RESEARCH ARTICLES

The Primate Community of the Lopé Reserve, Gabon: Diets, Responses to Fruit Scarcity, and Effects on Biomass

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The diets of all diurnal primates (*Gorilla g. gorilla, Pan t. troglodytes, Mandrillus sphinx, Colobus satanas, Cercocebus albigena, Cercopithecus nictitans, C. pogonias, C. cephus*) in the Lopé Reserve, central Gabon, are described from qualitative and quantitative data collected over 10 years. A total of 397 foods were recorded, of which 91% were from plants. The diets of seven of the eight species were numerically dominated by fruit, the exception being *Colobus satanas* with a diet dominated by seeds. When proportion of feeding time was examined, fruit remained the dominant food class for six species, while *Cercocebus albigena,* like the black colobus, spent most time feeding on seeds. The number of foods recorded per species ranged from 46–220, but dietary breadth of the four species that have not been subjects of detailed study was certainly underestimated. Almost half of the foods (46%) were eaten by only one species, and only four (1%) were recorded for all eight species. At Lopé, fruit is scarce for 2–3 months during the annual dry season, and fruit crop failures can prolong this period of scarcity to as many as 8 months in some years. When fruit is scarce, the diets of all species changed to include more nonfruit foods, but chimpanzees and the three species of guenons maintained a fruit dominated diet. The total biomass of the Lopé primate community is 374 kg/km^2, which is low compared to other sites in tropical Africa. Within the Lopé community, biomass correlates negatively with degree of frugivory, suggesting that fruit availability may be critical, but this does not explain the low total biomass compared to other sites. Neither floristic diversity nor the composition of the primate community at Lopé can account for the low biomass. While historical events such as climate-induced changes in forest cover, disease, or impact of human activities cannot be ruled out, we conclude that the most likely explanation of low primate biomass is the occurrence of an ecological "catastrophe" in the fairly recent past from which populations have not

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yet recovered. We believe that the most likely scenario was climate-mediated disturbance of flowering of important fruit food species. Prolonged fruit scarcity would have caused mortalities and affected the most frugivorous species more severely. Am. J. Primatol. 42:1–24, 1997.

Key words: community ecology; diet; frugivory; biomass; seasonality; keystone resources

INTRODUCTION

Primates are the most important arboreal consumers in rain forest habitats of Africa [Emmons et al., 1983; Galat & Galat-Luong, 1985; Struhsaker & Leyland, 1979], South America [Chapman, 1987; Terborgh, 1983], and SE Asia [Leighton & Leighton, 1983; MacKinnon & MacKinnon, 1980]. Assemblages of 6–15 species occur sympatrically in such habitats, but, compared to detailed research on the ecology of individual species, few studies of primate communities have been made. Such studies are essential to answer questions about the evolution and adaptations of each species within the community, as the diet of each species and patterns of resource partitioning and niche separation evolved not in isolation but within communities [Waser, 1987].

Availability of most primate foods varies both in time and space. Plant reproductive parts (flowers, fruit, and seeds) are produced at intervals, and synchrony both within plant species and communities is the usual pattern in tropical forests, resulting in large seasonal variations in availability of these foods [Frankie et al., 1974; van Schaik et al., 1993]. In addition, the majority of tropical plants produce new leaves in regular bursts [Hladik, 1978; Leigh & Smythe, 1978], and so the availability of almost all plant foods, except mature leaves, bark, and pith of herbs, fluctuates between abundance and scarcity. Such seasonal variation tends to be regular and thus predictable, and it has exerted selective pressure during evolution—for example, on the timing of reproduction in seasonally breeding primates, which is often clearly related to peaks of food availability during pregnancy, lactation, or weaning [Butynski, 1988]. However, large interannual variations also occur in at least some tropical forests, and these lead to longer, unpredictable, periods of food scarcity [Foster, 1982; Tutin & Fernandez, 1993a]. Competition between species may occur whenever the availability of shared food resources is limited, and biomass has been taken as an indicator of evolutionary success at least within similar trophic levels [Eisenberg & Thorington, 1973].

During periods when fruit is scarce, certain foods sustain frugivores, and these have been called "keystone resources" [Gautier-Hion & Michaloud, 1989; Leighton & Leighton, 1983; Terborgh, 1986]. Studies of primate communities have shown that niche separation becomes clear-cut at such times [Terborgh, 1986; Gautier-Hion, 1980]. For example, Terborgh found at his study site at Manu, Peru, that of five frugivorous primates, the two larger species (*Cebus apella* and *C. albifrons*) relied on hard-shelled nuts during times of fruit scarcity, while two smaller species (*Sanguinus imperator* and *S. fuscicollis*) fed on nectar. The fifth species (*Saimiri sciureus*) maintained a fruit-dominated diet by concentrating on figs [Terborg, 1983, 1986]. Explicit references to the importance of "bottle-neck" periods of food scarcity in evolution have been made with respect to models of competitive interactions in primate communities [Skorupa, 1983; Waser & Case, 1981] and in explaining the lack of convergence of primate communities in tropical forests in different regions [Terborgh & van Schaik, 1987]. Long-term studies are therefore needed to quantify within-site variation in food availability, and to document the responses of each species in a community to both these crisis periods, and to regular seasons of fruit scarcity.

Eight species of diurnal primates share a tropical forest habitat in the Lopé Reserve in central Gabon. Research over the past 10 years has focused on the ecology of the two largest species, lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) [Tutin & Fernandez, 1993b; Tutin et al., 1991; Williamson et al., 1990]. Shorter studies have been made of black colobus (*Colobus satanas*) [Harrison, 1986; Harrison & Hladik, 1986] and grey-cheeked mangabeys (*Cercocebus albigena*) [Ham, 1994]. Opportunistic data have been amassed on the other four species: mandrills (*Mandrillus sphinx*) and three guenons (*Cercopithecus nictitans, C. pogonias, C. cephus*). The population densities and biomass of the eight primate species have been estimated by White [1994a] from repeated line-transect censuses. In addition, fruit availability was monitored at monthly intervals for 7 years.

Our data on primate diets present several problems for a community study, as primate species were studied with different intensities using different methods. However, the available information allows us to begin to examine some of the questions about the diets of these species, how they overlap, and their responses to fruit scarcity.

The aims of this paper are as follows:

1. to describe the diet of each of the eight primate species in terms of the relative importance of plant parts (fruit, seeds, leaves, etc.);

2. to examine the degree of overlap of foods within the primate community at Lopé;

3. to identify resources that are exploited by each species during periods of low fruit availability (keystone resources);

4. to relate the choice of keystone resources to morphological and social characters of the primates and to their biomass in the Lopé study area;

5. to try to identify critical factors that determine or limit the biomass of primates by comparing the data from Lopé with those from other sites in tropical Africa.

METHODS
Study Area

The study area covers about 50 km^2 (0°10'S, 11°35'E) in the northern part of the Lopé Reserve (5,000 km^2) in central Gabon. Within this study area, the forest is heterogeneous in both plant species and structure, but Marantaceae Forest, characterized by a dense herbaceous understory dominated by species of Marantaceae and Zingiberaceae is common [White, in press; White et al., 1995]. To date, 676 plant species have been identified, and the total number in the study area probably approaches 1,500 [Tutin et al., 1994]. Parts of the study area were selectively logged between 1960 and 1970. A single species, *Aucoumea klaineana,* was extracted at an average density of 1.5 trees per hectare. The area is well protected from hunting. Mean annual rainfall is 1,531 mm (1984–1994), and the climate is characterized by a dry season of about 3 months from mid-June to mid-September. Temperatures vary little over the year but are lowest during the dry season, when constant cloud cover during the daylight hours results in low evaporation rates and high relative humidity [Hladik, 1973].

Diets

The diets of gorillas and chimpanzees have been documented by observation and faecal analysis over a 10 year period [Tutin & Fernandez, 1993b; Williamson

et al., 1990]. Apes at Lopé have proven difficult to habituate to human presence [Tutin & Fernandez, 1990], but indirect methods of monitoring diets have produced useful data. In addition, for this comparative study, feeding observations made during a 3 year period (1990–1992 inclusive) were analyzed. This period was selected as most observations of gorilla feeding came from a semihabituated focal group, which we followed until early 1993 when the silverback male died. As observation conditions of apes rarely permitted regular scans, the feeding frequency method (feeding on a particular food scored only once per individual per observation period) was used. Harrison and Hladik [1986] quantified the diet of a group of black colobus using the same method during 5 consecutive days per month over 9 months from August 1983 to April 1984, and Ham [1994] used instantaneous scan samples [Altmann, 1974] at 15 min intervals to study the diet of a group of grey-cheeked mangabeys during 5 days per month for 15 months between April 1991 and August 1992.

Opportunistic data have been collected on foods consumed by all primate species over the 10 year study period. For each species, each confirmed food was recorded. In addition, all foods seen to be eaten by primates during Ham's [1994] 15 month study of mangabeys were listed, but each food was recorded only once per day per species, regardless of the number of feeders. The plant food categories used in this study were fruit (flesh surrounding seed: mesocarp, exocarp, or aril), seed, leaf, flower, pith, animal, and other (includes bark, roots, galls, and soil).

Fruit Availability

Fruit availability was monitored for 7 years (October 1986 to September 1993) by a monthly phenology circuit with data collected on the quantity of leaves (new, mature, and senescent), flowers, and fruit (immature and ripe) of 60 species of plant. The species were selected originally for their importance in the diet of gorillas and chimpanzees. Of the 60 species, 54 have succulent fruit and 6 arillate fruit.

