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Composition of the Diet of Lowland Gorillas at Lopé in Gabon

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This report describes the composition of the diet of lowland gorillas, *Gorilla gorilla gorilla*, at Lopé in central Gabon. This population inhabits mature evergreen tropical forest and is not habituated to human observers. Data were collected during 6 years of an ongoing long-term study, from feeding-trails and by direct observation, but mostly by fecal analysis. Gorillas ate 182 plant foods from 134 species and 36 families. The fruit diet was diverse: 95 species were consumed, most with succulent pulp, and some immature seeds were eaten. Fruit remains were recorded in 98% of dung. Vegetative parts of *Aframomum* and Marantaceae formed staple foods, as they were abundant, accessible, and available year-round. Soil and social insects were also ingested; remains of weaver ants were recorded in one third of feces. More foods have been recorded for gorillas at Lopé than elsewhere and this is the most frugivorous population studied so far.

Key words: *Gorilla gorilla gorilla*, feeding ecology, frugivory

INTRODUCTION

Dietary niche is one of the most important constraints on the behavioral ecology and evolution of a species. Chimpanzees and orangutans have been described as frugivores [e.g., Ghiglieri, 1987], and all the apes should have basically similar dietary requirements [Wrangham, 1979]. Gorillas, however, have been classified as folivores [e.g., Bourliere, 1985; Clutton-Brock & Harvey, 1980; Dunbar, 1988: 322], a generalisation based on knowledge of mountain gorillas [Fossey & Harcourt, 1977; Schaller, 1963; Vedder, 1984; Watts, 1984]. In comparison, the western lowland subspecies of gorilla has been poorly known.

Early reports noted the propensity of lowland gorillas to feed in plantations and secondary forest [e.g., Derochette, 1941; Liz Ferreira et al., 1945; Petit, 1920]. This may have been because such areas were associated with human habitation, and so were most accessible to naturalists. The image of western gorillas feeding in secondary forest was enhanced by two previous studies of lowland gorillas, which took place in degraded habitats [Calvert, 1985; Jones & Sabater Pi, 1971].

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These studies drew attention still further away from the majority of gorillas, which inhabit mature forest [Tutin & Fernandez, 1984] and are unlikely to consume equivalently large proportions of foliage given the diversity of fruit available.

There have been suggestions that the western subspecies of gorilla has frugivorous tendencies since the earliest accounts of their habits [e.g., Savage & Wyman, 1847; Jenks, 1911; Valker, 1931]. Even given his emphasis on foods from secondary forest species and on the gorillas' supposed inability to climb, Sabater Pi [1977] described lowland gorillas as being more frugivorous than mountain gorillas. The first real indication of the extent of the lowland subspecies' frugivory came from Tutin and Fernandez' [1985] systematic study in northeast Gabon, which concluded that lowland gorillas can no longer accurately be classed as folivores. This article describes the composition of the diet of *Gorilla gorilla gorilla* in central Gabon.

STUDY AREA AND METHODS

Research was carried out at the Station d'Etudes des Gorilles et Chimpanzés (SEGC) at 0°10'S, 11°35'E in the Lopé Reserve. The Reserve comprises 5,000 km^2 of mature evergreen tropical forest, where gorillas are sympatric with 10 other species of primates, including the chimpanzee, *Pan troglodytes troglodytes,* mandrill, *Mandrillus sphinx,* and black colobus monkey, *Colobus satanas.* About 40 km^2 of undulating forested hills form the study-area, parts of which were logged on a small scale between 1965 and 1979 to extract a single species of tree, *Aucoumea klaineana.*

The climate of this region is characterised by four seasons: a major rainy season from October to mid-December, a short dry season from mid-December to mid-February, a minor rainy season from mid-February to May, and a long dry season from June to September. Annual rainfall averaged 1,532 mm over 5 years. Mean monthly minimum and maximum air temperatures varied from 20.1 to 23.2°C and 27.0 to 32.8°C, respectively.

The long-term research goal at SEGC is the habituation, without provisioning, of several groups of gorillas to permit a detailed study of their behavioral ecology. Observation was limited as the gorillas were not habituated and visibility in the forest was poor. Under such conditions, a combination of direct observation and fecal analysis is the best way to obtain information on feeding [Moreno-Black, 1978], and additional data were collected on feeding-trails (the remains of food in situ).

