REVIEW ARTICLE

Western Gorilla Diet: A Synthesis From Six Sites

M. ELIZABETH ROGERS[1*], KATE ABERNETHY[2,3], MAGDALENA BERMEJO[4], CHLOE CIPOLLETTA[5], DIANE DORAN[6], KELLEY MCFARLAND[7], TOMOAKI NISHIHARA[8], MELISSA REMIS[9], AND CAROLINE E.G. TUTIN[2,3]
[1]ICAPB, University of Edinburgh, Edinburgh, United Kingdom
[2]CIRMF/SEGC, Libreville, Gabon
[3]Department of Biological Sciences, University of Stirling, Stirling, United Kingdom
[4]Departamento Biologia Animal, Universidad de Barcelona, Barcelona, Spain
[5]WWF, Bangui, Central African Republic
[6]Department of Anthropology, SUNY at Stony Brook, Stony Brook, New York
[7]Department of Anthropology, Graduate Center CUNY, New York, New York
[8]JWCS, Tokyo, Japan
[9]Department of Sociology and Anthropology, Purdue University, West Lafayette, Indiana

The objective of this paper is to collate information on western gorilla diet from six study sites throughout much of their current range, including preliminary information from two sites (Afi and Lossi), where studies of diet have begun only recently. Food lists were available from each site, derived from indirect signs of gorilla feeding (such as feces), with some observational data. Important staple, seasonal, and fallback foods have been identified, and a number of striking similarities across sites have been revealed based on a much larger data set than was previously available. It was confirmed that the western gorilla diet is always eclectic, including up to 230 items and 180 species. The greatest diversity is found among the fruit species eaten, fruit being included in western gorilla diets from all sites and throughout most or all of the year. Eight plant families provide important foods at five, or all six, sites, suggesting that it may be possible in the future to predict which habitats are the most suitable for gorillas. Gorillas exploit both rare and common forest species. Similarities and differences among sites can be explained superficially on the basis of geography and the past history of the forest. Gorilla density across sites appears to be most affected by the density of monocotyledonous bulk food plants, but its

*Correspondence to: Dr. Liz Rogers, ICAPB, University of Edinburgh, Kings Buildings, West Mains Road, Edinburgh EH93JT, Scotland, UK. E-mail: me.rogers@virgin.net

relationship to the density of important tree food species has yet to be tested. Am. J. Primatol. 64:173–192, 2004.   © 2004 Wiley-Liss, Inc.

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INTRODUCTION

Studying western gorilla (*Gorilla g. gorilla* and *Gorilla g. diehli*) diet has not proved easy, because of the difficulties experienced by observers in lowland forest [Tutin & Fernandez, 1991]. There are still few systematic measurements of western gorilla diet based on feeding time for different foods, or weights ingested, because regular observational data on feeding have rarely been obtained (but see Remis [1997]). Despite this, several study sites distributed over the entire range of western gorillas are now yielding long-term indirect data documenting the foods used throughout several years, including seasonal shifts in diet and variations across years [Doran & McNeilage, 2001; Doran et al., 2002]. This paper brings in new data from two more sites to add to the existing database, and attempts to sift out the common factors that characterize western gorilla diet, and to see the extent of its variation. Knowledge of the essential components of western gorilla diet now has a firmer base, which will inform conservation decisions wherever range restriction occurs, as well as hold intrinsic interest as the basis for explanations of ranging and social behavior.

Since the 1980s, systematic data on western gorilla diet from several sites have shown that a diverse array of fruit species are consumed throughout the year, often in large quantities [e.g., Doran & McNeilage, 1998, 2001; Doran et al., 2002; Goldsmith, 1999; Nishihara, 1995; Oates et al., 2003; Remis, 1997; Tutin & Fernandez, 1985]. The absence of succulent fruit in the diet of mountain gorillas (*Gorilla b. beringei*) is a consequence of its absence in their habitat [Hladik, 1988; Tutin & Fernandez, 1985; Watts, 1990; Williamson, 1988; Yamagiwa et al., 1992a]. Western gorillas also consume, along with fruit, large quantities of the nonreproductive parts of a range of trees and understory plants, and it is these foods that support them at times of fruit shortage and provide staple nourishment throughout the year [Doran & McNeilage, 1998, 2001; Kuroda et al., 1996; Rogers et al., 1988; Tutin & Fernandez, 1993a; Tutin et al., 1991; Watts, 1990; Williamson et al., 1990]. The major groups of food plants involved are the monocotyledonous families Arecaceae, Commelinaceae, Marantaceae, and Zingiberaceae. However, it is now clear that plants from other families of monocotyledons are as important in different habitats, notably in swamps [Blake et al., 1995; Nishihara, 1995]. Complete diet data are not yet available from most of these sites, particularly where observations of gorillas have been largely confined to open swampy areas (''bais''), where gorillas are easily seen in the bais, but which provide few dietary items overall (but see Magliocca and Gautier-Hion [2002]). Also still lacking is systematic, long-term dietary information from sites where monocotyledonous plants of any kind are sparse in the understory vegetation, as at Petit Loango, Gabon [Yamagiwa et al., 1995].

