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Composition of the Diet of Chimpanzees and Comparisons With That of Sympatric Lowland Gorillas in the Lopé Reserve, Gabon

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Over an eight-year period, a total of 174 food items were recorded for chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve in central Gabon. Plant foods, principally fruit, dominated the diet but insects were eaten regularly, and predation on at least three species of mammal occurred infrequently. The diversity of the vegetative component of the diet (leaves, stems, and bark) was probably underestimated by fecal analysis. Comparison of chimpanzee diet at Lopé with that of sympatric lowland gorillas showed the majority of foods were eaten by both species (73% of chimpanzee food items and 57% of gorilla food items). The overlap of fruit species was greater (82% and 79%, respectively) than that of other food classes. Both chimpanzees and gorillas harvested the majority of their plant foods arboreally (76% and 69%, respectively). The high degree of dietary overlap suggested that ecological competition between these two closely related species might exist. Few overt signs of competition for food either between or within species were observed but when fruit was scarce, the diets of the two species showed greatest divergence. The major differences between chimpanzee and gorilla diet at Lopé were the larger quantities of vegetative foods regularly eaten by gorillas and their ability to resort to a diet dominated by vegetative foods when fruit was scarce. In these respects, chimpanzees at Lopé resembled populations of *Pan troglodytes* studied elsewhere while Lopé gorillas resembled mountain gorillas (*Gorilla g. beringei*) and bonobos (*Pan paniscus*) in their greater dependence on vegetative foods.

Key words: chimpanzee, gorilla, diet, frugivory, keystone foods

INTRODUCTION

Description of the diet of wild primates contributes to understanding the behavioral ecology and evolution of the study species and allows comparisons of dietary niche of the same species in different habitats and of different species in a shared habitat. The diet of chimpanzees (*Pan troglodytes*) has been described from a number of habitats, ranging from a savanna-dominated area in Senegal [Mc-

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Grew et al., 1988], through woodland-forest mosaic in western Tanzania [Wrangham, 1977; Nishida, 1974; Nishida & Uehara, 1983] and in Guinea [Sugiyama & Koman, 1987], to tropical rain forest in Equatorial Guinea [Sabater Pi, 1979] and Gabon [Hladik, 1973]. The potential diet is defined by the availability of foods in each habitat but inter-site comparisons are often confounded by incomplete knowledge of the flora of different sites. The number of food items recorded has been found to vary both with habitat and with the duration of study. For example, Nishida [1974] listed 205 foods in the diet of chimpanzees of the Mahale Mountains, Tanzania, after 7 years of study but, after 16 years, the number of identified foods had increased to 328 [Nishida & Uehara, 1983]. Contrasting with this, chimpanzee diet in a savanna dominated habitat, at Mt. Assirik, Senegal, comprised only 68 foods after 5 years of study and it was estimated, from foods recorded for other primates but not directly for chimpanzees, that their diet in this marginal habitat could include a maximum of only 122 items [McGrew et al., 1988].

The tropical forest habitat of Gabon, on the west equatorial coast of Africa, has a highly diverse flora [e.g., Hladik, 1986; Reitsma, 1988] so a wide range of potential foods is available. Gautier-Hion [1983] has suggested that the greater diversity of plants in western African forests, compared to those of East Africa, allows monkeys to be more frugivorous in the western forests. Fruit and seeds dominate the diets of all of the eight species of diurnal primate in the Lopé Reserve in central Gabon. Fruit availability varies seasonally at Lopé [Tutin et al., 1991a] and succulent fruit is scarce during the 3-month dry season [Rogers et al., 1988]. Phenological monitoring of 60 tree species that produce fruit foods for apes at Lopé showed inter-annual as well as seasonal variation in the availability of ripe fruit with 4 to 24 of the 60 species bearing ripe fruit per month [Tutin et al., 1991a]. Terborgh [1986] and Gautier-Hion and Michaloud [1989] have demonstrated the dependence of frugivorous vertebrate communities in tropical forests on "keystone plant resources" during periods of fruit scarcity. In these tropical ecosystems niche differentiation between many sympatric primate species is clear-cut only at times when few fruit foods are available [Gautier-Hion, 1980; Terborgh, 1983]. Data from short-term studies of sympatric gorillas and chimpanzees suggested that the degree of dietary overlap increases with plant diversity, being highest in lowland tropical forest [Kuroda, 1992; Sabater Pi, 1977; Tutin & Fernandez, 1985; Yamagiwa et al., 1992]. But, as both seasonal and inter-annual variations in food availability are great, long-term data on foods consumed are essential in order to compare the diets of sympatric primate species and to examine ecological parameters such as niche separation and competition.

A recent paper by Williamson et al. [1990] described the diet of lowland gorillas (*Gorilla gorilla gorilla*) at Lopé. These lowland gorillas have the most diverse diet and are the most frugivorous of any population of *Gorilla* studied to date [Williamson et al., 1990]. While the degree of frugivory of gorillas is related to large differences in the availability of fruit between habitats [Watts, 1990], fruit dominates chimpanzee diet in all habitats [Peters & O'Brien, 1981]. The diet of bonobos (*Pan paniscus*) has been described at two study sites and resembles that of chimpanzees and of lowland gorillas at Lopé, with fruit being the dominant food class [Badrian & Malenky, 1984; Kano & Mulavwa, 1984].