Normally ten individual trees of each species were monitored, but this was not possible for some rare species (N = 6). Over 4–7 days at the beginning of each month, the 578 labelled trees were observed through binoculars, and the quantity of leaves, flowers, and fruit was recorded on a ten point scale from 0 (none) to 10 (maximum crop). A total fruit score was established each month for each species with the equation

$$\text{Total Fruit Score} = \frac{\sum \text{FS}}{\text{N Tr}}$$

where FS is the fruit score for each tree and N Tr the number of trees of that species monitored. Periods of fruit scarcity were defined as months when six or fewer species in the phenology sample had total fruit score ≥ 5 [Tutin et al., 1991].

Population Density, Group Size, and Biomass of Primates

Population density of primates in the study area came from transect censuses [see Whitesides et al., 1988]. A 5 km straight line transect was placed across the drainage system. The transect was walked 43 times over a 2 year period to census all diurnal mammals [White, 1994a]. Mean group sizes were used to convert census counts to population density, and data on body weights allowed estimation of biomass for each of the eight primate species [White, 1994a].

Complete counts of primate groups have been made whenever observation

conditions allowed over the 10 year period. Only counts in which the observer was confident that all individuals had been seen and which were considered independent (defined here as counts made at locations separated by 1–3 km depending on the species or counts from similar locations but separated by two or more years) were used in calculations of biomass. Ape group counts were taken from the number of night nests at all fresh nest sites (less than 1 week old) seen on the 43 censuses along the 5 km transect. This ignores unweaned individuals sharing the mothers' nest, but these immature individuals contribute little to biomass [Tutin & Fernandez, 1984]. Densities of apes from nest counts and from observations during transect-censusing were similar [White, 1994a].

Body weights were taken from published sources [Gautier-Hion & Gautier, 1974; Haltenorth & Diller, 1977; Jungers & Susman, 1984; Harrison, 1988], and the weight of an "average" individual was calculated following Oates et al. [1990].

RESULTS
Overall Diets

The total number of foods recorded for the eight species was 397, of which 362 (91%) were plant foods from 202 different species, 33 (8.3%) animal, and 2 (0.5%) mineral. The foods include 144 species of fruit, 73 leaves, 74 seeds, 28 flowers, 26 piths, 15 barks, 14 invertebrates, 12 galls, 7 vertebrates, 3 roots, 2 types of earth, 1 wood, and 1 fungus. The number of food species recorded in each food category for the eight species of primate is listed in Table I. The number of feeding observations recorded in each food category for the eight primate species is listed in Table II.

Fruit is the most numerous food class in terms of number of species eaten for seven of the eight species. The exception, *Colobus satanas,* has a diet dominated by seeds. The number of feeding observations is also highest for the fruit category for all the species except *Colobus satanas* and *Cercocebus albigena.* However, all eight species have mixed diets, and, even for the most frugivorous species (*Pan troglodytes, Cercopithecus pogonias,* and *C. cephus*), 38–40% of dietary items are nonfruit. A comparison of Tables I and II shows consistency in the first and second ranked category of food for seven of the eight species. The exception, *Cercocebus albigena,* has a diet numerically dominated by fruit but spent the most time feeding on seeds. However, statistically significant correlations emerged between the data sets in Tables I and II for all eight species: Spearman rank correlation coefficients ranged from 0.714 (*C. albigena*) to 0.98 (*C. nititans*) (N = 7, *P* < 0.001) for all except gorillas, chimpanzees, and mangabeys (for which *P* < 0.05).

All primates at Lopé, including the three terrestrial species (gorillas, chimpanzees, and mandrills), obtain the majority of their foods from trees. The percentage of foods harvested terrestrially ranges from 0 (for the three Cercopithecus) to 32% (for gorillas). Herbs provide important foods for the three terrestrial species [Tutin & Fernandez, 1993b; White et al., 1995].

Dietary Overlap

Of the 397 different foods of the primate community at Lopé, 183 (46%) were recorded for only one species, and only four foods (1%) were recorded for all eight primate species (see Fig. 1). Figure 2 compares sharing levels for the three commonest food categories, fruit, seeds, and leaves. There were significantly fewer exclusive fruit foods than was the case for seeds and leaves (X^2 = 120.3, df = 2, *P* < 0.001). The total number of food items recorded reflects the intensity of study

TABLE I. Diets of Eight Diurnal Primates at Lopé Showing the Number of Foods Recorded

| Primate species | Percentage (and number) of species eaten | | | | | | | Total |
	Fruit	Seed	Leaf	Pith	Flower	Animal	Other[a]	
Gorilla g. gorilla	45.5 (100)	9.6 (21)	21.8 (48)	7.3 (16)	1.4 (3)	4.6 (10)	10.0 (22)	220
Pan t. troglodytes	62.6 (114)	7.7 (14)	10.4 (19)	4.4 (8)	3.3 (6)	9.3 (17)	2.2 (4)	182
Mandrillus sphinx	50.7 (37)	26.0 (19)	8.2 (6)	6.8 (5)	2.7 (2)	4.1 (3)	1.4 (1)	73
Colobus satanas	19.6 (20)	43.1 (44)	22.5 (23)	4.9 (5)	6.9 (7)	2.0 (2)	1.0 (1)	102
Cercocebus albigena	38.1 (59)	25.8 (40)	13.5 (21)	3.9 (6)	9.0 (14)	6.5 (10)	0.7 (1)	155
Cercopithecus nictitans	55.3 (47)	9.4 (8)	20.0 (17)	2.4 (2)	9.4 (8)	3.5 (3)	0	85
Cercopithecus pogonias	60.9 (28)	10.9 (5)	8.7 (4)	2.2 (1)	10.9 (5)	6.5 (3)	0	46
Cercopithecus cephus	62.1 (36)	6.9 (4)	15.5 (9)	1.7 (1)	6.9 (4)	6.9 (4)	0	58

[a]Includes bark, roots, wood, soil and fungi.

TABLE II. Diets of Primates at Lopé Showing the Frequency of Feeding Records for Each Food Category

Primate species	Percentage (and number) of total feeding observations							
	Fruit	Seed	Leaf	Pith	Flower	Animal	Other[a]	Total
Gorilla g. gorilla[b]	40.9 (447)	5.8 (63)	33.8 (369)	11.5 (126)	1.2 (13)	0.8 (9)	7.3 (80)	1,092
Pant. troglodytes	69.2 (421)	7.7 (47)	9.9 (60)	0.5 (3)	6.4 (39)	5.3 (32)	1.0 (6)	605
Mandrillus sphinx	46.7 (57)	34.4 (42)	5.7 (7)	5.7 (7)	0.8 (1)	4.9 (6)	1.6 (2)	122
Colobus satanas[c]	4.1 (80)	60.1 (1,184)	26.0 (511)	1.2 (24)	5.3 (103)	2.6 (51)	0.9 (18)	1,971
Cercocebus albigena[d]	24.0 (559)	41.4 (962)	4.5 (104)	1.6 (36)	3.3 (76)	25.3 (589)	0	2,326
Cercopithecus nictitans	59.3 (96)	11.1 (18)	16.0 (26)	0.6 (1)	9.9 (16)	3.1 (5)	0	162
Cercopithecus pogonias	68.8 (53)	9.1 (7)	6.5 (5)	0	9.1 (7)	6.5 (5)	0	77
Cercopithecus cephus	67.0 (59)	6.8 (6)	11.4 (10)	0	5.7 (5)	9.1 (8)	0	88

[a]Includes bark, roots, wood, soil and fungi.
[b]Data from 1990–1992 [SEGC, unpublished].
[c]Data from M.J.S. Harrison [unpublished].
[d]Data from Ham [1994].
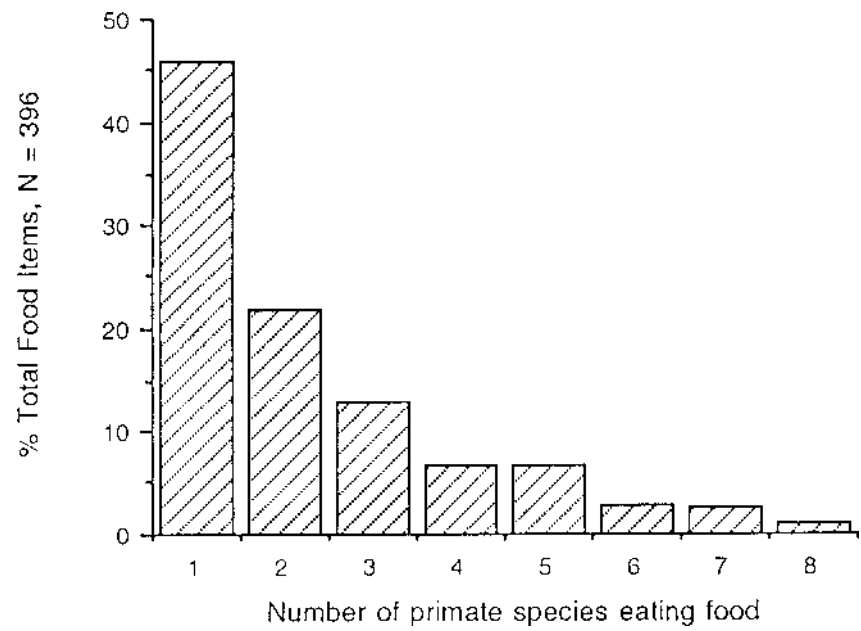
Fig. 1. Percentage of foods shared by the eight primate species at Lopé.
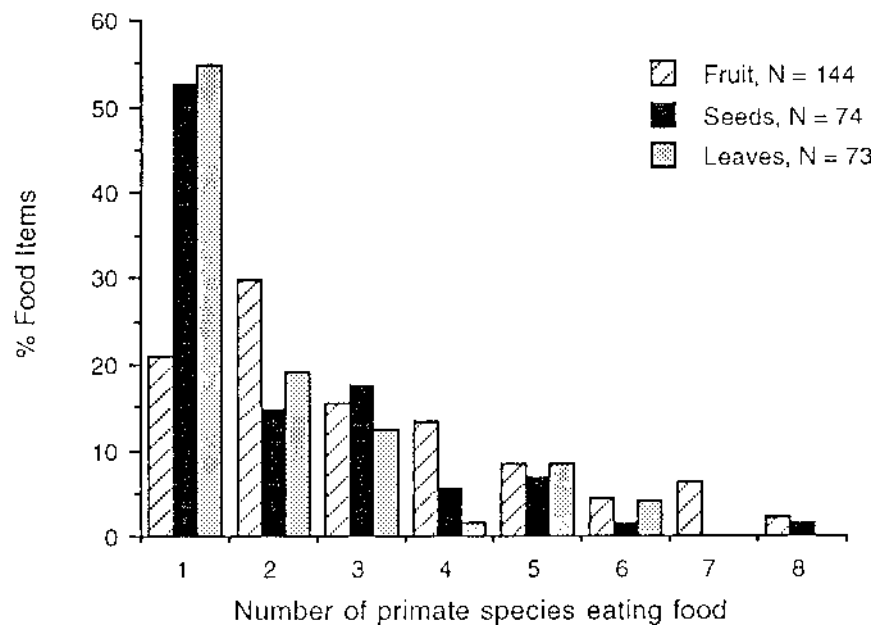