Another aspect of gorilla ecology is their highly selective feeding behavior. Nutritional analyses have shown that western gorillas select parts of the food plants that are the least fibrous and have more protein (leaves), or more sugar and less tannin (ripe fruit), than the discarded parts [Calvert, 1985; Remis, 2003; Remis et al., 2001; Rogers et al., 1990]. Nutritional data have also demonstrated that when fruit is scarce, western gorillas eat more fibrous and less proteinaceous

leaves and stems, and switch from sweet, succulent seasonal fruits to fibrous, less succulent fallback fruits that are usually ignored [Kuroda et al., 1996; Nishihara, 1995; Remis, 2003; Remis et al., 2001; Rogers et al., 1988, 1990]. Mountain gorillas also eat selectively [Waterman et al., 1983; Watts, 1996], but the extent of selectivity is more obvious in western gorillas because the plants available to them, and hence their diets, are much more heterogeneous. Another question, related to selectivity, is whether western gorillas are selective in their foraging for fruit, or they are fruit opportunists, exploiting mainly those species whose fruits happen to be common in the forest, with no significant foraging costs [Doran & McNeilage, 1998, 2001; Doran et al., 2002; Goldsmith, 1999; Kuroda et al., 1996; Remis, 1997, 2003; Williamson, 1988]. Evidence now accumulating strongly suggests that they are fruit ''pursuers,'' with strong preferences for particular and often rare fruit species, for which they will incur significant foraging costs [Doran & McNeilage, 1998, 2001; Doran et al., 2002; Goldsmith, 1999; Williamson, 1988]. When little fruit is available, western gorillas appear to adopt a ''low-energy'' strategy, by decreasing their day ranges and feeding more on lower-quality herbaceous foods and fibrous fruits [cf., DaSilva, 1992].

In spite of many remaining gaps in our knowledge, there is now much more scope for making generalizations about the common features of western gorilla diet across the whole species range. In this paper, we bring together diet composition data from the following study sites with at least 1 year's systematic data on diet: Afi, Nigeria (McFarland); Bai Hokou, Central African Republic (Cipolletta and Remis); Lope, Gabon (Abernethy, Rogers, and Tutin); Lossi, Republic of Congo (Bermejo); Mondika, CAR/Congo (Doran); and Nouabalé-Ndoki, Congo (Nishihara). We address the following questions: How variable is western gorilla diet across sites? What are its fundamental components, and how much do these vary across sites? What aspects of resource distribution and availability are most likely to determine western gorilla density?

MATERIALS AND METHODS

Sampling Biases

All basic methodology for studying western gorillas has been previously published, and was used across sites with modifications [Cipolletta, 2003; Doran et al., 2002; Goldsmith, 1996; Nishihara, 1995; Remis, 1994; Rogers & Williamson, 1987; Tutin & Fernandez, 1984, 1985, 1993a–c; Tutin et al., 1991; White, 1994a, b; White et al., 1995; Williamson, 1988, 1993; Williamson et al., 1990]. In this section, we give the general methodological framework, which was universal, and Table I gives site-specific details of practices on the ground. The information from Afi (McFarland, unpublished results) and Lossi is preliminary, pending publication of full details of these studies.

Food Availability

Phenology of new leaf, flower, and fruit production, and availability of food items from trees or monocotyledonous herbs has been monitored monthly along permanent transects at most sites (Table I) [Doran et al., 2002; Oates et al., 2003; Remis, 1994; Rogers et al., 1988; White et al., 1995; Williamson, 1988]. An arbitrary scoring method is used throughout for different phenophases, from 1 (rare) to 4 (abundant), or some modification thereof [Tutin & Fernandez, 1993c; Tutin & White, 1998; Williamson, 1993]. Fruitfall along transects has also been

TABLE I. Summary of the Methods Used to Obtain Gorilla Diet and Density Data from Each Site*

	Food availability	Evidence for diet	Importance criteria	Gorilla density
Afi Mountain, Nigeria Study began 1996[1,2]	Tree stems >10 cm dbh; 12 (250 × 5 m or 265 × 10 m) transects.[1] Monthly phenology, 880 inds. of 156 spp. Herb densities: stems in 1m² plots (n = 40,900 plots).[1]	Fecal samples: n = 1418.[1] Trails: n = 4181 feeding sites, 142 days.[1] No observations.[1,2]	1) eaten on trails ≥11 mo, ≥50% wk sampled, &/or ≥11% days sampled/mo; or 2) in any month: present in ≥20% fecal samples, or ≥10% trails, &/or ≥10% fruit feeding sites.[1]	Estimated, based on night nest counts from repeated censuses through study site.[1,2]
Bai Hokou, Central African Republic Study began 1990[3,4,5]	Trees >10 cm dbh within 5 m along 19 km of trails.[3,4] Monthly phenology, 973 trees, 152 spp.[3,4] Herb densities: stems in 1000 1 m² plots.[3,4]	Fecal samples: n = >859.[3,4] Trails: all fresh feeding sites separated by ≥2 m⁵. Observations: 826 1 min. samples.[3,4]	1) In trails &/or obs on ≥50% mo; or 2) ≥50% days in at least 1 mo, for foods occurring in >1% of all fecal samples.[3,4] (Cipolletta, unpub.)	Nest counts on 81.2 km of line transects.[6,7]
Lope, Gabon	Trees >70 cm dbh along 5 km × 50 m transect; >10 cm along 5 km × 5 m & in 50 20 × 20 m plots[14]	Fecal samples: n = >4675.[8,10–12]	1) In diet in ≥6 months of year; or 2) scored >50% in majority of fecal samples where it occurred, for foods occurring in >10% of samples[12] (Abernethy, unpub.)	Repeated nest counts on 5 km line transect[13]