Chimpanzees and gorillas are genetically close and show remarkable similarity in morphological features related to diet such as craniodental anatomy [Shea, 1983], gut morphology [Chivers & Hladik, 1984], and gut passage time [Milton, 1984]. The two species do differ in body size and in the degree of sexual dimorphism but sparse data compiled by Jungers and Susman [1984] on the weights of wild *Gorilla g. gorilla* and *Pan t. troglodytes* (the sub-species found at Lopé) indicate that, apart from the large adult male gorilla, body size differs less in forest habitats as female gorillas (N = 3) weighed 42%, and male (N = 3) and female (N = 3) chimpanzees 35% and 28%, respectively, of the mean adult male gorilla weight of 170 kg (N = 14).

This paper describes the composition of the diet of the Lopé chimpanzees, presenting data in the format used by Williamson et al. [1990] to describe the diet of gorillas at the same study site. Methods used to collect data on gorilla and chimpanzee diet at Lopé were the same and cover 8 consecutive years, allowing an assessment of the similarities and differences in utilization of the available food resources by the two species in a shared habitat.

STUDY AREA AND METHODS

The study area of the S.E.G.C. (Station d'Etudes des Gorilles et Chimpanzés) covers approximately 40 km^2 of tropical rain forest in the Lopé Reserve in central Gabon (0°10′S; 11°35′E). Within the study area, the forest is heterogeneous in both floristic composition and structure but areas with a dense understorey of herbs, dominated by species of Marantaceae and Zingiberaceae, are common [Rogers & Williamson, 1987]. Trees of the families Caesalpiniaceae, Burseraceae, Euphorbiaceae, Mimosaceae, Ochnaceae, and Sterculiaceae dominate the upper canopy, and the commonest smaller trees are members of the Annonaceae, Ebenaceae, and Rubiaceae [Williamson, 1988; White, 1992].

Average annual rainfall was 1,498 mm (1984–1991) and the climate was characterized by a 3-month dry season lasting from about mid-June to mid-September. Mean monthly minimum and maximum air temperatures varied from 20.1–23.2°C and 27.0–32.8°C, respectively.

Research began in late 1983 and is ongoing. Chimpanzees and gorillas occur at similar population densities of about one individual per square kilometer. Field procedure involved searching through the study area for chimpanzees and gorillas, or for indirect signs of their presence and activities. The chimpanzees were shy and, as visibility in many areas of forest was poor, observation was limited. Thus, in addition to observation, we used indirect methods to describe diet, systematically collecting fresh feces. Identification of non-fruit foods came from direct observation and we have also observed chimpanzees feeding on the majority (67%) of the fruit foods recorded below. Additional fruit, insect, and mammalian foods have been identified from fecal analysis, but only foods recorded in more than one fecal sample are included in the following analysis. Fecal analysis allows quantification of seasonal and inter-annual variation in diet and is an invaluable tool for the study of the diet of wild apes [McGrew et al., 1988; Kano & Mulavwa, 1984].

Fecal samples collected in the field were sealed in plastic bags and later were weighed and washed in sieves with 1 mm mesh. The particulate remains were examined macroscopically and the contents listed: large seeds were counted and small seeds rated on a four-point scale of abundance (abundant, common, few, rare). Non-fruit plant parts (leaves, stems, bark) could not be identified to species level macroscopically, so the volumes of the categories *fiber* (representing the characteristic remains of monocotyledon piths and of bark) and *green leaf fragments* (representing remains of ingested leaves) were assessed with respect to the total mass of the fecal sample and rated on the same four-point abundance scale. A numerical value for the proportion of non-fruit remains in feces was computed by converting the abundance ratings as follows: abundant = 4; common = 3; few = 2; rare = 1. The combined score of the categories fiber and green leaf fragments gave a foliage score for each fecal sample. Some food items (flowers, soft-bodied invertebrates) left no recognizable remains in feces (this problem is returned to

TABLE I. Composition of the Diet of Chimpanzees at Lopé, Gabon

Taxon/life-form	N species	Parts eaten	N items
Marantaceae	5	Young leaves	5
Zingiberaceae	5	Mature leaves	1
Acanthacaceae	1	Basal pith	2
Palmae	2	Stem pith	7
Total	13	Fruit	7
		Seeds	2
		Total	24
Trees	87	Pulp	99
Shrubs	5	Seed	10
Vines	11	Arils	5
Unknown	4	Total	114
Total	107		
Trees	11	Young leaves	12
Shrubs	2	Mature leaves	2
Vines	1	Total	14
Total	14		
Trees	5	Flowers	5
Trees	3	Bark	3
Trees	1	Galls	1
		Total plant food items	161
Soil	1		
Ants	>5		
Honey/bees	3		
Caterpillars	>1		
Mammals	>3		
Total	>13		
		Total food items	174

below) but fruit parts (seeds, skin, fiber) could be readily distinguished from non-fruit remnants allowing assessment of the relative importance of fruit and non-fruit plant parts in each fecal sample.

Samples of all plant foods were collected and specimens were identified at the Royal Botanic Gardens, Kew, the Museum of Natural History, Paris, Missouri Botanic Gardens, St. Louis, and the National Herbarium of Gabon, Libreville.

The data come from 8 years of continuous research (January 1984–December 1991) during which there were 857 contacts with at least two communities of chimpanzees. A total of 1,854 fecal samples were collected during 93 of the 96 months. Numbers of feces examined varied between years ($\overline{X}$ = 232, range 73–321) but the total sample was more evenly distributed over the calendar months ($\overline{X}$ by month = 156, range 114–229). Tables I and II follow the format of Williamson et al. [1990] to allow direct comparison of gorilla and chimpanzee diet at Lopé.