Fig. 2. Percentage of fruit, leaf, and seed foods shared by the eight primate species at Lopé.

of each species, and our data for *Cercopithecus pogonias* and *C. cephus* (and to a lesser degree mandrills and *C. nictitans*) are incomplete; therefore, the real overlap will be greater than that suggested by these data. Table III shows the percentage dietary overlap between pairs of species at Lopé. The incomplete data set means that for species pairs including *C. pogonias* and *C. cephus* (for which fewest data are available), the real dietary overlaps are likely to be higher. Three of the four largest species overlap most with gorillas, and two of the three smallest species overlap most with mangabeys. Gorillas and mangabeys both have eclectic diets, the former being a frugivore–folivore and the latter a gramnivore–frugivore–insectivore (Tables I, II).

Fruit Availability

Figure 3 shows the monthly means and ranges (over 7 years, from October 1986 to September 1993) of the number of tree species bearing ripe fruit out of the total phenology sample of 60. Of the 84 months, 55 (65%) were defined as good fruit months when 7–20 species in the sample had total fruit scores ≥5 (see Methods), and 29 (35%) were poor fruit months when only one to six species had total fruit scores ≥5. Nineteen of the 29 poor fruit months fell in the dry season (June–August). During the 3 month dry season in all years, fruit was scarce for either two (2 of 7 years) or three (5 of 7 years) consecutive months. Of the seven dry seasons, that of 1993 was the poorest for fruit, with only two species with fruit scores ≥5 for three consecutive months. In contrast, October–December was a consistent time of plenty, and no poor fruit months were recorded over the 7 year period. The longest period of fruit scarcity was eight consecutive poor fruit months (January–September 1991). Interannual variation in the number of species with ripe fruit in each month was statistically significant (Freidman two-way analysis of variance, $X_r^2 = 299.6$, df = 6, $P < 0.001$). In summary, the dry season is a consistent period of fruit scarcity, and in some years (three of the seven) crop failures of certain tree species resulted in additional poor fruit months between January and September.

Primate Diets During Periods of Fruit Scarcity

Figure 4 compares the overall diet of each of the eight species (ordered by decreasing overall frugivory) with diet during periods of fruit scarcity. During poor fruit months, fruit continued to dominate numerically the diets of six species, but for two of these species (*Mandrillus* and *Cercocebus*) the relative contribution of seeds to dietary variation increased to almost equal the number of fruit species eaten. The variety of fruit consumed by colobus and gorillas was much reduced in poor fruit months and was compensated by an increase in the number of species of leaves and flowers by the former and of leaves, pith, and bark by gorillas. The relative contribution of leaf and pith foods to the diets of chimpanzees and mandrills also increased in poor fruit months but less dramatically. The frequency of these food categories remained relatively constant in the diets of mangabeys and the three species of guenon. The variety of insects eaten by mangabeys increased during poor fruit months, and the number of flower species consumed by *P. troglodytes, C. albigena,* and *C. nictitans* (as well as by *Colobus*) was greater when fruit was scarce.

Most of the primate species retained varied diets during periods when their major food class (ripe fruit) was in short supply. The 29 poor fruit months represent 35% of the study period, and for seven of the eight species the number of foods recorded during poor fruit months represented 30–47% of all recorded foods.

TABLE III. Dyadic Dietary Overlap in Plant Foods Eaten by Primates at Lopé

	Gorilla g. gorilla	Pan t. troglodytes	Mandrillus sphinx	Colobus satanas	Cercocebus albigena	Cercopithecus nictitans	Cercopithecus pogonias	Cercopithecus cephus	Number of foods
Gorilla		58.8[a]	20.8	18.6	30.3	22.6	10.0	16.7	220
Pan	76.5[a]		26.5	20.6	38.2	26.5	15.3	20.0	182
Mandrillus	67.6[a]	66.2		26.5	47.1	39.7	23.5	30.9	73
Colobus	37.3	31.8	16.4		59.1[a]	30.9	20.0	20.0	102
Cercocebus	44.1[a]	42.8	21.1	42.8		40.1	26.3	25.0	155
C. nictitans	61.7	55.6	33.3	42.0	75.3[a]		40.7	54.3	85
C. pogonias	47.8	56.5	34.8	47.8	87.0[a]	71.7		54.3	46
C. cephus	64.9	59.7	36.8	38.6	66.7	77.2[a]	43.9		58

[a]Indicates the species with the highest number of shared foods. Species are listed in descending order of body weight.
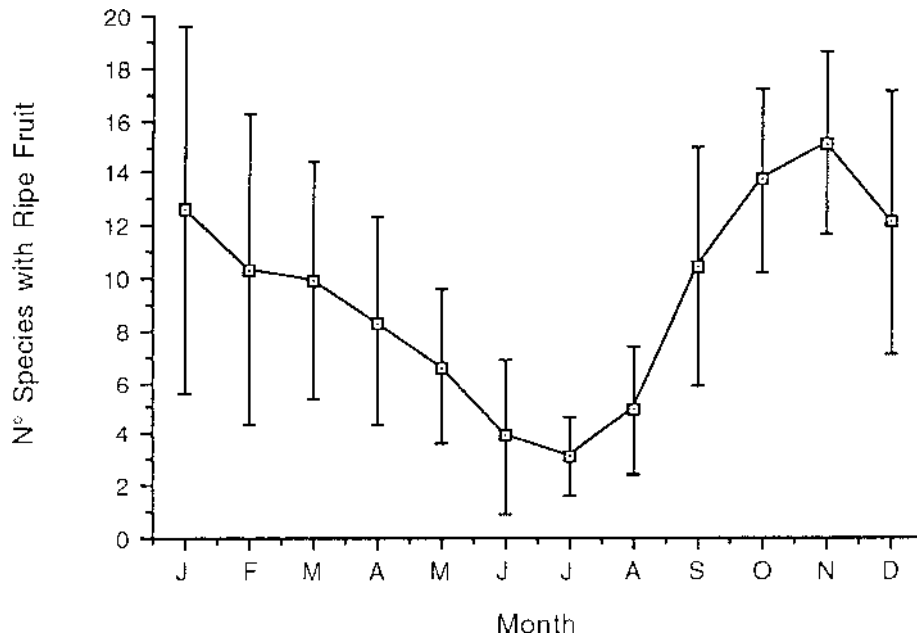
Fig. 3. Number of the 60 monitored tree species bearing ripe fruit: 7 year mean and observed range (1987–1993).

Only gorillas (with 20% of total recorded foods eaten during poor fruit months) seemed to reduce dietary variety markedly when fruit was scarce.

During the annual dry season, gorillas at Lopé eat large amounts of bark (more correctly bast, as only the inner part is consumed) of a common tree species, *Milicia (Chlorophora) excelsa* (Moraceae) and pith of two species of aquatic herbs, *Marantachloa cordifolia* and *M. purpurea* (Marantaceae). These foods are constantly available but are almost never eaten at other times of year, even in poor fruit months [Rogers et al., 1988, 1994; Tutin et al., 1991]. Chimpanzees rely heavily on the fruit of the oil palm (*Elaeis guineensis*) during the dry season, as this species fruits asynchronously with fruit ripening a few at a time over long periods. Fibrous fruit such as *Detarium macrocarpum* (which ripen progressively starting in July or August) increase in importance in the diet of gorillas during the dry season, but chimpanzees do not eat this fruit. Guenons and mangabeys share the fruits of *Elaeis guineensis, Pseudospondias longifolia,* and *Pycnanthus angolensis* with chimpanzees and *Detarium macrocarpum* with gorillas, but, rather than depending on a few key species, they also take advantage of small arillate fruits, notably of *Xylopia* spp. that are relatively common during the dry season [White, 1994b] but not eaten by apes.