Site	Phenology / density data	Methods	Definition criteria	Census / group notes
Study began 1983[8-14]	Monthly phenology, >670 trees, 67spp.[10] Herb densities: stems in 1 m² plots along 5 km transects.[9]	Trails: qualitatively, trail follows <2days old. n >1036 nest sites, >634 other trail follows. Quantitatively, 334 day follows (Abernethy, unpub.) No systematic observations.		Repeated group follows & individual recognition in restricted study area (Abernethy, unpub).
Lossi, Republic of Congo	No tree densities. Important fruit food trees located in home range (Bermejo, unpub.).	Fecal samples: n = 670.	1) In trails &/or obs on ≥ 50% of mo; or 2) ≥50% days in at least 1 mo. (Bermejo, unpub.)	No Lossi data; at least 8 groups (n = 136 gorillas).[15] In Odzala: nest counts, 7 transects, 68 km. Methods based on Tutin & Fernandez [1984].
Study began 1994[15]	No phenology data. No herb density data.	Trails: foods recorded when first encountered/day. Observations: 5 min scans, 1 min focals. N contact hours = 1099 hrs. (Bermejo, unpub.)		
Mondika, Central African Republic	Tree stems >10 cm dbh; 28 transects (200 × 100 m).[16] Monthly phenology, 10 inds. of 20 imp. food species.[16]	Fecal samples: n female = 315, n male = 400.[16]	Fecal samples: 1) present in 50% mo; or 2) 50% of fecal samples or mean abundance score of ≥2 in any month. Trails: occurs on ≥5% of trails[16].	No data. At least 9 gorilla groups.

TABLE I. Continued

	Food availability	Evidence for diet	Importance criteria	Gorilla density
Study began 1996[16]	Herb densities: stems in 136 4 m² plots.[16]	Trails: n = 619 > 200 m.[16] No observations.		
Nouabalé-Ndoki, Republic of Congo	Fruitfall census along transect 10 m × 37 km. Total N of fruiting trees & spp/mo.[17]	Fecal samples: n = 522.[17]	Fecal samples: 1) present in >50% mo; or 2) vol. % score at least 10% in at least one month.	Nest counts on line transects.[18,19]
Study 1991–92[17]	No herb density.	All feeding signs ≤2 days old.[17] Observations: n = 93, 60% were of foraging.[17]	Trails/obs: 1) present at high % in >50% mo; or 2) high % in at least 1 mo.[17]	

*References cited in the first column are the key sources for relevant methodology at each site. Methods used at Lopé in the 1980s were the basis for those at all other sites. Importance criteria distinguish between 1) staple and 2) seasonally important items.
[1]McFarland, dissertation in prep.; [2]Oates et al. [2003]; [3]Remis [1994,1997]; [4]Goldsmith [1996, 1999]; [5]Cipolletta [2003]; [6]Remis [2000a]; [7]Blom [2001]; [8]Tutin & Fernandez [1984,1985]; [9]Rogers & Williamson [1987]; [10]Williamson [1988, 1993]; [11]Williamson et al. [1990]; [12]Tutin & Fernandez [1993a,b]; [13]White [1994b]; [14]White [1995]; [15]Bermejo [1997, 1999]; [16]Doran et al. [2002]; [17]Nishihara [1995]; [18]Mitani et al. [1993]; [19]Nishihara [1994].

used to measure tree fruit availability at Lopé and Nouabalé-Ndoki [Nishihara, 1995; White, 1994a]. Where no phenology data are available (Lossi), the project was not originally set up to study feeding ecology [Bermejo, 1997].

Density of food plants in the habitat was calculated from the density or basal area of all trees >10 cm diameter at breast height (dbh) along transects sampling different habitat types used by gorillas (Table I) [Doran et al., 2002; Goldsmith, 1999; White, 1995; Williamson, 1993]. Herb densities were measured from 1- or 4-m^2 plots along transects or distributed at random across the study site (Table I) (Lopé [Rogers & Williamson, 1987; White et al., 1995], Bai Hokou [Goldsmith, 1999], and Mondika [Doran et al., 2002]). At Afi, herbs rooted within 0.5 m on either side of 40.9 km of transects placed at 1-km intervals across the study site were enumerated (Table I).

Observing Western Gorillas

Because of dense vegetation, and the tendency of gorillas to flee [Tutin & Fernandez, 1991], few studies of western gorillas have obtained extensive long-term observational data on food consumption (Table I). At Afi, gorilla observation is discouraged, because of the gorillas' highly precarious status in the area. At Bai Hokou, feeding has been quantified by 1-min focal samples of individuals chosen at random [Remis, 1997], and a similar feeding-frequency method was used at Lopé [Tutin et al., 1997]. Because of low visibility on the ground, these data are biased toward feeding in trees, but most plant foods are taken from trees (79% at Bai Hokou [Remis, 1997]). Regular observations have been made of western gorillas on the ground in open swampy areas (bais) in the Congo, but few of these were feeding observations (Odzala [Magliocca & Gautier-Hion, 2002]). Habituation of groups of western gorillas in the Lossi forest and at Bai Hokou has been partially successful and is yielding direct feeding data via focal and scan sampling [Bermejo, 1997; Cipolletta, 2001, 2003]. At Lossi, focal animals were observed for as long as they were visible during 1,099 contact hours over 4–30 days per month (Table I).

Indirect Evidence: Fecal Samples

The most extensive data regarding the composition of western gorilla diets at most sites have come from analyses of fecal samples (Table I), which contain fruit remains, such as seeds (from which fruit species can be identified), as well as remains of nonfruit foods and insects [Tutin & Fernandez, 1993b; Williamson, 1988; Williamson et al., 1990]. Without microscopic examination, fecal samples do not usually yield specific information about the nonreproductive plant parts that have been eaten. Instead, general categories such as ''fiber'' or ''green leaf fragments'' have been measured throughout by % weight or volume, or on a scale of abundance [Goldsmith, 1996, 1999; Nishihara, 1995; Remis, 1997; Tutin & Fernandez, 1993b; Tutin et al., 1991; Williamson, 1988].

