas and tree species, the pith and young leaves of sedges, and fibrous fruit [Nishida, 1976; Galdikas, 1988; Rodman, 1988; Tutin et al., 1991; Doran, 1997].

Western lowland gorillas prefer to eat fruit and modify their foraging, ranging, and perhaps grouping patterns to take advantage of ripe fruit resources

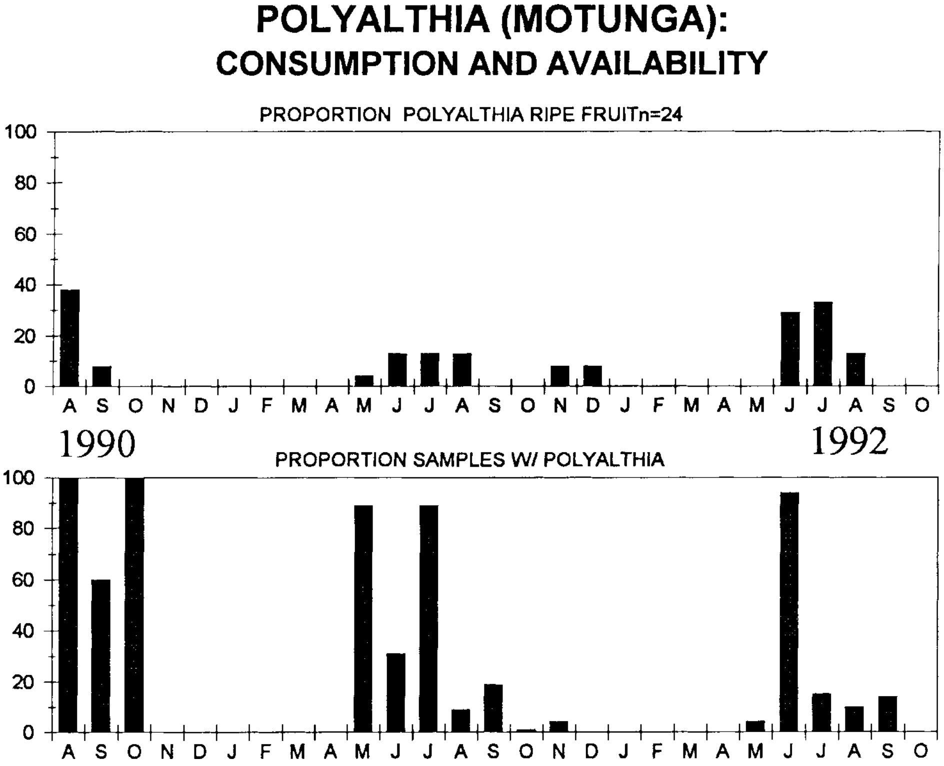

Fig. 8. *Polyalthia* availability and consumption. Monthly variation in the proportion of fecal samples containing *Polyalthia* is compared with the proportion of *Polyalthia* trees in fruit on phenology trails, 1990–1992.

[Remis, in review a]. Western lowland gorilla group size is generally smaller than among eastern populations, and their maximum group size may be constrained by within-group competition for fruit [Tutin, 1996]. Gorillas may be less committed full-time frugivores than chimpanzees, but they consume some fruit resources even when they are rare. The diversity of fruits eaten and the amount of fiber consumed by the gorillas varies with seasonal and interannual variation in fruit availability.

Herbs likely serve as a buffer against fruit shortages for eastern and western lowland gorilla populations [Yamagiwa et al., 1994], but the attractiveness of herbs as an alternative to fruit may vary with the abundance and the quality of the herbs [e.g., Wrangham et al., 1996]. Hence, gorillas with access to superabundant high quality swamp vegetation (i.e., *Hydrocharis sp.*) may have few incentives to pursue fruit when its abundance is low. As such, fruit has been described as an "alternative" food for the gorillas at Nouabalé-Ndoki [Nishihara, 1995].