The study-area was searched daily, to systematically collect evidence of the gorillas' activities. We used simple line maps, on a scale of 10 cm:1 km, drawn from aerial photographs, and onto which we had plotted old forestry roads, major animal paths, and streams, using compasses and a "Topofil Hipchain" to measure distance. The decision to search a given area was based on the results of the previous day's work, or on our knowledge of the location of fruiting trees which might attract gorillas. Researchers worked alone or in pairs, and trackers were not employed. Our equipment included compasses, binoculars, and Motorola HT90 radios which enabled contact between observers and better co-ordination of our movements.

The ease with which the gorillas' trails could be followed varied in relation to the density of food traces, and the time they had spent at any one location; for instance, traveling groups did not leave any food-remains. We often had to predict the gorillas' routes, as trails were rarely continuous. If a trail was lost we moved forward in parallel directions to pick it up again.

Remains were attributed to gorillas directly, by sight, sound, or smell, or by indirect evidence, such as knuckle- and foot-prints, association with nests or feces

[for a discussion of similar criteria, see McGrew et al., 1988]. All observation sites, nest-sites, and trails were examined, and food-items and fresh feces were collected. Feces were sealed in polythene bags and weighed with a spring balance.

Whole feces were washed in 1-mm mesh sieves and identifiable parts, such as seeds and fruit skins, were counted; fragments of leaves and stem-fibre, which became an indistinct mass, were assessed simply on a five-point scale of relative abundance: none, rare, few, common, abundant.

Samples of all foods were collected. Fruits were sectioned and dried, or preserved in 10% ethanol; leaves and flowers were pressed. Plant specimens were identified at the Royal Botanic Gardens in London and Edinburgh and at the Museum of Natural History in Paris.

The data come from 6 years of continuous research at Lopé (December 1983 to December 1989) and the examination of 3,565 feces, but the quantitative analyses of feces presented are based on a subset of 716 samples, collected during the first 17 months of the study.

RESULTS

Composition of the Diet

Gorillas at Lopé were found to eat 182 different parts of at least 134 species of plants from 36 taxonomic families. Table I summarises the diet, and Table II lists all plant species identified so far. Earth and at least three species of arthropods were eaten in addition to vegetable matter, making a total of 186 known food-items.

Plant foods. The herbaceous component of the diet, comprising 33 parts from 21 species, was dominated by two families: 10 species of Marantaceae and six species of Zingiberaceae. The majority of 277 feeding-trails included remains of *Aframomum spp.* (82%) and Marantaceae (77%), while 98% of 716 dung samples contained stem-fibre, which was common or abundant in 77%.

As unusual aspect of the gorillas' behavior was their feeding in streams and marshes on four species of Marantaceae: *Marantochloa cordifolia, M. filipes, M. purpurea,* and *Halopegia azurea* [Williamson et al., 1988]. The only trails with no *Aframomum* or Marantaceae were those crossing monospecific stands of an understorey shrub *Anisotes macrophyllus,* or *Marantochloa* marshes.

Leaves from 33 species of woody plants were identified after observation of feeding, or from trails. Petioles, new shorts, bracts, and vine tendrils were also eaten. Only the Marantaceae were common on trails: *Haumania liebrechtsiana* predominated, together with *Hypselodelphis violacea* and *Megaphrynium gabonense.* Leaf fragments were recorded in 90% of dung samples.

Bark was found in 9% of dung, and gorillas were often seen feeding on the bark of *Chlorophora (Milicia) excelsa* during the long dry season. Pieces of wood and roots were also identified in feces.

Feeding on the flowers of *Aucoumea klaineana, Pterocarpus soyauxii,* and one other species of unidentified tree was seen. Remains of flowers were not recorded in the dung, since such delicate structures would presumably have been destroyed by digestion.

Fruit remains, including many pieces of fruits and seeds which could not be identified, were found in 98% of the feces collected between January 1984 and May 1985. Gorillas ate 95 species of fruit, including one cultigen, the mango *(Mangifera indica).* Most types were succulent: 77% (78 species). Only four species of aril (a brightly coloured thin fatty layer adhering to a seed), and 16 types of seed were recorded. Immature seeds, including those of four species of *Diospyros,* were extracted from unripe fruits and chewed. In general, as fruits matured the seeds were