RESULTS

Composition of the Diet

Chimpanzees at Lopé were found to eat 161 different plant parts of at least 132 species from 34 taxonomic families. Table I summarises the diet, and Table II lists

TABLE II. Species of Plants Eaten by Chimpanzees at Lopé, Gabon

Scientific name	Family	Pulp	Seed	Leaf	Stem	Bark	Flower	Galls
Aframomum leptolepis	Zingiberaceae	x			x			
Aframomum longipetiolatum	Zingiberaceae	x			x			
Aframomum sp. ?nov.	Zingiberaceae	x			x			
Anisotes macrophylla	Acanthaceae			x				
Antidesma laciniatum[a]	Euphorbiaceae	x						
Antidesma vogelianum	Euphorbiaceae	x						
Antrocaryon klaineanum	Anacardiaceae	x						
Ataenidia conferta	Marantaceae			x				
Atractogyne gabonii[a]	Rubiaceae	x						
Aucoumea klaineana	Burseraceae						x	
Baillonella toxisperma	Sapotaceae	x						
Barteria fistulosa	Passifloraceae	x						
Beilschmeidia fulva	Lauraceae	x						
Beilschmeidia sp. #140	Lauraceae	x						
Canarium schweinfurthii	Burseraceae	x						
Celtis tessmannii	Ulmaceae	x						
Cissus dinklagei[a]	Vitaceae	x						
Cola lizae	Sterculiaceae	x		x	x			
Costus afer	Zingiberaceae				x			
Cryptosepalum staudtii	Caesalpiniaceae		x	x		x		
Dacryodes buettneri	Burseraceae	x				x		
Dacryodes igaganga	Burseraceae	x						
Dacryodes klaineana	Burseraceae	x						
Daryodes normandii	Burseraceae	x						
Dialium eurysephalum	Caesalpiniaceae	x						
Dialium lopense[a]	Caesalpiniaceae	x	x	x				
Dialium pachyphyllum	Caesalpiniaceae	x						
Dichapetalum sp. #264[a]	Dichapetalaceae	x						
Diospyros abyssinica	Ebenaceae	x						
Diospyros cf. cinnabarina	Ebenaceae			x				
Diospyros dendo	Ebenaceae	x	x					
Diospyros mannii[a]	Ebenaceae	x						
Diospyros piscatoria	Ebenaceae	x						
Diospyros polystemon	Ebenaceae	x	x					
Diospyros soyauxii	Ebenaceae	x						
Diospyros sp. #286	Ebenaceae	x						
Diospyros zenkeri[a]	Ebenaceae	x						
Discoglypremna coloneura	Euphorbiaceae	x						
Distemonanthus benthamianus	Caesalpiniaceae			x			x	
Duboscia macrocarpa	Tiliaceae	x	x					
Elaeis guineensis	Palmae	x			x			
Enantia chlorantha	Annonaceae	x						
Eremospatha carbrae	Palmae	x			x			
Ficus ingens	Moraceae	x						
Ficus polita	Moraceae	x						
Ficus bubu	Moraceae	x						
Ficus cf. dicranostyla	Moraceae			x				
Ficus macrosperma	Moraceae	x						
Ficus mucuso	Moraceae	x						
Ficus recurvata	Moraceae	x						
Ficus thonningii	Moraceae	x						
Ficus sp. #408	Moraceae	x						
Ficus sp. #441	Moraceae	x						

(continued on overleaf)

TABLE II. Species of Plants Eaten by Chimpanzees at Lopé, Gabon (Continued from previous page)

Scientific name	Family	Pulp	Seed	Leaf	Stem	Bark	Flower	Galls
Ficus sp. #443	Moraceae	x						
Gambeya africana	Sapotaceae	x						
Gambeya subnuda[a]	Sapotaceae	x						
Ganophyllum giganteum[a]	Sapindaceae	x						
Garcinia afzelii	Guttiferae	x						
Grewia coriacea	Tiliaceae	x						
Guibourtia tessmannii	Caesalpiniaceae		x					
Haumania liebrechstiana	Marantaceae		x	x				
Heisteria parvifolia	Olacaceae	x						
Hexalobus crispiflorus	Annonaceae	x						
Hypselodelphis violacea	Marantaceae		x	x				
Irvingia gabonensis	Irvingiaceae	x	x					
Irvingia grandifolia	Irvingiaceae	x						
Julbernardia brieyi[a]	Caesalpiniaceae		x	x		x		
Klainedoxa gabonensis	Irvingiaceae	x					x	
Klainedoxa microphylla	Irvingiaceae	x						
Landolphia cf. heudelotti[a]	Apocynaceae	x						
Leptoderris sp. #57	Papilionaceae			x				
Lecaniodiscus cupanoides	Sapindaceae	x						
Lophira alata	Ochnaceae							x
Mammea africana	Guttiferae	x						
Mangifera indica	Anacardiaceae	x						
Manilkara ? fouilloyara	Sapotaceae	x						
Megaphrynium gabonense	Marantaceae	x		x				
Megaphrynium macrostachya	Marantaceae	x		x				
Millettia sp. #102	Papilionaceae			x				
Monanthotaxis congensis	Annonaceae	x						
Monodora angolensis	Annonaceae	x						
Myrianthus arboreus	Moraceae	x						
Nauclea didderichi	Rubiaceae	x						
Nauclea vanderguchtii	Rubiaceae	x						
Ongokea gore	Olacaceae			x				
Parkia bicolor	Mimosaceae	x						
Parkia filicoidea	Mimosaceae	x						
Pentaclethra macrophylla	Mimosaceae			x			x	
Plagiostyles africana	Euphorbiaceae	x						
Polyathia suaveolens	Annonaceae	x						
Porterandia cladantha	Rubiaceae	x						
Pseudospondias longifolia	Anacardiaceae	x						
Pseudospondias microcarpa	Anacardiaceae	x						
Psidium guineensis[a]	Myrtaceae	x						
Psorospermum tenuifolium	Hypericaceae			x				
Psychotria peduncularis	Rubiaceae	x						
Psychotria vogeliana	Rubiaceae	x						
Pterocarpus soyauxii	Papilionaceae		x				x	
Ptychopetalum petiolatum	Olacaceae	x						
Pycnanthus angolensis	Myristicaceae	x						
Renealmia macrocolea	Zingiberaceae				x			
Santiria trimera	Burseraceae	x						
Scytopetalum sp. #168[a]	Scytopetalaceae	x						
Staudtia gabunensis	Myristicaceae	x						
Sterculia tragacantha	Sterculiaceae			x				
Treculia africana	Moraceae	x	x				x	