Fresh fecal samples are collected each month, attempting to equalize samples from adult males and females (distinguished by the size of the dung) (Table I). Samples are sieved through a 1-mm mesh; fruit components are identified, counted, or scored; and fiber/leaf fragments are quantified. The relative weights or volumes of each dietary category are determined so that seasonal changes in the relative consumption of fruit and fiber can be documented [Cipolletta, 2003; Doran et al., 2002; Goldsmith, 1996, 1999; Nishihara, 1995; Remis, 1997; Rogers

et al., 1988; Tutin et al., 1991; Williamson, 1988] (McFarland, unpublished results).

Indirect Evidence: Trail Analysis

Western gorillas leave characteristic remains of their feeding activities along their trails, because they are selective feeders and discard the least nutritious parts of their food plants [Calvert, 1985; Jones & Sabater Pi, 1971; Rogers et al., 1990, 1992; Tutin & Fernandez, 1985; Williamson, 1988]. Quantification of feeding remains has involved scoring each food item when it is first encountered on a fresh trail [e.g., Doran et al., 2002]. Another method is to count all, or a minimum number of, food items or feeding sites encountered along fresh gorilla trails, and then calculate the proportion of feeding remains each month from each category of food (e.g., leaf, pith, or shoot) or species [Goldsmith, 1996, 1999; Nishihara, 1995; Oates et al., 2003; Rogers et al., 1990]. Estimates of biomass consumed can also be made by comparing processed and unprocessed items [Rogers & Williamson, 1987; White et al., 1995] (McFarland, unpublished results). Most of the items are parts of leaves, stems, and shoots, which are the foods least easily identified species in fecal samples. Fruit remains may also be found on trails, but may not be attributable to gorillas if sympatric primates also eat them [Tutin et al., 1997; but see Doran et al., 2002]. Thus, analysis of feeding remains on trails complements that of fecal samples, which yields information mainly about fruit consumption [Tutin & Fernandez, 1993b]. However, trail data may miss leaf and bark foods from trees, unless the gorillas drop obvious feeding remains. At Mondika, recent adoption of focal sampling of diet during all-day follows of gorillas is greatly increasing the recorded diversity of leaf species consumed from trees and lianas, and therefore previous estimates of leaf diversity in the diet are much too low.

Important Foods

''Importance'' in the diet has been defined at all sites by the level of representation of a food in fecal samples, at feeding sites on trails, or during observations of feeding (Table I). The basic concept behind ''importance'' is that such foods should dominate the diet during some period in most or all years, and their availability should influence ranging [Tutin & Fernandez, 1993a]. Recently, important food species have been divided into three categories: 1) staple foods (eaten on a daily/weekly basis throughout the year), 2) seasonal foods (present in the majority of samples when available), and 3) fallback foods (always available, but eaten only or mainly during fruit-scarce months) [Doran et al., 2002]. We adopted these definitions in this study, with slight variation across sites.

Gorilla Density

All density data come from nest counts along line transects [e.g., Tutin & Fernandez, 1984; White, 1994b], except at Afi, where simultaneous searches for nests were conducted throughout the study site, but not along straight-line transects (Table I) [Oates et al., 2003].

OVERVIEW OF FINDINGS

General Composition of Western Gorilla Diet

Overall diet composition is now known from six sites where western gorillas have been studied for at least a year is now known. No sex differences in diet have been detected [Doran et al., 2002]. The average food species diversity is 148 species (n = 6 sites) for western gorillas, but only 71 species for mountain and eastern gorillas, even after many years of observation (n = 2 sites [Yamagiwa et al., 1996; Watts, 1996]). The total numbers of food items and species diversity may still increase for western gorillas, because there is a pronounced "length of study effect" [Tutin & Fernandez, 1993a], and some diet studies have been relatively short, as at Afi, Lossi, and Ndoki (Table I). Fruit species are the most diverse food category at all western gorilla sites, whether assessed indirectly or by direct observation (e.g., 70% of food species (Mondika), and 51% of feeding observations (Bai Hokou) Table II). Fruit is eaten year round, even when fruit

TABLE II. Important Food Plant Families & Plant Parts Eaten Across Western Gorilla Study Sites

	Parts eaten	Afi	BH	Lopé	Lossi	M'dika	Ndoki	Genera (Life form)
Staple foods								
Apocynaceae	P, B	√						Landolphia [Liane]
Commelinaceae	P						√	Palisota [H]
Marantaceae	P,B,YL,Sh	√	√	√	√	√	√	Haumania, Hypselodelphys, Megaphrynium, Thaumatococcus [H]
Moraceae	L	√						Ficus [T]
Zingiberaceae	P	√	√	√	√		√	Aframomum, Costus, Renealmia [H]
Seasonal foods (all trees except where indicated)								
Agavaceae	L	√						Dracaena
Anacardiaceae	F	√						Pseudospondias, Sorindeia, Trichoscypha
Annonaceae	F,Fl	√	√		√	√	√	Anonidium, Hexalobus, Monodora, Polyalthia, Uvariodendron
Apocynaceae	F,Se,L,St,B	√	√		√	√	√	Dictyophleba [Liane], Landolphia [Liane], Tabernaemontana
Araceae	L,P	√						Amorphophallus [H]
Burseraceae	F				√			Dacryodes, Santiria
Ebenaceae	F		√	√		√		Diospyros
Euphorbiaceae	F		√	√	√	√	√	Drypetes, Uapaca
Flacourtiaceae	F					√		Oncoba [Shrub]
Guttiferae	F		√		√			Garcinia, Pentadesma
Irvingiaceae	F,Se		√	√	√		√	Irvingia, Klainedoxa
Leguminosae	F,Se,L,B,Fl	√	√	√	√	√	√	Angylocalyx, Dialium, Erythrophleum, Parkia, Pterocarpus, Tetrapleura
Loganiaceae	F					√		Strychnos
Marantaceae	F		√		√	√		Haumania [H]
Meliaceae	L	√						Turreanthus
Menispermaceae	F						√	Tiliacora [Liane]