In contrast, at Bai Hokou many of the types of swamp vegetation that gorillas eat at other sites are rare [Harris, personal communication]. Gorillas consume fruits even when they are uncommon and travel long distances to get them. In addition, the constraints of within-group feeding competition on fruit-eating may vary with group size. For example, the numbers of feeding places within trees is limited for gorillas, and there is evidence of scramble competition among members of large groups to gain access to small fruit trees [Remis, 1995; Goldsmith, 1996]. Moreover, small groups travel far to take advantage of ripe fruits

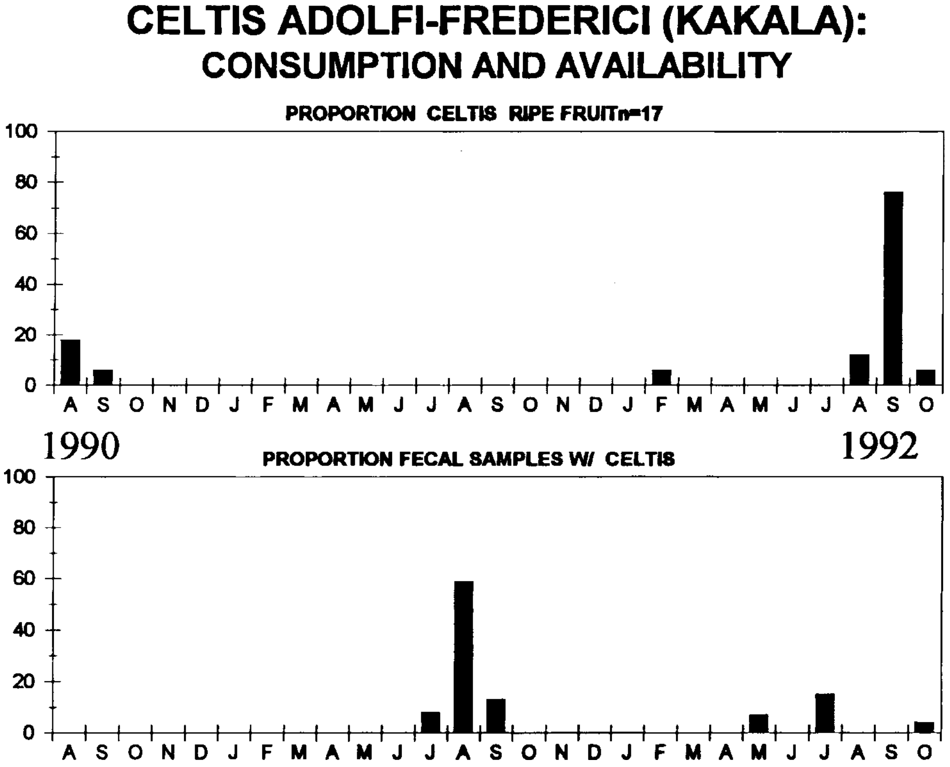

Fig. 9. *Celtis* availability and consumption. Monthly variation in the appearance of *Celtis* in the fecal samples of gorillas is compared with the proportion of *Celtis* trees in fruit on phenology trails, 1990–1992.

during periods of low fruit availability, whereas large groups may focus on fibrous foods and pursue time-minimizing strategies [Goldsmith, 1996].

Kuroda et al. [1996] contrast fruit-eating by gorillas with the foraging style of chimpanzees. They argue that, unlike chimpanzees, gorillas do not make repeated visits to individual fruit trees or persistently consume fruits of a single species and have short feeding bouts, even at large trees.

The data from Bai Hokou do not support this interpretation; the gorillas there are persistent and selective fruit eaters. They make repeated visits to individual trees in the course of circuits between individuals of a favored fruit species (e.g., *Dialium, Celtis,* and *Gambeya*). They respond to apparent microhabitat differences in the timing of fruit production by shifting their ranging habits in order to continue to feed on a particular species [Remis, 1994; also see Tutin, 1996]. In addition, they spend relatively long periods of time (at least up to 2 h) at large sources of *Celtis, Dialium,* or *Landolphia sp.* fruits. Moreover, the main study group, group C, occasionally split into two subgroups that foraged and slept apart, especially when concentrating on single species of fruits in the poor fruit season of 1991 [Remis, 1997b].