The larger monkeys (mandrills, mangabeys, and colobus) eat mechanically protected immature seeds of *Pentaclethra macrophylla, P. eetveldeana,* and *Ongokea gore* that are not eaten by guenons or apes. The three guenons eat some seeds of *Tetrapleura tetraptera,* but this species is more important to colobus and mandrills. At Lopé, neither *Pentaclethra* nor *Tetrapleura* seeds are eaten by apes, in contrast to other areas [Moutsamboté et al., 1994]. Gorillas do eat the seeds of *Detarium macrocarpum* and, with the exception of adult male mandrills, appear to be the only primate with the strength to bite through the hard protective shell.
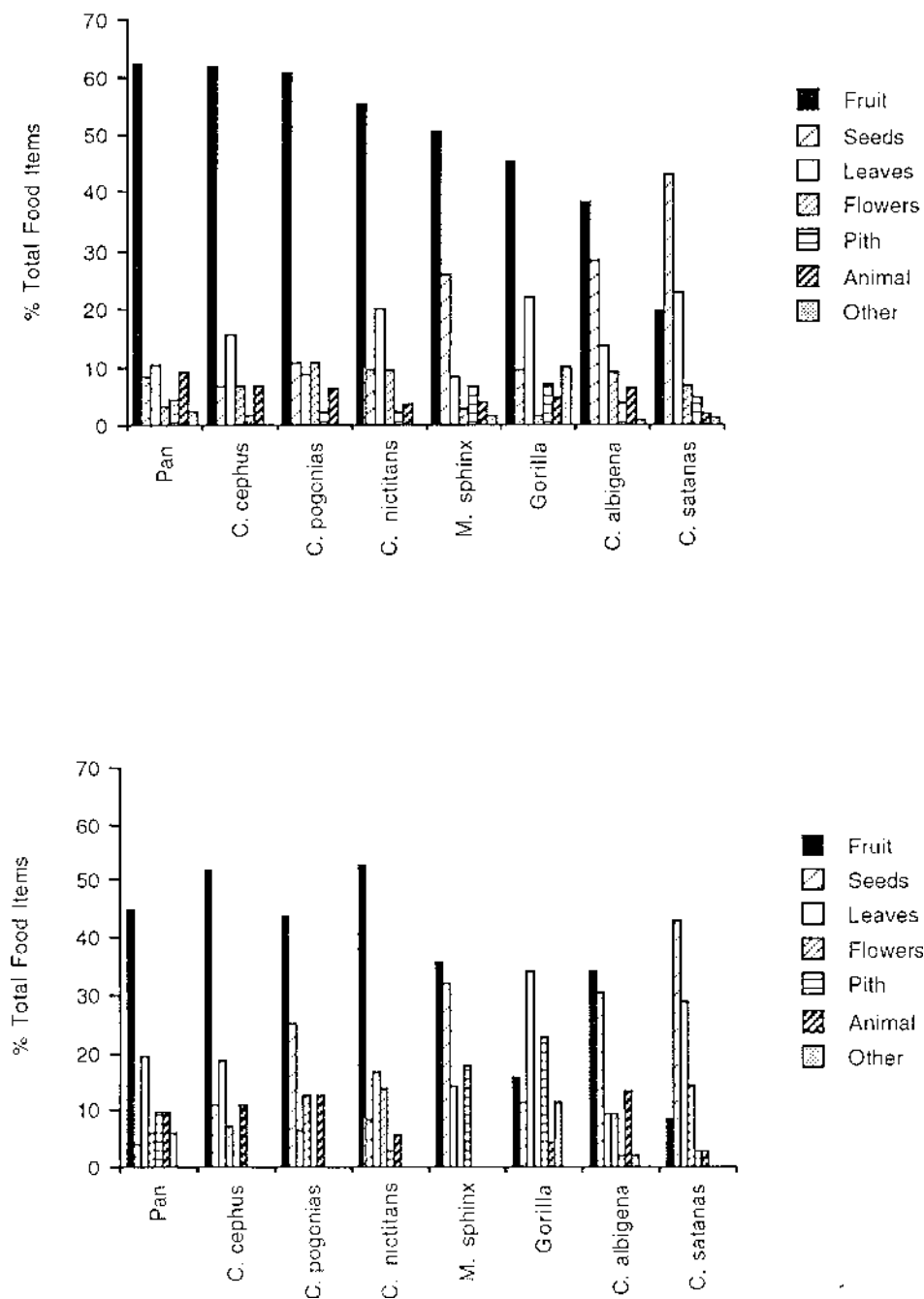
Fig. 4. **Top:** Proportion of different food classes in the diets of Lopé primates. The eight species are listed in order of decreasing frugivory. **Bottom:** Proportion of different food classes in the diets of Lopé primates during poor fruit months (see Methods for definition).

In 1992 exceptional climatic conditions led to a second fruiting by some common tree species such that a range of succulent fruit normally available only from December–April was again present in June–August during the dry season [Tutin & Fernandez, 1993a]. These fruits were heavily exploited by all of the primates. In all, 23 species produced some aseasonal fruit in the dry season of 1992, but most crops were small, scoring less than 5 for total fruit score (see Methods). An exception was *Pterocarpus soyauxii,* which produced a huge crop of flowers in May–June and winged seeds from June–September. First the flowers and then unripe seeds dominated the diets of all eight primate species during the dry season of 1992. The atypical availability of *Pterocarpus* flowers and seeds, which are popular foods but normally only available in December–February, suggests that many normal dry-season foods are not preferred or are less easy to harvest and process.

During poor fruit months outside the annual dry season, other foods are exploited. More young leaves are available in April–May than in July–August, and, in 1991, when few succulent fruit were available, flush leaves of *Irvingia grandifolia* and *Ficus* spp. were heavily exploited by all of the primates. Seeds of Caesalpiniaceae trees are abundant each year from March–May and are eaten consistently by monkeys, but apes eat these seeds only in years when succulent fruit is scarce. Processing of these seeds is time consuming, and observations of gorillas feeding on the winged seeds of *Hylodendron gabunense* showed clearly that feeding rate was limited by the slow speed of harvesting; gorillas had difficulty picking up the small seeds that carpeted the ground. Twelve species of *Ficus* occur in the study area [Tutin et al., 1994] and, although none are common, all fruit asynchronously. It was striking that fig crops available in poor fruit months attracted gorillas and chimpanzees without fail, but figs were often ignored in good fruit months when a variety of succulent fruit was available.

By definition, a keystone food must either be available at all times, as is true of mature leaves, pith, bark, and fruit of common species that reproduce asynchronously or must be consistently available during times of fruit storage. Table IV lists the major keystone foods for the Lopé primate community.

Population Density, Group Size, and Biomass of Primates

Data on diurnal primate densities, group size, and biomass are summarized in Table V. The eight primate species make up only 6% of total mammalian biomass at Lopé. Primate biomass is dominated by colobus, *C. nictitans,* and gorillas. *Cercopithecus pogonias* has the lowest biomass of all primates at Lopé. Mammalian biomass is dominated by forest elephants (*Loxodonta africana cyclotis*) that make up 89% of the total of 5,864 kg/km^2.

For primates, the percentage of feeding time spent eating leaves i.e., the degree of folivory of the eight species (Table III) showed a positive but not statistically significant correlation with biomass ($r_s = 0.57$, N = 8, $0.05 < P < 0.02$), while the percentage time spent feeding on fruit did show a significant negative correlation with biomass ($r_s = -0.667$, N = 8, $P < 0.05$). The percentage of all recorded foods that are leaves i.e., the breadth of the folivorous component of diet (Table I) was positively correlated with biomass ($r_s = 0.738$, N = 8, $P < 0.05$).

DISCUSSION
Diets of the Lopé Primates

The data on the diets of the Lopé apes, mangabeys, and colobus are likely to be representative although, even after 10 years of intensive study, new foods

TABLE IV. Keystone Foods of Primates at Lopé

Species	Family	Part eaten	Ggg	Ptt	Ms	Cs	Ca	Cn	Cp	Cc	Availability
Milicia excelsa	Moraceae	Bast	**X**								Permanent
Milicia excelsa	Moraceae	Leaves	x				x	x			Permanent
Marantachloa (2 species)	Marantaceae	Pith	**X**	**X**	**X**						Permanent
4 species herbs	Marantaceae	Leaves	**X**	**X**	**X**			x		x	Permanent
5 species herbs	Zingiberaceae	Pith	**X**	**X**	**X**						Permanent
Duboscia macrocarpa	Tiliaceae	Fruit	**X**	x	x		x				Permanent
Elaeis guineensis	Palmae	Fruit		**X**	x		**X**	x	x	x	Permanent
Pseudospondias longifolia	Anacardiaceae	Fruit	x	**X**	x		x	x		x	August
Detarium macrocarpum	Caesalpiniaceae	Fruit	**X**		x			x		x	August–November
Detarium macrocarpum	Caesalpiniaceae	Seed	**X**		x						August–November
Pentadesma butyracea	Guttiferae	Seed	**X**			**X**		**X**			July–January
Pentadesma butyracea	Guttiferae	Flower								**X**	February–August
Xylopia (4 species)	Annonaceae	Fruit			x		x	**X**	**X**	**X**	July–October
Ficus (12 species)	Moraceae	Fruit	x	**X**	x		**X**	**X**	**X**	**X**	Irregular
Ongokea gore	Olaceae	Seed			**X**	**X**	**X**		**X**		June–November
Pentaclethra (2 species)	Mimosaceae	Seed		**X**	**X**	**X**	**X**		x	**X**	July–October
Pycnanthus angolensis	Myristicaceae	Fruit					x	**X**	**X**	**X**	August–October
Berlinea bracteosa	Caesalpiniaceae	Insects				x	**X**	x	x	x	Permanent
Tetrapleura tetraptera	Mimosaceae	Seed			**X**	**X**	**X**	x	x	x	Permanent

Species

X, heavily exploited during annual dry season, July–August; x, eaten less frequently.