(continued)

TABLE II. Species of Plants Eaten by Chimpanzees at Lopé, Gabon (Continued)

Scientific name	Family	Pulp	Seed	Leaf	Stem	Bark	Flower	Galls
Trichoscypha acuminata	Anacardiaceae	x						
Trichoscypha patens	Anacardiaceae	x						
Uapaca heudelotti[a]	Euphorbiaceae	x						
Uapaca guineensis	Euphorbiaceae	x						
Uapaca cf. sansibarica	Euphorbiaceae	x						
Uapaca vanhouttei	Euphorbiaceae	x						
Uapaca sp. #299	Euphorbiaceae	x						
Uvaria sp. #162	Annonaceae	x						
Uvaria sp. #256	Annonaceae	x						
Uvariastrum pierreanum	Annonaceae	x						
Vitex doniana	Verbenaceae	x						
Xylopia aethiopica	Annonaceae	x						
Xylopia hypolampra	Annonaceae	x						
Xylopia quintasii	Annonaceae	x						
SEGC #117	Annonaceae	x						
SEGC #182	Annonaceae	x						
SEGC #347	Passifloraceae	x						
SEGC #385	Apocynaceae	x						
SEGC #428	Annonaceae	x						
SEGC #431	Menispermaceae	x						
Subtotals		105	12	19	8	3	6	1
Unidentified foods		6		1				
Totals		111	12	20	8	3	6	1

[a]Taxonomic errors or changes as compared to Williamson et al. [1990]: *Antidesma laciniatum = Antidesma sp. #251; Atractogyne gabonii* = SEGC #56; *Cissus dinklagei = Cissus sp. #145; Dialium lopense = Dialium cf. soyauxii; Diospyros mannii = Diospyros suaveolens; Diospyros zenkeri = Diospyros cf. iturensis; Gambeya subnuda = Chrysophyllum subnudum; Ganophyllum giganteum = Zanha golungensis; Julbernadia brieyi = Brachaystegia aff. eurycoma; Klainedoxa microphyllaa = Klainedoxa sp. #208; Landolphia cf. heudelotti* = SEGC #36; *Psidium guineensis = Psidium sp. #53; Scytopetalum sp. #168 = Scytopetalum ?klaineanum; Uapaca heudelotti = Uapaca acuminata.*

all plant species identified to date. Earth, from salines, at least nine invertebrate species, and three species of mammals were also eaten by chimpanzees, giving a total of 174 known food items.

Plant foods. Fruit dominated the chimpanzees' diet numerically with 111 different species being eaten. Remains of at least one species of fruit were found in 98.2% of the 1,854 feces analyzed, and the mean number of different fruit species per fecal sample was 2.7 (range 0–9). Fruit eaten by chimpanzees varied in size from the 5 mm drupes of *Antidesma* spp. and *Psychotria* spp. to the large composite fruit (120–150 mm diameter) of *Myrianthus arboreus.* Most of the fruits eaten (91%) had succulent pulp; a minority (5.4%) had lipid-rich arils or dry, fibrous, pulp (3.6%). Some, or all, of the seeds of the majority of fruit species eaten were swallowed and deposited intact in feces. Only the large seeds (> 5 cm^3 volume) of 10 species of succulent fruit were removed systematically by pre-ingestion processing.

Immature and ripe seeds of 12 species were eaten. In five cases, hard seeds of succulent fruit were selectively removed from immature fruit, the unripe pulp being rejected. For some of these species, a few seeds were deliberately crunched during feeding on ripe pulp but the quantity of seeds digested was small compared to those swallowed whole. The small seeds of two species of fibrous fruit, *Duboscia macrocarpa* and *Treculia africana,* were selectively removed from ripe fruit and relatively little pulp was eaten. The other five species of seeds were not embedded in pulp: two were large nuts of the lianescent Marantaceae, *Haumania liebrechstiana* and *Hypselodelphis violacea,* that were removed from the dehiscent husk, two were harvested from the ground having been mechanically dispersed by exploding pods of large Caesalpiniaceae trees, and lastly, winged seeds of *Pterocarpus soyauxii* were harvested from the tree whilst immature.