TABLE II. Continued

	Parts eaten	Afi	BH	Lopé	Lossi	M'dika	Ndoki	Genera (Life form)
Moraceae	F,Fl,Se,L,B	√	√	√	√	√		*Antiaris, Ficus, Milicia, Morus, Myrianthus, Treculia*
Myristicaceae	F,R				√			*Pycnanthus*
Myrtaceae	F				√			*Syzygium*
Olacaceae	F,L,Fl		√					*Strombosia*
Passifloraceae	F,L,Fl,B				√	√		*Barteria*
Rhamnaceae	F	√						*Maesopsis*
Rubiaceae	F				√	√		*Nauclea, Pseudogardenia*
Sapindaceae	F		√	√	√	√		*Ganophyllum, Lecaniodiscus, Pancovia*
Sapotaceae	F	√	√		√	v		*Chrysophyllum, Manilkara, Synsepalum*
Sterculiaceae	F	√		√				*Cola*
Tiliaceae	F						√	*Grewia*
Ulmaceae	F,L,Fl		√		√			*Celtis*
Verbenaceae	F,L	√	√			√		*Vitex*
Vitaceae	F,L				√			*Cissus [Liane]*
Zingiberaceae	F	√	√	√				*Aframomum [H]*
Fallback foods								
Acanthaceae	L		√			√		*Thomandersia, Whitfieldia [Shrubs]*
Apocynaceae	F,B,L,St		√					*Landolphia [Liane], Pycnobotrya [Liane]*
Araceae	L,P	√						*Stylochiton [H]*
Arecaceae	L,P		√		√			*Ancistrophyllum, Elaeis [Palms]*
Commelinaceae	P	√	√					*Palisota [H]*
Dioscoreaceae	L		√					*Dioscorea [Liane]*
Gnetaceae	L		√					*Gnetum [Liane]*
Irvingiaceae	F				√	√		*Klainedoxa [T]*
Leguminosae	B,F	√				√		*Pterocarpus, Tetrapleura [T]*
Marantaceae	P,F	√		√	√	√		*Marantochloa, Megaphrynium [H]*
Moraceae	F,B,L,St	√	√	√	√	√		*Ficus, Milicia, Morus, Musanga, Myrianthus [T]*
Myristicaceae	L	√						*Pycnanthus [T]*
Sapotaceae	F					√		*Chrysophyllum [T]*
Tiliaceae	F,B,L	√	√	√	√	√	√	*Desplatsia, Duboscia, Grewia [T]*
Ulmaceae	F,B,L					√	√	*Celtis [T]*
Zingiberaceae	F,P	√	√			√		*Aframomum, Costus [H]*
Swamp/marsh foods								
Cyperaceae	St	abs	√					*Rhynchospora [H]*
Hydrocharitaceae	R	abs	√		√	√	√	*Hydrocharis [H]*
Marantaceae	P	abs		√	√			*Marantochloa [H]*

B, bark; F, fruit; Fl, flowers; H, herb; L, leaves; P, pith; R, roots; Se, seeds; Sh, shoots; St, stem; T, tree; YL, young leaves.

availability is low, and is present in 90–100% of all fecal samples in both sexes [Cipolletta, 2003; Doran et al., 2002; Oates et al., 2003; Remis, 1997; Tutin et al., 1991; Williamson et al., 1990].

Many plant species also provide leaves, stems, pith, shoots, roots, and bark for western gorillas (e.g., 84 species at Lopé and Bai Hokou [Remis, 1997; Tutin & Fernandez, 1993a] (Table II). Such foods are present year round, in varying amounts, in 100% of gorilla dung at all sites. The diversity of these food plants will certainly be underestimated unless feeding remains on gorilla trails are analyzed regularly (e.g., Afi [Oates et al., 2003]); but equally, the diversity of these foods taken from trees will be underestimated unless regular observation of gorillas is possible, as at Lossi and, more recently, Mondika (Table I).

Key Foods for Western Gorillas

The diet of western gorillas is so diverse that one must find a way to define the most important foods in order to compare diets between sites (Table I, Materials and Methods section), and to decide which ecological factors are influencing gorilla ranging.

Table II shows a list of plant families and genera that provide important foods for western gorillas at six sites. Food lists were shortest at Lopé, where importance criteria were most stringent, and Ndoki, where the study period was short (Table I). Botanical families are listed instead of individual species to highlight similarities between sites, where the same family of plants may be used as food but the species differ (as with *Haumania* spp. in Congo and Gabon). Knowing the dominant families of food plants is also useful to know the dominant families of food plants when comparing them with forest composition data, which is usually described in the literature by dominant families, not species [e.g., White, 2001a]. From the table, it can be seen that there are some striking similarities across sites, and some differences involving families and species that are important foods at only one site. Afi has the highest proportion of ''unique'' families that provide important food species at no other site (31%), whereas 17% of all families are important across five or six of the sites. For example, species of Marantaceae (primarily *Haumania* spp.) are staple foods for western gorillas across all sites, whereas species of another herb family (Commelinaceae, *Palisota* spp.) are a staple food at Ndoki only. Leaves from a liana (*Landolphia*) are a staple at Afi only. Of the important seasonal foods (not all of which are fruit) five families stand out as food sources at nearly all, study sites (Annonaceae, Apocynaceae, Euphorbiaceae, Leguminosae, Moraceae). Of the important fallback foods, two families are critical providers of food: the Moraceae and Tiliaceae. Thus, the family Moraceae features prominently in all three important food categories and appears to be a key provider of food items to western gorillas. However, the food items involved do not come mainly from *Ficus* species, and are often nonfruit food items, such as bark and leaves (Table II) [Doran et al., 2002; Nishihara, 1995; Oates et al., 2003; Remis, 1997; Rogers et al., 1990; Tutin & Fernandez, 1993a; Williamson et al., 1990]. On the other hand, Table II shows differences between sites that remain to be explained. For example, gorillas eat the fruit of species of Burseraceae and Myristicaceae at Lossi, but eat them much less, or not at all, at other sites where they occur (notably at Lopé).