Gorillas will work hard to get fruit. The notion that gorillas are opportunistic fruit-eaters is not reflected in the Bai Hokou data. On the contrary, fruit-eating shapes the ranging patterns of the Bai Hokou gorillas. However, their large body size and digestive capacity differentiate gorillas from chimpanzees and provide them greater dietary flexibility to subsist entirely on fibrous foods when fruit is scarce.

TABLE 4. Feeding Data From Gorilla Field Studies

Study	Length of study (months)	Number of food species	Number of food items	Number of fruits	Fruit in diet (%)
Mountain gorillas (Rwanda)					
Schaller, 1963 (Kabara)	16	27, 29		3	6.1–10 items
Fossey and Harcourt, 1977	84	42			1.7 records
Vedder, 1984	18	21	30	1	3.3 items .4 time
Watts, 1984	17	38	75	3	4 items .3 time
Eastern lowland gorillas					
Schaller, 1963 (Congo)	3	12	—	0	0
Casimir, 1975, (KB, Zaire)	15	57	70	2	3 items
Goodall, 1977 (KB, Zaire)	7	78	160	3	2 items
Yamagiwa et al., 1994 (It, Zaire)	11	121	194	48	40 species 25 items
Western lowland gorillas					
Sabater-Pi, 1977 (Rio Muni, Eq. Guinea)	68	92	128	52	56.8 species 40.0 items
Calvert, 1985a,b (Campo, Cameroon)	15	51	79	21	41.2 species 26.6 items
Nishihara, 1995 (Congo)	12	152	182	115	76 species 63 items
Tutin et al., 1993 (Lopé, Gabon)	96	157	213	97	61 species 45 items
Tutin et al., 1997 (Lopé, Gabon)	120 36 (observed)		220	100	55 items 47 time
This study (Bai Hokou, C.A.R.)	27	138	239	77	45 species 35 items 51 times

TABLE 5. Feeding Data From Chimpanzee and Orangutan Studies

Study	Length of study (months)	Number of food species	Number of food items	Number of fruit species	Fruit in diet (%)
Chimpanzees					
Wrangham, 1977 (Gombe, Tanzania)	12	Not available	140	68	49 items 59 times
Nishida and Uehara, 1983 (Mahale, Tanzania)		198	328	100	Not available
Sugiyama and Koman, 1987 (Bossou, Guinea)	13	156	205	Not available	57 items
McGrew et al., 1988 (Mt. Assirik, Senegal)	47	43	60	34	56 items
Wrangham et al., 1991 (Kibale, Uganda)	40	Not available	Not available	66	72 time (observed time = 100 h)
Tutin and Fernandez, 1992 (Lopé, Gabon)	96	132	174	111	76 items
Pygmy chimpanzees					
Kano and Mulavwa, 1984 (Wamba, Zaire)	28	114	133	67	50 items
Badrian and Malenky, 1984 (Lomako, Zaire)	17	81	113	62	54 items
Orangutans					
Galdikas, 1988 (Tanjung Puting, Borneo)	48	229	310	169	61 time

CONCLUSIONS

1. Across their range, lowland gorillas consume large quantities of fruit whenever it is available. Herbaceous plants and fibrous fruits are consumed year-round and are important fallback foods during times of fleshy fruit scarcity.

2. Gorilla fruit resources are temporally discontinuous, and diet exhibits marked seasonal and interannual variation.

3. Seasonal fruit-eating shapes gorilla ranging patterns. Nevertheless, their large body size lends them greater dietary flexibility than chimpanzees during periods of fruit scarcity and enables them, when necessary, to subsist on a largely folivorous diet.

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