The herbaceous component of the diet, comprising 28 parts, came from 27 species: 10 herbs, 2 palms, 3 shrubs, 1 vine, and 11 trees. Young leaves or stem pith of four species of herb, *Aframomum* sp. ?nov., *Haumania liebrechstiana, Hypselodelphis violacea,* and *Megaphyrnium gabonense,* were consumed throughout the year but most other leaf feeding was highly seasonal, coinciding with bursts of leaf-flush by tree species. As leaf foods could not be identified to species level by fecal analysis, our data on the herbaceous component of the Lopé chimpanzees' diet is certainly incomplete. The same is perhaps true of feeding on flowers which was also highly seasonal and only recorded for six species of large tree. Flowers were eaten infrequently except for those of *Pterocarpus soyauxii* and *Pentaclethra macrophylla* that were eaten each year.

Feeding on bark was uncommon and remains of bark were found in less than 1% of feces. Galls formed by insects on young leaves of *Lophira alata* were selectively removed but no other gall-feeding was observed.

Of the 161 plant foods, 32 were defined as important foods that were eaten whenever available (as monitored by monthly phenology data from 580 trees of 60 food species) and the distribution of which influenced the ranging patterns of chimpanzees. Of these important foods, 27 were seasonally available tree fruits, one was the fruit of a herb, and four were stem-pith, or leaves, of herbs. Consumption of other plant foods was variable and often clearly related to the availability of important, and presumably preferred, foods. For example, the fibrous fruit of *Duboscia macrocarpa* were always available due to asynchronous fruiting, but chimpanzees only ate *Duboscia* seeds during the dry season each year and in April–May 1985 and 1988 when other fruit was scarce [Tutin et al., 1991a].

In a sample of 6.5 hectares of vegetation transects in the study area, 119 species of trees of ≥10 cm dbh (diameter at breast height) were identified [Williamson, 1988; White, 1992]. Of these species, 60 provided food for chimpanzees and 23 (85%) of the 27 important food tree species were represented. The vegetation sample included 2,482 trees and mean densities of the 23 species that produce important fruit foods ranged from 6,522 individuals per square kilometer (for *Cola lizae,* the commonest tree in the study area) to 15 individuals per square kilometer. Only 6 (22%) of the 27 important tree food species were among the 20 most common species in the vegetation sample, but 8 further species in the top 20 provided some food for chimpanzees.

Non-plant foods. Chimpanzees at Lopé ate at least five species of ants and honey of three bee species, and remains of insects were found in 31% of fecal samples [Tutin & Fernandez, 1992]. The most frequently eaten insect species was the weaver ant, *Oecophylla longinoda.* Chimpanzees used tools to obtain honey and to feed on two species of large ants [Tutin & Wrogemann, in preparation]. Feeding on caterpillars was observed once. Recognizable remains of caterpillars have not been seen in feces, suggesting that they are digested completely, so soft invertebrates may be eaten more commonly than the data suggest.

Chimpanzees have been seen eating mammalian prey four times. On three occasions the prey was an adult black colobus monkey (*Colobus satanus*) and meat was shared by 5–9 chimpanzees; on the fourth occasion, an adult female chimpanzee ate a juvenile grey-cheeked mangabey (*Cercocebus albigena*). Over the 8-year

TABLE III. Gorilla Foods Additions Since Williamson et al. [1990]

Scientific name	Family	Pulp	Seed	Leaf	Stem	Bark	Flower	Other[a]
Baillonella toxisperma	Sapotaceae	x						
Barteria fisulosa	Passifloraceae	x						
Berlinea bracteosa	Caesalpiniaceae							x
Caloncoba glauca	Flacourtiaceae						x	
Combretum platyperum	Combretaceae			x				
Corynathe sp. #373	Rubiaceae			x				
Dialium eurysephalum	Caesalpiniaceae	x						
Dichapetalum sp. #264	Dichapetalaceae			x		x		
Diospyros sp. #286	Ebenaceae	x						
Discoglypremna coloneura	Euphorbiaceae					x		
Duboscia macrocarpa	Tiliaceae		x					
Ficus barteri	Moraceae	x						
Ficus sp. #407	Moraceae			x		x		
Ficus sp. #443	Moraceae	x						
Hylodendron gabonense	Caesalpiniaceae		x					
Julbernardia brieyi	Caesalpiniaceae			x				
Leptoderris sp. #57	Papilionaceae							x
Lophira alata	Ochnaceae							x
Manniophyton sp. #379	Euphorbiaceae		x					
Milicia excelsa[b]	Moraceae							x
Mitragyna ciliata	Rubiaceae					x		
Mussaeuda debeauxii	Rubiaceae	x						
Ptychopetalum petiolatum	Olacaceae	x						
Sorindeia cf. judlandifolia	Anacardiaceae	x						
Trichilia monadelpha	Meliaceae		x					
Trichoscypha patens	Anacardiaceae	x						
Uapaca vanhouttei	Euphorbiaceae	x						
Uvaria sp. #256	Annonaceae	x						
Xylopia parvifolia	Annonaceae			x				
Subtotals		12	4	6	0	4	1	4
Williamson et al. [1990]		86	16	50	16	8	2	5
Totals		97	20	56	16	12	3	9

[a]Includes roots and galls.
[b]*Milicia exclesa = Chlorophora excelsa.*

period, remains of mammalian prey were found in 1.7% of feces at annual frequencies ranging from 0–3.7%. It was not always possible to identify the prey species from remains found in feces, but it seemed that black colobus were the most common victims of predation, and an additional prey species, the blue duiker (*Cephalophus monticola*), was positively identified from a hoof, jaw fragment, and hair.

Soil was found in less than 1% of feces and geophagy was observed only twice at salines created under tree roots by the digging of elephants. Soil from some salines had a high concentration of sodium compared to soil from other areas [M.J.S. Harrison, personal communication; L.J.T. White, personal communication].