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

Food class	Taxon/life-form	N species	Parts eaten	N items
Monocotyledons	Marantaceae	10	Leaf-bases	6
	Zingiberaceae	6	Leaves	4
	Commelinaceae	1	Non-emerged leaves	6
	Acanthacaceae	1	Basal pith	6
	Araceae	1	Stem-pith	10
	Palmae	2	Roots	1
		21	Fruits/seeds	8
				41
Dicotyledons				
Leaves	Trees	24	Leaf tissue	30
	Shrubs	5	Petioles	1
	Vines	4	Bracts	1
		33	New shoots	1
			Vine tendrils	1
				34
Bark	Trees	6	Bark	8
	Shrub	1		
	Vines	1		
		8		
Roots/wood	Unknown	≥ 2	Roots	≥ 1
			Wood	≥ 1
				≥ 2
Fruits	Trees	65	Pulp	72
	Shrubs	7	Seeds	14
	Vines	11	Arils	4
	Unknown	≥ 4	Indeterminate	3
		≥ 87		93
Flowers	Trees	3	Flowers	3
Other	Fungus	1		
	Soil	1		
	Ants	≥ 3		
		≥ 5		

either not eaten or not digested, although the ripe nuts of *Haumania liebrechtsiana, Hypselodelphis violacea,* and *Detarium macrocarpum* were eaten when available.

Gorillas fed on fruit, even though vegetative plant parts were available in large quantities [Rogers & Williamson, 1987]. However, some common types of fruit were avoided, notably some Caesalpiniaceae and Mimosaceae, whose seeds are wind dispersed and so not embedded in pulp (although young leaves of Mimosaceae were consumed). Gorillas also generally ignored several fruits with a high lipid content [Rogers et al., in prep.] and which formed a major part of the chimpanzees' diet [Tutin & Fernandez, 1985; unpub. data], namely *Canarium schweinfurthii, Dacryodes buettneri, Elaeis guineensis, Polyalthia suaveolens, Pycnanthus angolensis,* and *Staudtia gabonensis.*

Relatively few of the wide range of potential foods were eaten, for example, only 36% of the 138 tree species recorded on vegetation transects appeared in the

TABLE II. Species of Plants and Their Parts Eaten by Gorillas at Lopé, Gabon

Scientific name	Family	Pulp	Seed	Leaf	Stem	Bark	Other
Aframomum longipetiolatum	Zingiberaceae	x			x		
Aframomum sp. nov.	Zingiberaceae	x			x		
Aframomum ?leptolepis	Zingiberaceae	x			x		
Anchomanes difformis	Araceae			x	x		
Anisotes macrophyllus	Acanthaceae			x			
Antidesma vogelianum	Euphorbiaceae	x					
Antidesma sp. #251	Euphorbiaceae	x					
Anthocleista ?vogelii	Loganiaceae			x			
Antrocaryon klaineanum	Annonaceae	x					
Ataenidia conferta	Marantaceae			x			
Aucoumea klaineana	Burseraceae						Flowers
Berlinea bracteosa	Caesalpiniaceae			x			
Brachystegia aff. eurycoma	Caesalpiniaceae		x				
Celtis tessmannii	Ulmaceae	x		x			
Chlorophora excelsa	Moraceae			x		x	
Chrysophyllum subnudum	Sapotaceae	x					
Cissus leonardi	Vitaceae	x					
Cissus sp. #145	Vitaceae	x		x			
Cola lizae	Sterculiaceae	x		x			
Costus afer	Zingiberaceae			x			
Cryptosepalum staudtii	Caesalpiniaceae		x	x			
Dacryodes normandii	Burseraceae	x					
Detarium macrocarpum	Caesalpiniaceae		x	x			
Dialium sp. #79	Caesalpiniaceae	x	x	x			
Dialium sp. #118	Caesalpiniaceae	x					
Dichapetalum ?unguiculatum	Dichapetalaceae		x				
Diospyros abyssinica	Ebenaceae	x					
Diospyros cf. iturensis	Ebenaceae	x	x				
Diospyros cf. viridicans	Ebenaceae			x			
Diospyros dendo	Ebenaceae	x	x				
Diospyros polystemon	Ebenaceae	x	x				
Diospyros suaveolens	Ebenaceae	x	x				
Drypetes sp. #264	Euphorbiaceae	x					
Duboscia macrocarpa	Tiliaceae	x					
Enantia chlorantha	Annonaceae	x					
Eremospatha cabrae	Palmae	x		x	x		
Ficus macrosperma	Moraceae	x					
Ficus mucuso	Moraceae	x		x			
Ficus ?polita	Moraceae	x					
Ficus recurvata	Moraceae	x					
Ficus thonningii	Moraceae	x					
Gambeya africana	Sapotaceae	x					
Grewia sp. #343	Anacardiaceae	x					
Halopegia azurea	Marantaceae			x	x		
Haumania liebrechtsiana	Marantaceae		x	xx			
Heisteria parvifolia	Olacaceae	x		x			
Heisteria sp. #110	Olacaceae			x			
Hexalobus crispiflorus	Annonaceae	x					
Hypselodelphis violacea	Marantaceae		x	xx			
Irvingia gabonensis	Irvingiaceae	x					
Irvingia grandiflora	Irvingiaceae	x					
Klainedoxa gabonensis	Irvingiaceae	x					
Klainedoxa sp. #208	Irvingiaceae	x					