TABLE V. Biomass of Primates at Lopé

Species	Mean group size	Biomass (kg/km^2)
Gorilla g. gorilla	5.3	78
Pan t. troglodytes	2.4	27
Mandrillus sphinx	150	15
Colobus satanas	12.1	114
Cercocebus albigena	18.9	35
Cercopithecus nictitans	13.5	81
Cercopithecus pogonias	12.6	11
Cercopithecus cephus	9.6	13
Total diurnal primate biomass		374
Total mammalian biomass		5,864.2

continue to be recorded for gorillas and chimpanzees. Our data on the other four primate species are certainly incomplete, and small food items such as leaf buds and particularly invertebrates are under-represented. For example, Lahm [1986] found 44 species of invertebrates in her analysis of mandrill stomachs in Gabon, although invertebrates accounted for only 5% dry weight of the contents of the 12 stomachs examined. Despite the limitations of our data, they paint a similar picture to studies of mandrills and guenons in other areas of Gabon, indicating that no systemic bias exists. Published lists of plant foods of mandrills in Gabon correspond closely to our data, with fruit and seeds dominating [Jouventin, 1975; Lahm, 1986]. In detailed studies of the feeding ecology of the same *Cercopithecus* species in NE Gabon, 160 km from Lopé, both observations and stomach analysis showed all three to be frugivorous with high degrees of dietary overlap [Gautier-Hion, 1980]. In a review of *Cercopithecus* diet, Gautier-Hion [1988:266] reported that while a total of about 100 plant foods per species is usual, "in all species studied, about 80% of the diet is acquired from about 30 plant species." At Lopé, 43, 54, and 82 plant foods have been identified for *C. pogonias, C. cephus,* and *C. nictitans,* respectively (Table I), and, while the data on feeding frequencies are limited, it is unlikely that many major foods have been missed.

While we do not expect additional data on guenon diet at Lopé to change the general picture, more data are needed to clarify niche separation and patterns of interspecific interactions among these three species that differ little in body size or social organization. For example, the data on dietary overlap (Table III) show that, for the majority of pairwise comparisons involving guenons, dietary overlap is much higher from the guenons' perspective (e.g., chimpanzees eat between 56 and 60% of guenon foods, while guenons eat only 15–27% of chimpanzee foods). No detailed analysis of the frugivore niche of primates at Lopé can be made before systematic data are collected on the feeding ecology of guenons.

There can be no doubt that the most accurate way to describe the diet of wild primates is to quantify the weights of foods ingested. However, this is rarely possible for species living in tropical rain forest habitats. A list of foods eaten (Table I) indicates dietary breadth but does not necessarily reflect accurately the relative importance of different food categories in the species' diet. Data on the frequencies of feeding on different food items (Table II) allow quantification of diet in terms of relative amounts of time spent eating different classes of foods, but even this measure may not be directly related to the weights of different foods ingested, as processing times vary widely [Hladik, 1977]. A comparison of Tables I and II show that for seven of the eight primates at Lopé the quantitative data are similar to those derived from lists of foods, with the first and sec-

ond most important classes of foods being the same. The exception is *Cercocebus albigena,* which would be described as a frugivore–gramnivore from the food species list but becomes a gramnivore–insectivore–frugivore when feeding frequency data are considered. Mangabeys at Lopé have a diverse diet throughout the year, and the proportions of time spent feeding on seeds, insects, and fruit are similar overall but values vary greatly from month to month [Ham, 1994]. Similarly, the diets of apes at Lopé show great variation both within and between years depending on the availability of fruit [Tutin et al., 1991].

Flexibility in the diets of primates occurs both over time at the same study site [e.g., Dasilva, 1994; Chapman, 1987; Kinzey, 1977; Struhsaker, 1975; Waser, 1977] and for the same species at different sites [e.g., Oates, 1977; MacKinnon & MacKinnon, 1980; Maisels et al., 1994; Watts, 1990]. Most species of primate appear to have a preferred category of food (succulent fruit, seeds, leaves) which dominates the diet if available. Other foods are eaten regularly in smaller quantities and are probably critical in providing a nutritionally balanced diet. All eight primate species at Lopé have diverse diets (46–220 food items per species Table I), and each fed on three to five food classes for at least 5% of feeding time (Table II).

Niche Overlap and Keystone Resources

Seven of the eight species eat a diverse array of fruit, and the eighth (*Colobus satanas*) has a diet dominated by seeds. There is considerable overlap of fruit foods, with relatively few being exclusive (Fig. 4; Table IV). Flesh of succulent fruit is the only food class that is "designed" to be eaten (i.e., feeding on seeds, leaves, and pith is never advantageous to plants), and thus it is not surprising that it figures strongly in the diets of primates. Seventy-five percent of plant species at Lopé have fruit adapted for animal dispersal [White, 1994b], and, as pointed out by Gautier-Hion [1983], the high plant species diversity in Gabon provides a wide frugivorous niche. To date we have identified 676 plant species in the Lopé study area, including all common and most large trees, although it is likely that a total of 1,200–1,500 plant species occurs within the study area [Tutin et al., 1994]. The primate community eats foods from at least 202 species. Therefore, a minority of plant species (about 15–30%) is used, demonstrating selectivity.

The diets and the choices of keystone resources of the different primate species can be related to morphological and social characters. Among the monkeys, the greater size and stronger dentition of mangabeys, colobus, and mandrills enable them to exploit mechanically protected seeds, which appear to be inaccessible to the smaller guenons. Similarly, the larger monkeys and the apes are able to eat seeds of immature fruit, which may give them a competitive advantage when fruit crops are small [Ham, 1994]. Differences in gut morphology allow species to digest different foods or the same foods to a different extent. The compartmentalized stomach of colobus allows greater extraction of energy from fiber and detoxification of secondary compounds that protect seeds from predation, permitting colobus a more gramnivorous and folivorous diet [Davies & Oates, 1994]. Gorillas have long colons with many entodiniomorph ciliates which aid in cellulose digestion [Collet et al., 1984]. This allows them to subsist on fibrous fruits, mature leaves, bark, and stems when succulent fruit is scarce [Rogers et al., 1990, 1994].

The four species (*P. troglodytes* and the three *Cercopithecus*) which maintain diets dominated by fruit, even in periods of scarcity (Fig. 4), appear to lack the

dietary flexibility shown by gorillas, mandrills, colobus, and mangabeys and might be defined as obligate frugivores. Our data on guenon diets at Lopé are limited, but a detailed study of the same species in NE Gabon showed that diets of all three were dominated by fruit throughout the year [Gautier-Hion, 1980] (Fig. 1). However, *Cercopithecus wolfi* (which, like *C. pogonias,* is a member of the *mona* superspecies) diet is dominated year-round by seeds in Salonga, Zaire, where tree species that produce succulent fruit are rare [Gautier-Hion et al., 1993]. All field studies of chimpanzees have found diet to be dominated by fruit, but pith, seeds and bark have been recorded as important foods when fruit is seasonally scarce [McGrew et al., 1988; Nishida, 1976; Wrangham et al., 1991]. This suggests that chimpanzees and guenons are not obligate frugivores in the strict sense of the term, but, at Lopé, they are more frugivorous than gorillas, mandrills, or mangabeys. It seems that all primate species have potential dietary flexibility, although the full extent of this may emerge only from comparisons of diet of the same species in different habitats. The different reactions to fruit scarcity of the eight species at Lopé reflect the different constraints (physical, physiological, and social) that influence choice when faced with the same array of foods. An elegant example of the complexity of food choice comes from Gautier-Hion's [1980] finding of greater intraspecific than interspecific variance in diet among sympatric forest guenons.

Other adaptations aid survival during periods of hardship, such as the fission–fusion social organization of chimpanzees and the large group spread of mangabeys, which allows individuals to feed in smaller subgroups when fruit is scarce [Ham, 1994; Wrangham, 1977]. Primates possess extensive knowledge of food resources and are able to travel long distances to find food. For example, during our study, a group of gorillas travelled 4 km in two days to reach the far west of their range, where they spent a week feeding on the seeds of *Treculia obvoidea* which occurs only in that area; and an habituated group of colobus moved 2 km out of their normal home range to feed for 5 days in a single *Ceiba pentandra* that was producing new leaves. Home range size and day range length vary among species, and wide-ranging species such as the apes and mandrills are able to exploit scattered resources more easily than are the smaller primate species.

What is clear at Lopé is that no one plant species, or genus, can be identified as a keystone resource for any one species and certainly not for the whole primate community. Several authors have stressed the importance of *Ficus* spp. in the diets of primates in South America [Terborgh, 1986] and Africa [Wrangham et al., 1993]. At Lopé, figs are not a dependable resource since their rarity means that the availability of fruit is far from constant. Likewise, Gautier-Hion and Michaloud [1989] showed that figs are uncommon and not a keystone resource for primates in NE Gabon. Instead, they found fruit of *Coelocaryon preussi, Pycnanthus angolensis,* and *Polyalthia suaveolens* to be important keystone resources in this part of Gabon. At the Lopé, 160 km to the southwest, *Pycnanthus angolensis* is the only one of these species important in the diet of primates during the dry season. It is a common tree, but its arillate fruit does not ripen until late August, when the annual period of fruit scarcity at Lopé is nearing its end. However, monkeys eat immature *P. angolensis* seeds throughout the dry season, and for the guenons they are an important keystone resource (see Table IV). *Polyalthia suaveolens* and *Coelocaryon preussi* both bear ripe fruit in November–December; these are eaten by primates at Lopé but are not keystone resources, as they are not available during poor fruit months. The differences in keystone foods between study areas and between species within the same area show that the identification of such resources can be complex [see also Gautier-Hion et al.,

1993]. Different foods are important during regular, predictable periods of food scarcity (the annual dry season) compared to irregular and unpredictable periods of hardship, and this emphasizes the importance of long-term studies. Similarly, phenological patterns can vary between years at the same site [Tutin & Fernandez, 1993a] and between sites as close as Lopé and NE Gabon, making generalizations difficult.