Comparison of Chimpanzee and Gorilla Diets at Lopé

Table III lists 31 additional foods recorded for lowland gorillas at Lopé since the species list published in Williamson et al. [1990]. Table IV compares both the total number of species in each food class eaten by chimpanzees and gorillas, and

TABLE IV. Comparison of the Diets of Chimpanzees and Gorillas at Lopé, Gabon

Food class	No. species eaten by chimpanzees		No. species eaten by gorillas	
	Total	Exclusive	Total	Exclusive
Pulp	106	18	94	15
Arils	5	2	3	0
Seeds	12	2	20	10
Leaves	20	6	56	32
Stems	8	3	16	11
Bark	3	3	12	12
Flowers	6	4	3	1
Other[a]	1	0	9	8
Non-plant foods	13	10	8	5
Totals	174	48	221	94

[a]Includes galls, roots, and fungus.

the number of foods eaten by only one species. Fruit pulp is the most numerous class of food for both species of ape, and fruit parts (pulp, arils, and seeds) account for 76% of chimpanzee and 55% of gorilla plant food items. Many more vegetative foods have been recorded for gorillas than for chimpanzees at Lopé, and this is reflected by the higher number of exclusive foods in the categories leaves, stems, and bark. Overall, only 27% of chimpanzee plant foods were not eaten by gorillas while 43% of gorilla foods have not been recorded as being eaten by chimpanzees. The degree of dietary overlap is highest for fruit pulp and lowest for bark and non-plant foods. Records for fruit and non-plant foods are the most complete data sets for both species as fruit seeds and insect/mammalian remains can be identified most reliably to species level in feces.

Table V lists the important plant foods of gorillas and chimpanzees, defined as those that dominate the diet on a regular or irregular (in the case of some fruit species) basis and influence ranging patterns [see also Appendix 1 in Tutin et al., 1991b]. Chimpanzees at Lopé have 28 important fruit foods and only 4 important vegetative foods, while gorillas have fewer important fruit species and more important vegetative foods than do chimpanzees. These differences are qualitative, and we do not yet have sufficient observational data to compare time spent feeding on different foods. However, foliage scores (see Methods) allow comparison of the relative importance of non-fruit vs. fruit remains in feces, and Figure 1 compares the mean monthly foliage scores recorded from feces over a 4-year period (1987–1990). While both species showed similar seasonal variation in foliage scores, gorillas consistently ate larger amounts of vegetative foods than did chimpanzees. The maximum foliage score is 8, corresponding to fecal samples with no, or very few, fruit food remains, and scores for gorillas in July and August were 7.5 and 7.2 compared to 5.4 and 4.5 for chimpanzees. Succulent fruit is scarce during the dry season (mid-June to mid-September) and it is at this time that gorillas resort to a diet dominated by non-fruit foods while chimpanzees continue to find considerable quantities of fruit [see also Rogers et al., 1988; Tutin et al., 1991a].

Table VI compares the number of foods that chimpanzees and gorillas at Lopé ate on the ground, either harvesting them from herbs and shrubs, or, in the case of fruit that abcise on ripening, feeding on fallen fruit. The majority of foods of both chimpanzees (76%) and gorillas (69%) at Lopé are eaten in trees but gorillas have more terrestrially harvested fruit and vegetative foods than do chimpanzees.

TABLE V. Comparison of Important Foods of Chimpanzees and Gorillas at Lopé

Scientific name	Part eaten	Life-form	Chimpanzee[a]	Gorilla[a]
Aframomum sp. ?nov.	P/F	Herb	x	x
Beilschmeidia sp. #140	F	Tree	x	0
Canarium schweinfurthii	F	Tree	x	0
Celtis tessmannii	F	Tree	x	x
Cola lizae	F	Tree	x	x
Dacryodes buettneri	F	Tree	x	0
Dacryodes normandii	F	Tree	x	x
Dialium lopense	F	Tree	x	x
Diospyros dendo	F	Tree	x	x
Diospyros polystemon	F	Tree	x	x
Elaeis guineensis	F	Palm	x	0
Gambeya africana	F	Tree	(x)	x
Gambeya subnuda	F	Tree	x	(x)
Ganophyllum giganteum	F	Tree	x	x
Grewia coriacea	F	Tree	x	(x)
Haumania liebrechstiana	L	Herb	x	x
Heisteria parvifolia	F	Tree	x	(x)
Hypselodelphis violacea	L	Herb	x	x
Irvingia gabonensis	F	Tree	x	x
Lecaniodiscus cupanoides	F	Tree	x	x
Marantchloa cordifolia	P/L	Herb	0	x
Megaphrynium gabonense	L	Herb	x	x
Milicia excelsa	Bast/L	Tree	0	x
Nauclea didderichi	F	Tree	x	(x)
Parkia bicolor	F	Tree	x	(x)
Parkia filicoidea	F	Tree	x	(x)
Pentadesma butyracea	F/Sd	Tree	0	x
Polyalthia suaveolens	F	Tree	x	0
Pseudospondias microcarpa	F	Tree	x	(x)
Psidium guineensis	F	Shrub	(x)	x
Pycnanthus angolensis	F	Tree	x	0
Santiria trimera	F	Tree	x	x
Scytopetalum sp. #168	F	Tree	x	(x)
Trichoscypha acuminata	F	Tree	x	(x)
Uapaca guineensis	F	Tree	x	x
Uvariastrum pierreanum	F	Tree	x	(x)
Important Fruit Foods			28	15
Important Vegetative Foods			4	8

[a]x = important food; (x) = eaten but not important in diet; 0 = not eaten.