(*continued on next page*)

TABLE II. Species of Plants and Their Parts Eaten by Gorillas at Lopé, Gabon (Continued from previous page)

Scientific name	Family	Pulp	Seed	Leaf	Stem	Bark	Other
Leptoderris sp. #57	Papilionaceae			x			
Lecaniodiscus cupanoides	Sapindaceae	x					
Lophira alata	Ochnaceae			x			
Mammea africana	Guttiferae	x					
Mangifera indica	Annonaceae	x					
Marantochloa cordifolia	Marantaceae			x	x		
Marantochloa filipes	Marantaceae				x		
Marantochloa purpurea	Marantaceae			x	x		
Megaphrynium gabonense	Marantaceae	x		xx	x		Roots
Megaphrynium macrostachyum	Marantaceae	x		xx	x		
Milletia versicolor	Papilionaceae			x		x	
Monanthotaxis congensis	Annonaceae	x					
Monodora angolensis	Annonaceae	x					
Myrianthus arboreus	Moraceae	x				x	
Nauclea didderichi	Rubiaceae	x					
Nauclea vandeguchtii	Rubiaceae	x					
Oncoba spinosa	Flacourtiaceae			x			
Palisota ambigua	Commelinaceae				x		
Parkia bicolor	Mimosaceae	x					
Parkia filicoidea	Mimosaceae	x					
Pausinystalia macroceras	Rubiaceae			x			
Pavetta puberula	Rubiaceae			x			
Pentaclethra eetveldeana	Mimosaceae			x			
Pentaclethra macrophylla	Mimosaceae			x			
Pentadesma butyracea	Guttiferae	x	x				
Piptadeniastrum africanum	Mimosaceae		x				
Plagiostyles africana	Euphorbiaceae	x					
Porterandia cladantha	Rubiaceae	x					
Pseudospondias longifolia	Anacardiaceae	x					
Pseudospondias microcarpa	Anacardiaceae	x					
Psidium sp. #53	Myrtaceae	x					
Psychotria peduncularis	Rubiaceae	x					
Psychotria vogeliana	Rubiaceae	x					
Pterocarpus soyauxii	Papilionaceae		x	x			Flowers
Renealmia cincinnata	Zingiberaceae				x		
Renealmia macrolea	Zingiberaceae				x		
Rutidea dupuisii	Rubiaceae	x					
Saccoglottis gabonensis	Humiriaceae	x					
Santiria trimera Types I–II	Burseraceae	x					
Scyphocephalium ochocoa	Myristicaceae			x			
Scytopetalum ?klaineanum	Scytopetalaceae	x					
Swartzia fistuloides	Caesalpiniaceae			x			
Testulea gabonensis	Luxemburgiaceae			x			
Trachyphrynium braunianum	Marantaceae				x		
Treculia africana	Moraceae	x					
Trichoscypha acuminata	Anacardiaceae	x					
Uapaca ?acuminata	Euphorbiaceae	x					
Uapaca guineensis	Euphorbiaceae	x					
Uapaca cf. sansibarica	Euphorbiaceae	x					
Uapaca sp. #299	Euphorbiaceae	x					
Uvaria sp. #256	Annonaceae	x					
Vitex doniana	Verbenaceae	x					
Xylopia aethiopica	Annonaceae	x					

(*continued*)

TABLE II. Species of Plants and Their Parts Eaten by Gorillas at Lopé, Gabon (Continued)