Determinants of Biomass

Total primate biomass at Lopé is low [White, 1994a]. Equivalent figures from seven sites in tropical Africa range from a high of about 3,000 kg/km^2 at Kibale, Uganda, to a low of 217 kg/km^2 at Douala-Edéa, Cameroun [Bourlière, 1985; Oates et al., 1990; Struhsaker, 1975; Thomas, 1991]. Much of the variation in primate biomass between sites in central Africa is a direct result of differences in colobine biomass [Oates et al., 1990]. However, even when the colobus biomass is removed from the equation, Lopé, with 259 kg/km^2 of noncolobine primates, ranks lower than all sites except Douala-Edéa [Bourlière, 1985; Oates et al., 1990; Thomas, 1991]. Variations in primate densities between sites have been suggested to result from the presence or absence of competitive species [Harrison & Hladik, 1986], historical events (such as disease) [Butynski, 1990], variation in the plant species composition and structural heterogeneity of the habitat [Oates et al., 1990], and patterns of seasonal change in the availability of food [Oates et al., 1990].

The explanation of the low primate biomass at Lopé is not clear. Interspecific competition seems unlikely to be responsible as, at all but one of the above-mentioned sites, there are as many or more different primate species and biomass does not correlate with species diversity (r_s = 0.14, N = 7, ns). Elephant densities at Lopé are high, but, although elephants share many of the primates' foods, direct competition is limited, as elephants are restricted to feeding on terrestrial foods and fallen fruit, while all Lopé primates feed mostly in trees.

Historical events cannot be eliminated as the cause of the present-day low primate biomass at Lopé. Butynski [1990] concluded that the large difference in population densities of *Cercopithecus mitis* at two study sites, only 10–15 km apart, at Kibale, Uganda, was probably due to an unknown historical event such as disease. At Lopé, low primate biomass is not restricted to the area in which we studied primate diets, as White [1994a] found similar densities at four other sites within 30 km. While we can be only speculative, archaeological research in central Gabon is perhaps relevant. Evidence from stone tools, pottery, furnaces, and radiocarbon dating shows that humans have inhabited the Lopé area for at least 60,000 years [Oslisly, 1993]. There is, however, a period of 700 years between 1400 and 700 years BP when the area was void of humans [Oslisly, 1996]. The reason for this hiatus is unknown, but, if the same events affected nonhuman primate populations, present-day densities may still be below the carrying capacity of the forests.

The possibility of population declines of primates at Lopé in the more recent past as a result of either selective logging or hunting also seems unlikely, apart perhaps from chimpanzees (see below), as disturbance levels have been slight compared to some sites with high primate biomass, such as Kibale [Struhsaker, 1975] and Tiwai [Fimble, 1994]. The low level of selective logging which occurred in parts of our study area 20–25 years ago has been shown to have no detectable impact on primate populations with the exception of chimpanzees, which do show a significant decrease in population density after logging and take 15–25 years to recover [White, 1992; White & Tutin, in press]. The study area has been effectively protected from poaching since at least 1960. It is unlikely ever to have

been subjected to significant hunting pressure (i.e., with firearms), as the few inhabitants of this sparsely populated region (human population density for the Reserve averages 0.4 km^{-2}) are primarily fishermen and live close to the Ogooué and Offoué rivers, 15 km or more from the study area. In addition, densities of ungulates in the study area are comparable to or higher than those recorded elsewhere, and total mammalian biomass is the highest recorded for an African forest [White, 1994a].

The flora at Lopé is diverse and the habitat heterogeneous [Tutin et al., 1994], but this does not rule out plant species composition as contributing to the low primate biomass. For example, the diets of primates in the Salonga National Park, Zaire, are dominated by seeds and leaves of Leguminosae trees [Gautier-Hion et al., 1993; Maisels et al., 1994]. At Salonga, this botanical tribe dominates the vegetation (45.6% of trees) and produces some fruit in 11 of 12 months [Maisels et al., 1994]. In the Lopé study site, only 9.2% of trees are Leguminosae [White, 1992], and most produce fruit for a limited period between January and March [White, 1994b]. Only one species (*Swartzia fistuloides*) has an extended fruiting period, but it is not an important food for primates, as only mandrills occasionally eat the seeds. While this kind of difference in vegetation may be critical in determining biomass, more comparative data are required (on primate diets and biomass, and on plant species composition and fruiting phenology) before conclusions can be reached.

Oates et al. [1990] suggested that primate biomass may be determined by the availability of food during ecological "crunches." Differences in plant species composition and the heterogeneity of the habitat may interact with seasonality to determine primate densities. Fruit production at Lopé is highly seasonal, with a long dry season of 2–3 months during which little succulent fruit is available. This leads to an annual "bottleneck" period for frugivores. In some years the crunch imposed by poor fruit months can extend for up to eight months because of crop failures. It follows that species which are able to switch readily to a largely folivorous diet have a better chance of surviving long periods of low fruit availability. At Lopé, colobus, *C. nictitans,* and gorillas (the primates with the most foliage in their diets) have the highest biomasses of the diurnal primates (see Table V). The correlation between biomass and folivory reinforces the suggestion of a relationship between frugivory and low biomass within the primate community [see also Robinson & Redford, 1986], but this does not explain the low total biomass of primates compared to other sites.

While we cannot rule out historical factors such as disease, the low primate biomass at Lopé could be the result of vegetation history. Climatic changes in the region have had large impacts on vegetation in the past 25,000 years, and the extent of forest cover was much reduced as recently as 2,500 years ago [Maley, 1993]. Under present climatic conditions, forest actively colonizes the remaining Pleistocene savannas in the north of the Reserve except where regular burning blocks this succession [White, in press]. The forests of our study area date from 700–1,400 years ago, when the absence of humans greatly reduced the occurrence of fires and allowed major forest expansion. It is possible that populations of primates are still expanding to fill the naturally expanding forests, but it seems unlikely that such a process would not be complete after several hundred generations.

Less dramatic and more recent changes in climate could have had a profound impact on the availability of fruit foods within the forest. Many tree species at Lopé flower only if minimum temperatures of 19°C or less are experienced [Tutin & Fernandez, 1993a]. In years that are warmer than this critical temperature (three of ten), fruit is scarce from February to September, and this will

affect the most frugivorous species more than those with eclectic diets. During the study period we have seen one exceptional year (1992) when low temperatures occurred twice in the same year, triggering a second flowering episode in 23 normally annual tree species that produce fruit eaten by primates. The repercussions of this episode are still apparent in some of the tree species which, 3 years later, are flowering and fruiting in a less synchronized way than previously and producing small crops [unpublished data]. We have no evidence that the years of extended fruit scarcity had a negative effect on primates, but longer periods of scarcity, or several successive years of crop failure, would probably reduce birth rate and increase mortality of infants and juveniles [cf. Dittus, 1985; Foster, 1982] even if adults survived. Both the ease of dietary switching and the choice of keystone resources will influence vulnerability to extended periods of fruit scarcity.

In conclusion, comparable data from other sites in tropical Africa suggest that primate biomass at Lopé is low. The explanation for this is not clear, but it appears not to be a result of plant species composition or of competition between primate species. Historical events related to climate-induced changes in the extent of forest cover in the area, disease, or human-related impact through hunting or selective logging cannot be ruled out but seem unlikely. The biomasses of the eight species in the Lopé community are negatively correlated with degree of frugivory, suggesting that fruit availability may be critical. Little fruit is available each year during the dry season, but in some years, in part related to climatic variables, crop failures lead to more prolonged periods of fruit scarcity. No obvious impact of these poor fruit years was detected in the present study, but it is possible that an ecological catastrophe, such as several successive years with above normal temperatures in the quite recent past, led to mortalities. If this was indeed the case, it could be that populations, especially of the more frugivorous species, have not yet recovered.

A number of predictions emerge from our hypothesis. Some, related to competitive abilities within the frugivore guild, can be tested with systematic data on guenon feeding ecology at Lopé. For example, the relatively high biomass of *Cercopithecus nictitans* compared to the other frugivorous primates (see Table V) suggests evolutionary success [Eisenberg & Thorington, 1973], but whether this was achieved by out-competing other frugivores for limited fruit resources in the recent past or reflects dietary flexibility that buffered this species during past bottlenecks remains to be shown. Simple answers are unlikely to emerge, as neither the recent nor longer-term history of individual species can be reconstructed in detail, but more community studies and intersite comparisons should advance our understanding of the factors that determine and regulate primate biomass.