Forest composition data were available from four of the six sites, and showed that whereas herbaceous species that provide staple foods are always common, a relatively small proportion (9% (Lopé) to 19% (Mondika)) of tree species that provide important seasonal foods are among the most common (top 10) in the

forest. Therefore, the gorillas are selecting seasonal foods mainly from rarer tree species. Plant species that provide important fallback foods can be common or relatively rare (e.g., *Celtis mildbraedii* cf. *Duboscia macrocarpa* at Mondika [Doran et al., 2002]).

Dietary Overlap Between Sites

The dietary overlap [Tutin et al., 1997] between important food-plant species for western gorillas at different study sites should reflect forest composition. Table III shows a dyadic comparison for all six sites, in which food species lists for each dyad were compared and the percent overlap calculated. Food species were used here, not plant families, in order to reflect differences in diet at the species level, and to avoid overemphasizing similarities at the family level (Table II). The table shows that important food species at Afi, the most isolated site, overlap the least with all other sites. Lopé food species are the most similar to those at Afi. Bai Hokou, Mondika, and Ndoki show the highest levels of overlap with each other.

The data used to calculate dietary overlap refer only to ''important'' food species; however, thresholds determining ''importance'' have not yet been standardized (Table I), and similarities between sites in less important foods are excluded. Gorillas eat many of the same species at different sites, but at different frequencies, so affecting their importance value [e.g., Nishihara, 1995; Remis, 1997]. Thus, the total dietary overlap would be much higher.

Gorilla Density

If the important staple foods for western gorillas must be abundant in order to maintain such large primates, and since most important staples are monocotyledonous herbs, then can one predict gorilla density by herb densities? Available data on this question are very patchy, and are often derived from a few censuses in heterogeneous habitats, but some preliminary conclusions can be reached (Table IV). The highest densities of western gorillas are always in Marantaceae or swamp forest. The high densities recorded by Mitani et al. [1993] and Nishihara [1994] in the Ndoki forest were in an area where the habitat is a mosaic of mixed forest, monodominant *Gilbertiodendron* forest, and swamp forest. The lowest densities, recorded at Petit Loango, Gabon, were in an area where no herbs from the Marantaceae and Zingiberaceae were recorded in 800 m^2 [Furuichi et al., 1997; Morgan, 2001]. These were minimal estimates, because gorilla nests cannot always be distinguished from those of chimpanzees, since both apes nest in trees there [Furuichi et al., 1997]. The data in Table IV, though

TABLE III. Dyadic Dietary Overlap (%) in Important Plant Food Species Between Food Lists From the Six Study Sites

	Afi	Lopé	Lossi	Bai Hokou	Mondika	Ndoki
Afi	–	21	15	18	10	8
Lopé	47	–	41	35	24	24
Lossi	24	32	–	28	28	16
Bai Hokou	23	20	23	–	50	27
Mondika	14	14	25	57	–	29
Ndoki	23	23	31	62	62	–

TABLE IV. Densities of Gorillas and Monocotyledonous Herbs in Western Gorilla Sites Across Central Africa*

	Afi	Lopé	Odzala	BHokou	Mondika	Ndoki	Likouala	PLoango
Gorillas (ind/km²)								
Overall	1.0	0.8	5.44[1]	0.9[2]	n/a	0.2[3]		0.08[7]
						1.9–2.6[4]		0.21[8]
						3.9–5.5[5]		
Mat. forest		0.48	1.1					0.03[8]
Mar. forest	Absent	1.0	11.3	Absent	Absent	Absent	Absent	Absent
Sav. galls	Absent	0.5		Absent	Absent	Absent	Absent	
Sw. forest	Absent	Absent					2.7[6]	
Raphia sw.	Absent	Absent	Absent				5.9	Absent
Monocots (/metre²)								0.46[7]
Overall	1.16			1.11	0.78	n/a	n/a	0[8]
Marants.	0.51	1.75	High		0.6	High		0[8]
Zingibers	0.51	0.13			0.07			
Palisota	0.06	n/a			0.11	High		
Sw. herbs & palms	Absent	Absent	High	Rare	High	High	High	

*Gorilla densities (weaned individuals/km²) were measured by line transect censuses and nest counts; herb densities are stem counts/metre² from plots along transects (Table 1). "Absent" refers to absence of the habitat type at that site; n/a, no data available.

Mat. forest, mature forest; Mar. forest, marantaceae forest; Sav. galls, savanna gallery forests; Sw. forest, swamp forests; Raphia sw, swamp forests with dominant *Raphia* palms; Marants., all Marantaceae species; Zingibers, all Zingiberaceae species; Palisota, all Commelinaceae.

[1]All density data for Odzala National Park, Congo, from Bermejo [1999]; [2]Remis [2000a]; [3]Fay & Agnagna [1992]; [4]Nishihara [1994]; [5]Mitani et al. [1993]; [6]Both density figures from Likouala swamps, Congo, Blake et al. [1995]; [7]Morgan [2001]. The mean herb density value was for "non-woody terrestrial vegetation". [8]Furuichi et al. [1997].

fragmentary, emphasize that mean values (e.g., in "lowland forest") conceal large variations in density in different habitat types, and gorilla distribution can be very clumped locally [Yamagiwa, 1999] (E.A. Williamson, personal communication).