Scientific name	Family	Pulp	Seed	Leaf	Stem	Bark	Other
Xylopia hypolampra	Annonaceae	x					
Xylopia ?quintasii	Annonaceae	x					
Zanha golungensis	Sapindaceae	x					
SEGC No. 36	Apocynaceae	x					
SEGC No. 46	Apocynaceae	x					
SEGC No. 58	Apocynaceae	x					
SEGC No. 56	Celastraceae	x					
SEGC No. 319	Melastomataceae			x			
SEGC No. 351	Palmae				x		
SEGC No. 288	Rubiaceae	x					
SEGC No. 291	Rubiaceae	x					
SEGC No. 369	Rubiaceae			x			
SEGC No. 318	Sapotaceae	x					
Subtotals		79	14	43	16	3	3
Unidentified foods		6	2	7		5	4
Totals		85	16	50	16	8	7

diet [see Williamson, 1988]. Gorillas were also selective at other levels, choosing between individual plants and their parts. Entire plants were never eaten, but instead specific parts were removed, such as the bases of developing *Haumania* leaves, the inner pith of *Aframomum* stems, and the bases of *Marantochloa* stems.

Non-plant foods. Evidence of insectivory came from trails and one-third of dung samples; 31% contained hundreds of undigested heads of weaver ants, *Oecophylla longinoda*. Weaver ants were deliberately consumed: crushed leaves from arboreal nests with a few dead ants remaining on them were found on gorillas' feeding-trails. The presence in dung of wings and heads of the reproductive castes, as well as those of the worker forms of weaver ant, and pieces of mature Marantaceae leaves, not normally eaten by gorillas, indicated that whole nest contents had been swallowed.

The other 2% of dung samples included two types of black ant, ticks, bees, or, in one case, a caterpillar. The large numbers of black ants, *Crematogaster depressa* and *C. stadelmanni*, in the dung suggested that their consumption had also been intentional. The ticks were larval forms of *Amblyomma thollini*, probably swallowed during grooming; the bees and caterpillar were probably ingested inadvertently with vegetable matter.

Soil or gravel was found in 4% of dung, and geophagy was observed at salt-licks. These licks were created in the banks of streams by elephants, and enlarged through use by other species of mammal, including buffalo, antelope, chimpanzee, and colobus monkey (unpub. data). Soil from these sites had a relatively high concentration of sodium (M. Harrison, pers.comm.).

Food Acquisition

Foraging on the ground. The density of food remains on trails varied. Foraging seemed to be intense early in the day, as large numbers of *Aframomum* stems were split and flattened in the vicinity of nest-sites. Feeding on *Marantochloa* was similarly concentrated, as gorillas waded through marshes and streams, uprooting hundreds of stems. Gorillas consumed little herbaceous vegetation when they moved directly from one fruiting tree to another.

Feeding in trees. Gorillas of all age-classes were often seen to feed in trees, at heights of up to 30 m. Terminal branches were bent to within reach, often without breaking them; fruits and leaves were plucked directly with the lips, or pulled off by hand and transferred to the mouth. Arboreal vines were pulled through the canopy and run through a closed fist, leaving a bunch of leaves in the fingers. Food was also collected from neighbouring trees. Both sitting and standing positions were adopted for feeding. Arboreally feeding adults often broke off branches and backed toward the trunk or to a major fork to eat from a more secure position. Branches were later dropped to the ground, some with fruit still on them. Gorillas sometimes spent more than an hour feeding continuously in single trees, turning around or shifting position every few minutes.

One especially destructive technique used by adult males was the bending and breaking of saplings to feed on their foliage, fruit, or on vines growing around them. *Diospyros,* in particular, suffered from the activity of gorillas, since many were small trees incapable of supporting an adult gorilla's weight, and branches were pulled towards the ground and snapped off.

Processing of Foods

Structural plant parts. Examples of ways in which gorillas processed foods are given below.

Aframomum spp. Stems were anchored in the teeth and pulled with the hands to split the tough outer sheath and expose the inner pith, which was ingested.

Anchomanes difformis. Stems of this fleshy, herbaceous plant were peeled and the inner tissues were consumed. Leaves were stripped from petioles with the teeth.

Anisotes macrophyllus. Stems were bent and broken, while still rooted; leaves were bitten in half or drawn through the teeth, stripping away the tissues and leaving behind the midribs.

Chlorophora excelsa. Branches were broken off and stripped of bark; bunches of terminal leaves often remained attached to dropped branches.

Dialium sp. Only the tips of young leaves were swallowed; leaf bases and petioles were spat out in little heaps.