CONCLUSIONS

1. A community of eight species of diurnal primates in the Lopé Reserve, central Gabon (*Gorilla g. gorilla, Pan t. troglodytes, Colobus satanus, Cercocebus albigena, Mandrillus sphinx, Cercopithecus nictitans, C. pogonias, C. cephus*) share a tropical rain forest habitat. The diets of the first four species have been quantified over periods ranging from 9 months to 10 years, and all identified foods of all species have been recorded opportunistically over the whole study period (1984–1993). Despite the disparity of methods and amounts of quantitative data, a general picture emerges of the use of shared food resources by this primate community. A total of 397 different foods were recorded, and all primates had diverse diets, with 46–220 foods recorded per species. The diets of all eight primate species were dominated by

fruit or seeds but included leaves, flowers, and invertebrates. Other foods such as vertebrates, bark, and galls were eaten by a minority of the primate species.

2. Of the total foods, 183 (46%) were recorded for only one species, and only four foods (1%) were shared by all eight primates. Compared to seeds and leaves, significantly more fruit foods were shared. All primate species, including the three terrestrial ones, obtain the majority of their foods from trees. The proportion of foods harvested arboreally ranged from 64–100%.

3. The availability of fruit varied from month to month, and interannual fluctuations also occurred. During the annual 3 month dry season, fruit was scarce each year, and in some years crop failures led to additional months of scarcity. When fruit was scarce, the diets of all species changed to include more leaves, flowers, and insects, but only for gorillas was dietary breadth notably reduced. Keystone foods during periods of fruit scarcity varied: in some cases, choice was related to morphological characters (e.g., only species with powerful jaws fed on mechanically protected seeds). The guenons and chimpanzees maintained a relatively high intake of fruit by exploiting small arillate fruit and palm nuts, while gorillas ate large amounts of pith from herbaceous plants and inner bark of a common large tree. Some keystone resources were not preferred foods, as, despite constant availability, they were eaten only when fruit was scarce.

4. The total biomass of primates in the Lopé study area, 374 kg km^{-2}, is low compared to other forest sites in Africa. Within the primate community, biomass is positively correlated with the degree of folivory, suggesting a relationship between diet and biomass.

5. The low primate biomass at Lopé is not easily explained, but the most likely hypothesis to emerge is that in the recent past successive, or grouped, years of fruit scarcity occurred as a result of higher than normal temperatures (known to inhibit flowering in some major fruit-producing tree species at Lopé). We suggest that a prolonged period of fruit scarcity would have caused mortalities and that the most frugivorous species would have been worst affected.

REFERENCES

Altmann, J. Observational study of behavior: Sampling methods. BEHAVIOUR 49:227–267, 1974.
Bourlière, F. Primate communities: Their structure and role in tropical ecosystems. INTERNATIONAL JOURNAL OF PRIMATOLOGY 6:1–26, 1985.
Butynski, T.M. Guenon birth seasons and

correlates with rainfall and food. Pp. 284–322 in A PRIMATE RADIATION: EVOLUTIONARY BIOLOGY OF THE AFRICAN GUENONS. A. Gautier-Hion; F. Bourlière; J.-P. Gautier; J. Kingdon, eds. Cambridge, Cambridge University Press, 1988.

Chapman, C. Flexibility in diets of three species of Costa Rican primates. FOLIA PRIMATOLOGIA 49:90–105, 1987.

Collet, J.-Y.; Bourreau, E.; Cooper, R.W.; Tutin, C.E.G.; Fernandez, M. Experimental demonstration of cellulose digestion by *Troglodytella gorillae,* an intestinal ciliate of lowland gorillas. INTERNATIONAL JOURNAL OF PRIMATOLOGY 5:328–1984.

Dasilva, G.L. Diet of *Colobus polykomos* on Tiwai Island: Selection of food in relation to its seasonal abundance and nutritional quality. INTERNATIONAL JOURNAL OF PRIMATOLOGY 15:655–680, 1994.

Davies, A.G.; Oates, J.F. COLOBINE MONKEYS. Cambridge, Cambridge University Press, 1994.

Dittus, W.P.J. The influence of leaf-monkeys on their feeding trees in a cyclone disturbed environment. BIOTROPICA 17:100–106, 1985.

Eisenberg, J.F.; Thorington, R.W., Jr. A preliminary analysis of a Neotropical mammal fauna. BIOTROPICA 5:150–161, 1973.

Emmons, L.H.; Gautier-Hion, A.; and Dubost, G. Community structure of the frugivorous-folivorous forest mammals of Gabon. JOURNAL OF ZOOLOGY 199:209–222, 1983.

Fimble, C. The relative use of abandoned farm clearings and old forest habitats by primates and a forest antelope at Tiwai, Sierra Leone, West Africa. BIOLOGICAL CONSERVATION 70:277–286, 1994.

Foster, R.B. Famine on Barro Colorado Island. Pp. 151–172 in THE ECOLOGY OF A TROPICAL FOREST: SEASONAL RHYTHMS AND LONG-TERM CHANGES. E.G. Leigh; A.S. Rand; D.M. Windsor, eds. Washington DC, Smithsonian Institution Press, 1982.

Frankie, G.W.; Baker, H.G.; Opler, P.A. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. JOURNAL OF ECOLOGY 62:881–919, 1974.

Galat, G.; Galat-Luong, A. La communaute de primates diurnes de la foret de Tai, Cote-d'Ivoire. TERRE ET VIE 40:3–32, 1985.

Gautier-Hion, A. Seasonal variation of diet related to species and sex in a community of *Cercopithecus* monkeys. JOURNAL OF ANIMAL ECOLOGY 49:237–269, 1980.

Gautier-Hion, A. Leaf consumption by monkeys in western and eastern Africa: A comparison. AFRICAN JOURNAL OF ECOLOGY 21:107–113, 1983.

Gautier-Hion, A. The diet and dietary habits of forest guenons. Pp. 257–283 in A PRIMATE RADIATION: EVOLUTIONARY BIOLOGY OF THE AFRICAN GUENONS. A. Gautier-Hion; F. Bourlière; J.P. Gautier; J. Kingdon, eds. Cambridge, Cambridge University Press, 1988.

Gautier-Hion, A.; Gautier, J.P. Les associations polyspécifiques chez les Cercopithèques du plateau de M'passa, Gabon. FOLIA PRIMATOLOGIA 22:134–177, 1974.

Gautier-Hion, A.; Michaloud, G. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. ECOLOGY 70:1826–1833, 1989.

Gautier-Hion, A.; Gautier, J.P.; Maisels, F. Seed dispersal versus seed predation: An inter-site comparison of two related African monkeys. VEGETATIO 107/108:237–244, 1993.

Haltenorth, T.; Diller, H. A FIELD GUIDE TO THE MAMMALS OF AFRICA INCLUDING MADAGASCAR. London, Collins, 1977.

Ham, R.M. BEHAVIOUR AND ECOLOGY OF GREY-CHEEKED MANGABEYS (*Cercocebus albigena*) IN THE LOPE RESERVE, GABON. Ph.D. thesis, University of Stirling, 1994.

Harrison, M.J.S. Feeding ecology of black colobus (*Colobus satanas*) in central Gabon. Pp. 31–38 in PRIMATE ECOLOGY AND CONSERVATION. J.G. Else; P.C. Lee, eds. Cambridge, Cambridge University Press, 1986.

Harrison, M.J.S. The mandrill in Gabon's rain forest—ecology, distribution and status. ORYX 22:218–228, 1988.

Harrison, M.J.S.; Hladik, C.M. Un primate granivore: Le Colobe noir dans la forêt du Gabon: Potentialité d'évolution du comportement alimentaire. TERRE ET VIE 41:281–298, 1986.

Hladik, A. Phenology of leaf production in rain forest of Gabon: Distribution and composition of food for folivores. Pp. 51–72 in THE ECOLOGY OF ARBOREAL FRUGIVORES. G.G. Montgomery, ed. Washington DC, Smithsonian Institution Press, 1978.

Hladik, C.M. Allimentation et activité d'un group de chimpanzés reintroduits en fôret Gabonais. TERRE ET VIE 27:343–413, 1973.

Hladik, C.M. A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *P. entellus.* Pp. 481–501 in PRIMATE ECOLOGY: STUDIES OF FEEDING AND RANGING BEHAVIOUR IN LEMURS MONKEYS AND APES. T.H. Clutton-Brock, ed. New York, Academic Press, 1977.

Jouventin, P. Observations sur la socio-écologie du mandrill. TERRE ET VIE 29:493–532, 1975.

Jungers, W.L.; Susman, R.L. Body size and skeletal allometry in African apes. Pp. 131–177 in THE PYGMY CHIMPANZEE: EVOLUTIONARY BIOLOGY AND BEHAVIOR. R.L. Susman, ed. New York, Plenum Press, 1984.

Kinzey, W.G. Diet and feeding in *Callicebus torquatus*. Pp. 127–151 in PRIMATE ECOLOGY. T.H. Clutton-Brock, ed. London, Academic Press, 1977.

Lahm, S.A. Diet and habitat preference of *Mandrillus sphinx* in Gabon: Implications of foraging strategy. AMERICAN JOURNAL OF PRIMATOLOGY 11:9–26, 1986.

Leigh, E.G.; Smythe, N. Leaf production, leaf consumption and the regulation of folivory on Barro Colorado Island, Pp. 33–50 in THE ECOLOGY OF ARBOREAL FRUGIVORES. G.G. Montgomery, ed. Washington DC, Smithsonian Institution Press, 1978.

Leighton, M.; Leighton, D.R. Vertebrate response to fruiting seasonality within a Bornean rain forest. Pp. 181–196 in TROPICAL RAIN FOREST: ECOLOGY AND MANAGEMENT. S.L. Sutton, T.C. Whitmore, A.C. Chadwick, eds. London, Blackwell Scientific, 1983.