DISCUSSION

Table II emphasizes that western gorillas everywhere have eclectic but very selective diets consisting of 1) staple piths, leaves, roots, and shoots from abundant, monocotyledonous plant species in the understory of various terra firma forest types, and/or in swampy areas; 2) seasonal ripe fruits from a wide variety of species, common or rare in the forest; and 3) fallback foods, which are often of lower nutritional quality, consisting of piths, leaves, barks, and fibrous fruits from herbaceous and tree species of many of the same families that fall into categories 1 and 2. These data also confirm the position of western gorillas at the top end of a range of diet diversity and frugivory in the genus *Gorilla*: at its minimum in the highest altitude populations of mountain gorillas, at intermediate levels in lower altitude populations of eastern lowland gorillas, and at highest levels in western gorilla populations in the Congo basin and Nigeria. Data from the latter (Afi) emphasize this assessment, because the Afi site is geographically the farthest west from other sites where western gorillas were already known to have diverse diets and eat large quantities of fruit (e.g., Lopé [Williamson et al., 1990]). However, sampling biases (see Materials and Methods) could be affecting our ability to detect the details of dietary variation among sites,

and good observational data are still needed urgently. The use of a standardized methodology among sites is also needed, particularly with regard to definitions of ''important'' food species. We strongly recommend that in the future the criteria described by Doran et al. [2002] for determining the importance of western gorilla foods be used as a standard at all sites, so we can have a universal baseline for intersite comparisons and keep updating this post-hoc analysis.

The value of different foods to gorillas throughout the annual cycle and between years has only become clear after years of collecting data. This overview allows us to see which foods are most important at each site, and to make predictions about what foods might be crucial at any new site. The biomass of fallback foods available at crunch times, such as the annual dry season, may constrain the population density or biomass of primates in tropical forests [Terborgh, 1983, 1986]. In addition, it has been argued that the distribution of staple foods has a strong influence on ape social systems [Wrangham 1979, 1986], and the distribution of seasonal foods that are strongly preferred (particularly fruit) can profoundly affect ranging while they are available [Goldsmith, 1999; Remis, 1997; Tutin et al., 1991] (Klein, unpublished data). Thus, the data presented in Table II should help researchers assess the potential of any future site as a habitat for gorillas under a variety of circumstances, including range restriction as a result of human disturbance.

Dietary overlap data are used here to express levels of similarity among food species lists from different sites, and to make inferences about underlying similarities in forest composition. The different western gorilla study sites from which diet data are currently available are situated in different forest types, but all are within the Guineo-Congolian regional center of endemism [White, 2001a]. Geography, as well as forest composition and history, may explain some of the differences and similarities among sites. Afi and Lopé are part of a chain of centers of biodiversity and endemism in moist evergreen forest from the Biafran forest (Cross River to Sanaga River) to West Cameroon and the Massif du Chaillu in Gabon, which relates to previous arid phases [Maley, 2001; White, 2001a]. However, Lopé has experienced extensive savanna recolonization as well, which explains the existence there of Marantaceae forest [White, 2001b]. This feature is also found at Lossi, which is south of the Odzala National Park, where savannas and Marantaceae forest are also extensive [Bermejo, 1997]. Therefore, Marantaceae forest is the principal vegetation link between Lopé and Lossi, and the principal difference between them and all other sites. On the other hand, Lossi includes forest types that are characteristic of the west Congo basin as well, such as swamp forest [White, 2001a]. Thus, food species at Lossi ought to overlap to some extent with those at Bai Hokou, Mondika, and Ndoki, as can be seen in Table III. The latter three sites should show the highest levels of overlap in important food species because they are closest geographically and have the same forest types, even if the proportions of each forest type differ. There is overlap also with Lopé and Lossi, suggesting that many of the same tree species occur at all five sites, even if their density rankings are not the same. This would be predicted, because all western gorilla sites are within the Guineo-Congolian region [White, 2001a]; and even at Afi, which is completely isolated, there is still a large variety of trees are still available as food for gorillas (Table II) (McFarland, unpublished results).

Considering their density, the strong suggestion is that western gorillas are at higher densities in areas where their staple food is most abundant. Marantaceae forest is a distinct forest type with a dense understory of herbs in the families Marantaceae, Zingiberaceae, and Commelinaceae [White, 2001b];

but, these same herbs can also be common in the understory of other forest types, as at Ndoki (in mixed forest [Nishihara, 1995]; see also Afi, Table IV). Moreover, it is probably not just the commonest herbaceous species that matter, for less common ones often serve as fallback foods, and have been shown to be more fibrous and contain less protein or sugar than the species used as staples [Kuroda et al., 1996; Nishihara, 1995; Remis, 2003]. The overall status of swamp food plants in western gorilla diet is currently unclear (Cyperaceae, *Hydrocharis*; Table II), because gorillas visit swamps sporadically; however, they are likely to be important fallback or seasonal foods because of their abundance, nutritional value, and mineral content [Doran & Greer, in press; Doran et al., 2002; Kuroda et al., 1996; Magliocca & Gautier-Hion, 2002; Nishihara, 1995]. The marsh plant *Marantochloa cordifolia* (Marantaceae) is certainly an important fallback food species at Lopé (Table II) [Williamson et al., 1988], where it is very common locally, and the stem base has a high sodium content [White et al., 1995] (Abernethy and Tutin, unpublished data). In addition, swamp forest contains trees (both palms and other species) that could also provide important food items, such as pith (*Raphia* spp.) and fruit (*Uapaca* spp.) (Likouala swamps [Blake et al., 1995]).