Eremospatha cabrae. Leaves were pulled through the teeth, leaving the ribs behind.

Haumania liebrechtsiana* and *Megaphrynium gabonense. Bases of young leaves were bitten off, and developing leaves removed from inside stems or shoots.

Marantochloa spp.* and *Halopegia azurea. Ten to 15-cm portions of the tender, pink stem-bases were eaten, and the rest was discarded.

Milletia versicolor. Saplings were completely stripped of bark, except for the base of the trunk. An unidentified shrub was stripped in the same manner.

Fruits. Many succulent fruits were swallowed whole after the fruit skin had been pierced with the teeth. Seeds of only a few species were selectively extracted, rather than swallowed passively with pulp (e.g., *Detarium macrocarpum, Diospyros spp., Pentadesma butyracea).* Some large seeds were rarely *(Irvingia grandifolia, Klainedoxa gabonensis)* or never *(Mammea africana, Saccoglottis gabonensis)* swallowed. Examples of ways in which fruits were manipulated follow.

Dialium sp. The brittle, flattened seed cases were bitten in half and processed at a rate of 20–30 per minute. Seeds and pulp were swallowed and the cases spat out.

Detarium macrocarpum. This large fruit with dense green pulp encases a

hard discoid seed, 6–7 cm in diameter. Gorillas are not known to use tools in the wild [McGrew, 1989] and depend on the strength of their jaw musculature to break open the seeds to gain access to the kernels. The pulp was discarded.

Duboscia macrocarpa. This species was a major food-item, though seemingly unpalatable. The 4–6 cm ribbed fruits have a brown, velveteen skin, and the "pulp" has the texture of a scrubbing brush. The remains of a meal resembled apple cores.

Myrianthus arboreus. These large, yellow, composite fruits have a thick skin, similar to that of a pineapple. They consist of about 70 segments each containing a single seed encased in sugary pulp. Gorillas broke off pieces, extracted the seeds and pulp, then discarded the empty segments together with some sucked and spat-out seeds.

Pentadesma butyracea. The size of a small melon, these are the largest soft fruits found at Lopé. The orangey-pink pulp, sticky with latex, was eaten; the 3 cm seeds were chewed when unripe, but usually discarded when ripe.

DISCUSSION

A high dependence on fecal analysis in evaluating diet can lead to a bias against soft digestible plant parts, and in favour of hard items, such as seeds. However, after six years of the present study, many structural plant parts have been identified on trails, or gorillas have been seen eating them. More food-items have been recorded for the gorillas at Lopé than for any other population of gorillas; the highest numbers of foods listed previously were 160 in Zaire [Goodall, 1977] and 128 in Equatorial Guinea [Sabater Pi, 1977]. We found that gorillas living in mature forest depended heavily on fruits, although the proportions of each food-class in the diet remain to be determined. Over half (55%) of recorded items were fruits, and almost 100 fruit species were eaten. It has been suggested that access to fruit is restricted, as adult gorillas are poor climbers [e.g., Sabater Pi, 1977], but even silverbacks are capable of climbing and do so often at Lopé. This contrasts with Watts' [1984] report that mountain gorillas are terrestrial during 96% of their feeding time.

Fruits were usually swallowed whole, even though the increased load of seeds offsets the benefits of feeding on pulp [Herrera, 1981]. The cost of filling the gut with indigestible seeds is thought to outweigh the increase in handling time necessary to extract seeds from pulp [Milton, 1984]. Some seeds were eaten when immature, but in general ripe seeds passed through the gut undigested. Many seeds contain high concentrations of secondary compounds [Rogers et al., in prep.], and gorillas do not seem to have specialisations of the digestive tract necessary to metabolise such compounds [Andrews & Aiello, 1984; Chivers & Hladik, 1984].

The amount of fruit eaten during different months varied according to fruit availability, and one of the ways lowland gorillas coped with succulent fruit shortages was to eat more herbaceous vegetation [Rogers et al., 1988; Williamson, 1988]. *Aframomum* is a major food for gorillas in Cameroon [Butzler, 1980; Calvert, 1985], Equatorial Guinea [Sabater Pi, 1977], Gabon [Tutin & Fernandez, 1985], and Zaire [Schaller, 1963:151]. Similarly, *Aframomum* and *Haumania* form the gorillas' staple foods at Lopé, as they are abundant, perennially available, easily accessible on the ground, and the herb layer is comparatively less toxic than the canopy [Hladik, 1981; Waterman, 1984]. Such permanent food sources may play an important role in the ecology of gorillas and bonobos by alleviating competition for other foods [Wrangham, 1986].