DISCUSSION

Diet of the Lopé Chimpanzees

Fruit dominates the diet of chimpanzees at Lopé in numerical terms, and remains of at least one species of fruit were found in over 98% of analyzed feces. The advantages and disadvantages of fecal analysis as a method for describing primate diets are discussed by Moreno-Black [1978] but, as pointed out by Kano and Mulavwa [1984] and by Tutin and Fernandez [1992], this method does allow accurate assessment of the diversity and frequency of fruit consumption and that of mammals and invertebrates with chitinous body parts. However, the number of species of vegetative foods (leaves, stems, and bark), flowers, and soft-bodied invertebrates is underestimated by a dependence on fecal analysis. It is likely that

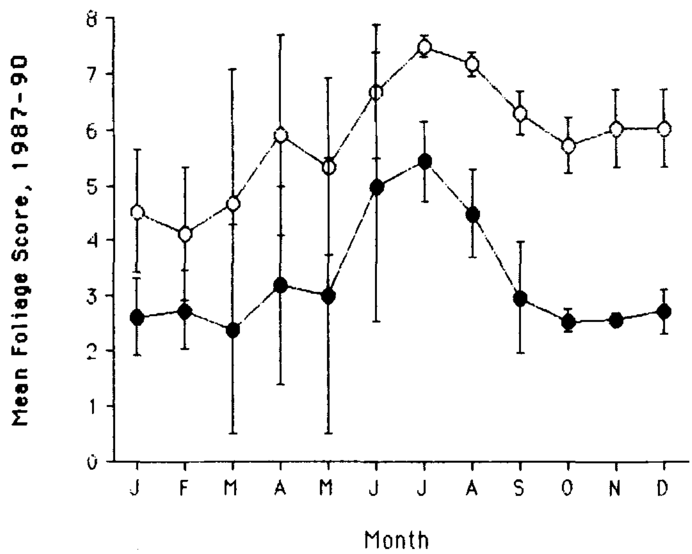

Fig. 1. Mean foliage scores with standard deviations for chimpanzees (closed circles) and gorillas (open circles) at Lopé, 1987–1990.

TABLE VI. Comparison of Number of Foods Harvested Terrestrially by Chimpanzees and Gorillas at Lopé, Gabon

	Chimpanzees		Gorillas	
Foot item	No. species	Percentage of total	No. species	Percentage of total
Fruits[a] of herbs and shrubs	14	11.4	16	13.7
Tree fruits usually eaten when fallen	12	9.8	16	13.7
Leaves/stems of herbs and shrubs	13	46.4	33	45.8
Other	0	—	2	8.3
Total foods eaten terrestrially	39	24.2	67	31.5

[a]Includes pulp, arils, and seeds.

more of these foods will be recorded with continued study and increased close-range observation.

In general, the diet of Lopé chimpanzees resembles that of populations studied elsewhere, being dominated by succulent fruit pulp, supplemented by a regular intake of vegetative foods (Fig. 1) and insects [Tutin & Fernandez, 1992]. This dependence on fruit leads to large seasonal and inter-annual variation in diet as most fruit foods are produced seasonally—that is, at the same time of year but not necessarily each year [Nishida & Uehara, 1983; Tutin et al., 1991a]. The predominance of fruit of tree species among the important foods of chimpanzees (Table V) leads to non-random ranging, as chimpanzees congregate in areas where fruit-bearing species are commonest or travel long distances between dispersed individuals of the rarer tree species. At Lopé, succulent fruit is scarce every year during the 3-month dry season [Rogers et al., 1988; Tutin et al., 1991a] and, at such times, chimpanzees increase their consumption of vegetative foods (Fig. 1) but also depend heavily on the continuously available fruit of *Elaeis guineensis* [Tutin et al., 1991a]. In some years, because fruit crops of important food species fail, succulent fruit is scarce for longer periods, and wind- and mechanically dispersed seeds of trees of the Caesalpiniaceae and Papilioniaceae, if available, are eaten in large quantities at such times.

The number of plant food items (161) and food species (132) recorded for chimpanzees at Lopé shows a dietary breadth of a similar order to other studied populations of both *Pan troglodytes* and *Pan paniscus*. Six studies of the diet of *Pan troglodytes* recorded an average of 165 plant food items (range 55–328) from an average of 119 species (range 43–198) [Goodall, 1968; Hladik, 1973; Nishida & Uehara, 1983; McGrew et al., 1988; Sabater Pi, 1979; Sugiyama & Koman, 1987; Wrangham, 1975]. Two studies of *Pan paniscus* diet found a similar pattern of plant food use with an average of 123 items eaten (range 113–133) from 98 species (range 81–114) [Badrian & Malenky, 1984; Kano & Mulavwa, 1984]. Dietary overlap between sites is generally low which is perhaps not surprising, given the range of habitats in which *Pan* has been studied: average overlap of plant food species of the Lopé chimpanzees with other populations was 17% (Range 5–35%). Food lists from the sites closest to Lopé, Makokou in NE Gabon [Hladik, 1973] and Okorobiko in Equatorial Guinea [Sabater Pi, 1979], showed the highest percentage overlap with 28% and 35% of plant food species, respectively, being shared with Lopé chimpanzees. However, 9% of food species at both of these sites occur at Lopé but were not eaten by chimpanzees. Similar differences in diets were found between neighboring study sites in Tanzania, with only 59% of 286 available plant foods eaten by chimpanzees both at Gombe and at Mahale [Nishida et al., 1983].