MacKinnon, J.R.; MacKinnon, K.S. Niche differentiation in a primate community. Pp. 167–190 in MALAYAN FOREST PRIMATES: TEN YEARS STUDY IN TROPICAL RAIN FOREST. D.J. Chivers, ed. New York, Plenum Press, 1980.

Maisels, F.; Gautier-Hion, A.; Gautier, J.P. Diets of two sympatric colobines in Zaire: More evidence on seed-eating in forests on poor soils. INTERNATIONAL JOURNAL OF PRIMATOLOGY 15:681–701, 1994.

Maley, J. The climatic and vegetational history of the equatorial regions of Africa during the upper Quaternary. Pp. 43–52 in THE ARCHAEOLOGY OF AFRICA. T. Shaw, P. Sinclair, B. Andah, A. Okpoko, eds. London, Routledge, 1993.

McGrew, W.C.; Baldwin, P.J.; Tutin, C.E.G. Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal. I. Composition. AMERICAN JOURNAL OF PRIMATOLOGY 16:213–223, 1988.

Moutsamboté, J.M.; Yumoto, T.; Mitani, M.; Nishihara, T.; Suzuki, S.; Kuroda, S. Vegetation and list of plant species identified in the Nouabalé-Ndoki Forest, Congo. TROPICS 3:277–294, 1994.

Nishida, T. The bark-eating habits in primates with special reference to their status in the diet of wild chimpanzees. FOLIA PRIMATOLOGIA 25:277–287, 1976.

Oates, J.F. The guereza and its food. Pp. 276–321 in PRIMATE ECOLOGY. T.H. Clutton-Brock, ed. London, Academic Press, 1977.

Oates, J.F.; Whitesides, G.H.; Davies, A.G.; Waterman, P.G.; Green, S.M.; Dasilva, G.L.; Mole, S. Determinants of variation in tropical forest primate biomass: New evidence from West Africa. ECOLOGY 71:328–343, 1990.

Oslisly, R. PRÉHISTOIRE DE LA MOYENNE VALLÉE DE L'OGOOUÉ (GABON). TRAVAUX ET DOCUMENTS MICROEDITES NO. 96. Paris, ORSTOM Editions, 1993.

Oslisly, R. The middle Ogooué valley, Gabon, from 3500 yrs. bp: Cultural changes and palaeoclimatic implications. ANZANIA 14/15:324–331, 1996.

Robinson, J.G.; Redford, K.H. Body size, diet and population density of Neotropical forest mammals. THE AMERICAN NATURALIST 128:665–680, 1986.

Rogers, M.E.; Maisels, F.; Williamson, E.A.; Tutin, C.E.G.; Fernandez, M. The diet of the gorillas in the Lopé Reserve, Gabon: A nutritional analysis. OECOLOGIA 84:326–339, 1990.

Rogers, M.E.; Tutin, C.E.G.; Williamson, E.A.; Parnell, R.J.; Voysey, B.C.; Fernandez, M. Seasonal feeding on bark by gorillas: an unexpected keystone food? Pp. 37–43 in CURRENT PRIMATOLOGY, VOL. 1: ECOLOGY AND EVOLUTION. B. Thierry, J.R. Anderson, J.J. Roeder, N. Herrenschmidt, eds. Strasbourg, Université Louis Pasteur, 1994.

Skoropa, J.P. Monkeys and matrices: A second look. OECOLOGIA 57:391–396, 1983.

Struhsaker, T.T. THE RED COLOBUS. Chicago, University of Chicago Press, 1975.

Struhsaker, T.T.; Leland, L. Socioecology of five sympatric monkey species in the Kibale forest Uganda. ADVANCES IN THE STUDY OF BEHAVIOUR 9:159–228, 1979.

Terborgh, J. FIVE NEW WORLD PRIMATES. Princeton, Princeton University Press, 1983.

Terborgh, J. Keystone plant resources in the tropical forest. Pp. 330–344 in CONSERVATION BIOLOGY: THE SCIENCE OF SCARCITY. M.D. Soulé, ed. Sunderland, MA, Sinauer Associates, 1986.

Terborgh, J.; van Schaik, C.P. Convergence vs. nonconvergence in primate communities. Pp. 205–226 in ORGANISATION OF COMMUNITIES: PAST AND PRESENT. J.H.R. Gee, P.S. Giller, eds. Oxford, Blackwell Scientific Publications, 1987.

Thomas, S.C. Population densities and patterns of habitat use among anthropoid primates of the Ituri Forest, Zaire. BIOTROPICA 23:68–83, 1991.

Tutin, C.E.G.; Fernandez, M. Nationwide census of gorilla (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) popula-

tions in Gabon. AMERICAN JOURNAL OF PRIMATOLOGY 6:313–336, 1984.

Tutin, C.E.G.; Fernandez, M. Responses of wild chimpanzees and gorillas to the arrival of primatologists: Behaviour observed during habituation. Pp. 187–197 in PRIMATE RESPONSES TO ENVIRONMENTAL CHANGE. H.O. Box, ed. London, Chapman and Hall, 1990.

Tutin, C.E.G.; Fernandez, M. Relationships between minimum temperature and fruit production in some tropical forest trees in Gabon. JOURNAL OF TROPICAL ECOLOGY 9:241–248, 1993a.

Tutin, C.E.G.; Fernandez, M. Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. AMERICAN JOURNAL OF PRIMATOLOGY 30:195–211, 1993b.

Tutin, C.E.G.; Fernandez, M.; Rogers, M.E.; Williamson, E.A.; McGrew, W.C. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY OF LONDON SERIES B 334:179–186, 1991.

Tutin, C.E.G.; White, L.J.T.; Williamson, E.A.; Fernandez, M.; McPherson, G. List of plant species identified in the northern part of the Lopé Reserve, Gabon. TROPICS 3:249–276, 1994.

van Schaik, C.P.; Terborgh, J.W.; Wright, S.J. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. ANNUAL REVIEW OF ECOLOGICAL SYSTEMATICS 24:353–377, 1993.

Waser, P.M. Feeding, ranging and group size in the mangabey *Cercocebus albigena.* Pp. 182–222 in PRIMATE ECOLOGY. T.H. Clutton-Brock, ed. London, Academic Press, 1977.

Waser, P.M. Interactions among primate species. Pp. 210–226 in PRIMATE SOCIETIES. B.B. Smuts; D.L. Cheyney; R.M. Seyfarth; R.W. Wrangham; T.T. Struhsaker, eds. Chicago, Chicago University Press, 1987.

Waser, P.M.; Case, T.J. Monkeys and Matrices: On the coexistence of "omnivorous" forest primates. OECOLOGIA 49:102–108, 1981.

Watts, D.P. Ecology of gorillas and its relation to female transfer in mountain gorillas. INTERNATIONAL JOURNAL OF PRIMATOLOGY 11:21–45, 1990.

White, L.J.T. VEGETATION HISTORY AND LOGGING DISTURBANCE: EFFECTS ON RAIN FOREST MAMMALS IN THE LOPÉ RESERVE, GABON. Ph.D. thesis, University of Edinburgh, 1992.

White, L.J.T. Biomass of rain forest mammals in the Lopé Reserve, Gabon. JOURNAL OF ANIMAL ECOLOGY 63:499–512, 1994a.

White, L.J.T. Patterns of fruit-fall phenology in the Lopé Reserve, Gabon. JOURNAL OF TROPICAL ECOLOGY 10:289–312, 1994b.

White, L.J.T. Forest-savanna dynamics and the origins of 'Marantaceae Forest' in the Lopé Reserve, Gabon. In AFRICAN RAIN FOREST ECOLOGY AND CONSERVATION. B. Weber; L.J.T. White; A. Vedder; H. Simons-Morland, eds. New Haven, Yale University Press, in press.

White, L.J.T.; Tutin, C.E.G. Why chimpanzees and gorillas respond differently to logging: A cautionary tale from Gabon. In AFRICAN RAIN FOREST ECOLOGY AND CONSERVATION. B. Weber; L.J.T. White; A. Vedder; H. Simons-Morland, eds. New Haven, Yale University Press, in press.

White, L.J.T.; Rogers, M.E.; Tutin, C.E.G.; Williamson, E.A.; Fernandez, M. Herbaceous vegetation in different forest types in the Lopé Reserve, Gabon: Implications for keystone food availability. AFRICAN JOURNAL OF ECOLOGY 33:124–141, 1995.

Whitesides, G.H.; Oates, J.F.; Green, S.M.; Kluberdanz, R.P. Estimating primate densities from transects in West African rain forest: A comparison of techniques. JOURNAL OF ANIMAL ECOLOGY 57:345–367, 1988.

Williamson, E.A.; Tutin, C.E.G.; Rogers, M.E.; Fernandez, M. Composition of the diet of lowland gorillas at Lopé in Gabon. AMERICAN JOURNAL OF PRIMATOLOGY 21:265–277, 1990.

Wrangham, R.W. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. Pp. 504–538 in PRIMATE ECOLOGY. T.H. Clutton-Brock, ed. London, Academic Press, 1977.

Wrangham, R.W.; Conklin, N.L.; Chapman, C.A.; Hunt, K.D. The significance of fibrous foods for Kibale Forest chimpanzees. PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY OF LONDON SERIES B 334:171–178, 1991.

Wrangham, R.W.; Conklin, N.L.; Etot, G.; Obua, J.; Hunt, K.D.; Hauser, M.D.; Clark, A.P. The value of figs to chimpanzees. INTERNATIONAL JOURNAL OF PRIMATOLOGY 14:243–256, 1993.