Only four of the gorillas' food-items were not obtained from plants: earth and three species of insects. Ants were the predominant animal matter eaten by all primates at M'passa in north-east Gabon [Gautier-Hion et al., 1980], and *Oecophylla,* the weaver ant, comes closest to being the universal insect food for chimpanzees [McGrew, 1983]. Many social insects can be exploited without much expenditure of energy, but *Oecophylla* are particularly convenient as they bind leaves together into compact nests, each containing about 5 g of eggs, larvae, pupae, and adults [Hladik, 1973]. Although ants are regularly eaten by apes, they usually form only a small portion of the diet in relation to plant matter. For example, invertebrates, including weaver ants, formed only 3–4% by weight of the annual diet of chimpanzees at M'passa [Hladik, 1973].

Harcourt and Harcourt [1984] considered nutrient content of the thousands of insects inadvertently ingested by mountain gorillas to be trivial, as these amounted to less than 2 g per day. And Watts [1989] found that although some mountain gorillas fed on driver ants, they did so too rarely for the ants to be an important source of protein. However termite-eating by chimpanzees *is* nutritionally significant [e.g., Redford, 1987]. Furthermore, the larvae of *Oecophylla* have a high amino acid content (72%) in a readily digestible form [Hladik, 1977], which complements the protein obtained from leaves [Hladik & Viroben, 1974]. There is a striking similarity in the proportions of gorillas' dung which contained insects at Lopé and at Belinga in northeast Gabon [31.1% this study; 30.5% Tutin & Fernandez, 1983], so it seems likely that weaver ants and termites have interchangeable roles in the gorillas' nutrition.

Eastern gorillas are known to eat earth [Schaller, 1963:166; Fossey, 1983:52], and geophagy was seen at Lopé. There have been two main interpretations of soil ingestion: 1) that animals eat earth to obtain minerals or trace elements; and 2) that fine soils adsorb some of the secondary compounds present in leaves. Mahaney et al. [1990] have also suggested that mountain gorillas' consumption of soil may simply be a behavioural tradition, with no nutritional role.

Soils have been analysed from many sites, and sodium, in particular, has been measured in higher concentrations at salt-licks than in the surrounding areas [e.g., Schaller, 1963:371; Stark, 1986]. Some studies have denied any apparent physiological benefits of geophagy [Stark, 1986; Ganzhorn, 1987], but salt-licking by chimpanzees at Gombe correlated with changes in body weight, suggesting that salt requirement increased with metabolic stress [Wrangham, 1977]. Hladik and Gueguen [1974] found that the sodium content of soils seemed insignificant compared to that of some food plants, especially *Hypselodelphis* shoots, and they emphasised the physical action of earth in the gut. This view point was reiterated by Harrison and Hladik [1986], as geophagy by *Colobus satanas* coincided with peaks of leaf ingestion. Similarly, the occurrence of earth in gorillas' dung at Lopé correlated with consumption of leaves during the 1st year of study (Pearsons' $r(629) = .1232$, $P = .002$). However, as this soil was also relatively high in sodium, no firm conclusions have been drawn from these preliminary data.

This is the first long-term study of western lowland gorillas, and is particularly important as these gorillas inhabit an area of mature tropical forest and are sympatric with chimpanzees. One of our most interesting findings is that gorillas eat a great diversity of fruit. Seasonal variation in fruit consumption and the importance of fruit in the gorillas' diet have not been discussed here, but will be dealt with in future articles [Tutin et al., in prep.; Williamson, in prep.]. If lowland gorillas are truly frugivores, every aspect of their lives will be influenced by their feeding ecology, and a complete revision of the accepted view of gorillas as folivores is needed.

CONCLUSIONS

1. More food types have been recorded at Lopé than for any other population of gorillas: 182 parts of 134 plant species.

2. Gorillas consumed 95 species of fruits, and 98% of feces contained fruit remains.

3. Small quantitites of immature seeds were eaten; seeds of most ripe fruits were not ingested, or not digested.

4. All age-classes of gorillas fed in trees, up to 30 m above the ground.

5. Leaves and pith of 21 species of herbs, including *Aframomum, Haumania,* and *Megaphrynium,* were eaten as staple foods throughout the year.

6. Earth and at least three species of ants were also consumed.

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