The important features of all of these food species that could influence gorilla population density, and hence the value of a site for their future conservation, are long-term availability in bulk, provision of items with high protein and low fiber (high-quality forage), low levels of digestion inhibitors, provision of minerals, low foraging costs and low inter- and intragroup competition when the animals are feeding on them [Calvert, 1985; Doran & McNeilage, 1998, 2001; Doran et al., 2002; Goldsmith, 1999; Nishihara, 1995; Remis, 2003; Rogers et al., 1990; Wrangham, 1986]. Obviously, staple foods should be abundant if a large-bodied primate is to be maintained on them [Gaulin, 1979], and where there are little or sparse herbaceous monocotyledonous plants, as at Petit Loango, gorillas must have another bulk food source as yet unknown.

Other factors affecting gorilla density may be the density of preferred seasonal fruit foods, and competition with other large mammalian consumers, particularly chimpanzees and forest elephants (*Loxodonta africana cyclotis*). There is no particular physiological imperative for gorillas to choose abundant seasonal foods, if foraging costs incurred by searching for rare foods are not too high, and if a variety of preferred species are available, but the density of seasonal fruit trees may still be important. All western gorilla sites appear to have at least one food species that supplies important seasonal fruits, that is one of the commonest tree species in the forest (e.g., *Cola lizae* at Lopé, and *Anonidium mannii* at Ndoki and Mondika), and an array of less-common species that provide ripe, sweet, succulent fruit as well, plus various other food items, including seeds, leaves and bark (Table II). It is doubtful whether any of these are as essential as the density of staple and fallback foods, particularly since gorillas can survive without any fruit at high altitudes, at certain times of the year at low altitudes, or in disturbed lowland forest where fruit diversity is low [Calvert, 1985; Tutin et al., 1991a; Watts, 1996]. However, the relationship between the density of the most important seasonal fruit foods and western gorilla density across sites has not been tested and must be investigated in the future. Perhaps there is something to be learned from forest elephants, which have diets with fluctuating fruit content, but, like gorillas, have been thought of as folivores [White et al., 1993]. Yet, surprisingly, it has recently been shown that the most important factor determining their distribution in undisturbed forest is fruit availability, not browse [Blake, 2002].

As to competition with other large mammals, proof is notoriously hard to obtain. However, it has been suggested that gorilla densities are lower where they are sympatric with chimpanzees and elephants, because there is considerable dietary overlap among them [Tutin & Fernandez, 1993a; Tutin et al., 1991; White et al., 1994]. This may be the case at Lopé, where the biomass of forest elephants in Marantaceae forest is very high (5,225 kg/km^2 [White, 1994b]), but a preliminary analysis of long-term data did not reveal a negative correlation between the presence of elephants in the central study area and the presence of gorillas (unpublished Lopé data). At Petit Loango, Gabon, there is some tentative evidence for a negative correlation between the density of elephants and that of apes (S. Suzuki, personal communication). If these findings are confirmed, it may be that the low density of herbaceous ground vegetation at Petit Loango constrains both elephants and gorillas, which consume large quantities of such vegetation at other sites, whereas at Lopé the dense understory vegetation in the Marantaceae forest provides enough food for all throughout the year [White, 1994b; White et al., 1995]. Competition between gorillas and sympatric chimpanzees may occur at times, or in areas, of fruit scarcity [Tutin & Fernandez, 1993a; Tutin et al., 1991; Yamagiwa et al., 1992b]. In such circumstances their diets are most different, for gorillas compensate for low fruit availability by consuming more fibrous foods (low-quality pith, leaves, shoots, and fibrous fruit), whereas chimpanzees may also eat more nonfruit foods, but always continue to eat quantities of fruit (e.g., from figs and palms), and modify their social behavior by foraging in smaller groups to do so [Doran, 1997; Kuroda et al., 1996; Tutin & Fernandez, 1993a; Tutin et al., 1991a; Yamagiwa, 1999; Yamagiwa et al., 1992b, 1996]. Earlier work suggested that there was little competition between gorillas and chimps in Ndoki swamp forest, because chimpanzees did not feed in swamps there [Kuroda et al., 1996; Malenky et al., 1994].

The emerging new information on western gorilla diet reinforces earlier conclusions from more limited data–for example, that there are some strong similarities among sites [Nishihara, 1992]. These similarities probably reflect the fact that all extant western gorillas live in the lower Guinea through Congolia subdivisions of the Guineo-Congolian forest [White, 2001a], which have certain universal features. The heterogeneity of the remaining forest, derived from its original diversity, probably explains the fact that western gorillas have an eclectic but highly selective diet even when confined to small ''islands'' of the original forest, as at Afi Mountain (Table II). However, before any future conservation decisions are made involving range restriction of western gorillas, more data are needed to probe the relationship between food choices and forest composition, particularly as regards fruit. For example, some might say that western gorillas can survive well in degraded forest, but it is a notable feature of studies in such areas that crop-raiding or the use of old plantations provides some of gorillas' foods [Calvert, 1985; Jones & Sabater Pi, 1971]. This may just reflect convenient availability, but probably also means that their diet without crop-raiding is of relatively low quality, or the biomass available is lower than it seems [Malenky & Stiles, 1991; Watts, 1984; White et al., 1995]. The flexibility of gorilla diet as regards the proportions of fruit and nonfruit components, and the smaller home range that flexibility can allow, mean that gorillas can live in some fragmented, degraded, and high-altitude forests that cannot support smaller-bodied frugivorous primates, such as chimpanzees [Remis, 2000b; Yamagiwa & Mwanza, 1994]. Predicting which forest sites are best for gorillas could be crucial for their future

conservation, and the broad database presented here is a foundation for such predictions.

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