Chimpanzee and Gorilla Diet at Lopé

The similarity between the diets of sympatric apes at Lopé is striking, with 73% of chimpanzee foods and 57% of gorilla foods eaten by both species (Table IV). For fruit foods, the most numerous and most completely documented food category, the degree of overlap is higher, being 82% and 79%, respectively. Of the minority of chimpanzee fruit foods not eaten by gorillas, six are important foods (Table V). Five of these species have oily, lipid-rich pulp or arils, suggesting that gorillas at Lopé avoid high-lipid foods [Rogers et al., 1990; Tutin et al., 1991a]. However, other populations of lowland gorillas eat at least some of these fruits [Nishihara, 1992; M. Fay, personal communication], so local differences in patterns of plant food consumption exist between gorilla populations, as they do between those of chimpanzees [Nishida et al., 1983].

Given the high degree of overlap of the fruit component of the diet of these sympatric apes, ecological competition might be expected. It has been suggested that competition is avoided because gorillas are less arboreal than chimpanzees and obtain the majority of their foods on the ground [Sabater Pi, 1977]. However, as Williamson et al. [1990] reported, all age-classes of gorillas at Lopé climb frequently and feed at heights up to 40 m and, as shown in Table VI, the majority of both fruit and vegetative foods of gorillas at Lopé are harvested arboreally.

Behavioral evidence of competition for food between gorillas and chimpanzees at Lopé is sparse: of 48 inter-specific encounters observed in 8 years only two interactions were clearly related to access to food [Tutin & Fernandez, in preparation]. Similarly, overt evidence of competition over food between individuals within each species is rare. This does not mean that competition does not occur but, if it does, subtle behavioral mechanisms regulating access to food must exist and be effective, as few "mistakes," needing detectable "correction," are made. During the annual dry season when fruit availability is limited, the diets of gorillas and chimpanzees diverge [see also Gautier-Hion, 1980; Terborgh, 1983] and gorillas concentrate on abundant vegetative foods. Bonobos also turn to vegetative foods when fruit is scarce in their tropical forest habitat [Badrian et al., 1981; Kano, 1983; Badrian & Malenky, 1984] and, like lowland gorillas, bonobos consume more herbaceous foods than do chimpanzees even when fruit is abundant [Malenky & Stiles, 1991]. Forest-living *Pan t. schweinfurthii* in the Kibale Forest, Uganda, also depend heavily on the piths and leaves of herbs when fruit is scarce [Wrangham et al., 1991]. Differences in body size, though poorly documented at present for all species of apes in the wild [Jungers & Susman, 1984], may explain the consistently larger intake of vegetative foods by Lopé gorillas (Fig. 1) but cannot account for the variation in the importance of vegetative foods as keystone resources described above. The herbaceous plants that are keystone foods [sensu Terborgh, 1986] for lowland gorillas at Lopé, for chimpanzees at Kibale, and for bonobos at Lomako are common, and the foods they provide appear to be superabundant. However, as pointed out by Malenky and Stiles [1991], a ubiquitous distribution of food plants does not necessarily mean unlimited supplies of food, as apes are very selective feeders [see also Rogers & Williamson, 1987]. Nutrient content and the avoidance of plant defences (secondary compounds and fiber) are known to influence the choice of plant foods [Altmann & Wagner, 1978; Freeland & Janzen, 1974; Glander, 1982; Milton, 1979] but not enough is known yet about the nutritional requirements and digestive physiology of apes to allow interpretation of the choice of keystone foods made by each species. Also, the influence of social factors remains unclear (i.e., the degree to which the increased costs of intra-specific competition, from feeding in groups, influences or dictates choice of keystone foods by African apes) [Malenky & Stiles, 1991; Tutin et al., 1991b; White & Wrangham, 1988; Wrangham, 1979]. More data on inter- and intra-specific competition for food, digestive physiology, nutritional requirements, and natural body weights of the three species of African ape are needed before these enigmas about dietary differences and their relationship to the evolution of social structure and ultimate influence on reproductive success [Tutin, in preparation; Wrangham, 1979, 1986] can be resolved.

CONCLUSIONS

1. The diet of chimpanzees in tropical forest habitat in the Lopé Reserve, Gabon, included 174 food items. Insects and mammalian prey were eaten, but fruit dominated the diet with 111 species being eaten. The diversity of vegetative food was probably underestimated by fecal analysis.
2. Of the plant foods, 27 species of tree fruit were important foods that dominated the diet whenever they were available and influenced ranging patterns. Only six of these were among the 20 commonest tree species in the study area.
3. Comparison of the diets of Lopé chimpanzees and sympatric gorillas revealed that the majority of foods were eaten by both species. Dietary overlap was highest for fruit foods, and only 18% of chimpanzee fruits and 21% of gorilla fruits were not eaten by the other species.
4. The majority of plant foods of both chimpanzees and gorillas at Lopé were harvested arboreally.
5. The major differences between the diets of the two ape species at Lopé were the larger amounts of vegetative foods eaten by gorillas throughout the year and the ability of gorillas to subsist on a diet dominated by vegetative foods when fruit was scarce.
6. The diets of chimpanzees and gorillas differed most when fruit was scarce.

Gorilla keystone foods were leaves, stems, and bark; chimpanzees also increased their consumption of leaves and stems but continued to find more fruit than did gorillas.

7. The high degree of dietary overlap and dietary divergence when fruit was scarce suggested potential ecological competition between these two closely related species. As little overt evidence of either inter- or intra-specific competition for food was detected, it appeared that sufficient niche separation exists and may be related to body size, although data from other field studies of apes suggest additional factors may also be involved.

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