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FOOD SELECTION BY WESTERN GORILLAS IN RELATION TO FOOD
CHEMISTRY AND SELECTIVE LOGGING IN CAMEROON, WEST AFRICA

University of California, Los Angeles

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Food Selection by Western Gorillas
in Relation to Food Chemistry and Selective Logging
in Cameroon, West Africa

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Anthropology

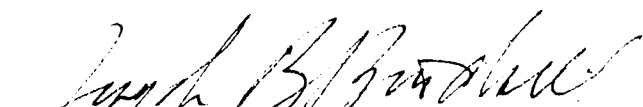
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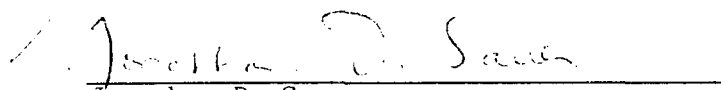
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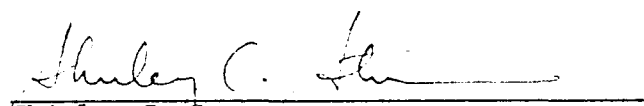
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1985

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ACKNOWLEDGEMENT

The second paper in this dissertation titled Food Selection by Western Gorillas (G.g.gorilla) in Relation to Food Chemistry first appeared in the journal Oecologia (Berlin), volume 65, 1985. Permission to reproduce the article here as part of the doctoral dissertation was kindly granted by Springer-Verlag, the publisher of Oecologia (Berlin).

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- Webb, J.C., Bullock, S.H. (1977) Cameroon: Project 1199--gorilla conservation. In: World Wildlife Fund Yearbook 1976-1977 (P.Jackson, ed.) p.61-63. Morges, Switzerland: World Wildlife Fund.
- Calvert, J. (1982, August) Ecology of western gorillas. Paper presented at the joint meeting of the International Primatological Society and the American Society of Primatologists, Atlanta, Georgia.
- Calvert, J. (1985) Food selection of western gorillas (G.g.gorilla) in relation to food chemistry. Oecologia (Berl.) 65:236-246.

ABSTRACT OF THE DISSERTATION

Food Selection by Western Gorillas
in Relation to Food Chemistry and Selective Logging
in Cameroon, West Africa

by

Julie Jean Calvert

Doctor of Philosophy in Anthropology

University of California, Los Angeles, 1985

Professor Donald G. Lindburg, Chair

Western gorillas were studied for 15 months in mature and disturbed, lowland rain forest of southern Cameroon. 1)The diet consists of shoots, stems, leaves, bark, roots and fruit throughout the year. There was no evidence of animal matter ingested. The bulk of the diet consists of stems and shoots. Gorillas stimulate regeneration of some food plants, effectively staggering visits to specific food patches while foods regenerate to a visitable quality. Associations of food plant species render food choices complex and highly interdependent. 2)Samples from the Cameroon diet including stems, leaves, shoots and fruit (N=36) were analyzed for nutrients, digestibility and digestion-inhibiting substances. Analysis of food chemistry in relation to food preference indicates that lignin, digestibility and crude protein are the most significant factors in food selection at this site. Food chemistry of western gorillas is compared to food chemistry of mountain gorillas in the montane forest of East Africa. Foliage consumed by western gorillas contains more condensed tannin than does foliage consumed by mountain gorillas. The greater content of condensed tannin in the

leaves consumed by western gorillas is related to the greater representation of woody plants in the western diet. 3) In Cameroon gorillas consume plants from mature forest, subsistence farms and forest which has been selectively logged. In 759 plots, data were collected on vegetation structure and composition including the abundance of 8 major food plants. Plots were located in fields, mature forest and forest logged 3, 4 and 6 years earlier. Logged and cultivated areas exceed mature forest in the number of plots of high resource abundance. The abundance of most foods decreases from the third to the sixth year after logging. The impact of logging and cultivation on gorillas is evaluated in an evolutionary context and compared to the long-standing relationship of elephants and gorillas.

The Diet and Feeding Pattern of Western Gorillas
in Cameroon, West Africa

Summary

Western gorillas were studied for 15 months in mature and disturbed forest of southern Cameroon. The diet consists of shoots, stems, leaves, bark, roots and fruit throughout the year. There was no evidence of animal matter ingested. The bulk of the diet consists of stems and shoots. Many foods are characteristic of early stages of succession in the forest. Associations of food plant species in habitats render food choices complex and highly interdependent. Gorillas stimulate regeneration of some food plants by their visitation patterns and foraging techniques. Gorillas effectively stagger visits to specific food patches while foods regenerate to a visitable quality. The most important foods are infrequently consumed by other mammals.

Introduction

Gorillas provide an interesting focus for feeding studies as they are the largest of all the primates and the most herbivorous of the hominoids. The literature on gorilla diet is limited and disproportionately focused on Gorilla gorilla berengei (mountain gorillas). Little is known of the other two subspecies, G.g.graueri (eastern lowland) or G.g.gorilla (western). The literature on gorilla diet through 1963 is reviewed in Schaller (1963). In the last 23 years mountain gorillas have been extensively studied. Studies of mountain gorilla feeding have focused in three areas: Kabara in the western Virunga Volcanoes, Zaire [(1)Schaller,1963]; Bukavu, Zaire [(2)Casimir & Butenandt,1973; (3)Casimir, 1975;

(4)Goodall,1977], and at Mt.Visoke in the eastern Virungas of Rwanda [(5)Fossey,1974; (6)Caro,1976; (7)Elliott,1976; (8)Fossey & Harcourt,1977; (9)Harcourt & Stewart,1978; (10)Watts,1980]. Schaller (1963) additionally includes ecological information gathered by Emlen and Schaller in their broad, six-month survey of gorillas in Rwanda, Uganda and Zaire. The duration of the above studies include less than seven months (6,7), one to two years (1-4,10) and five to seven years (5,8,9). Two of the shorter studies focus on ranging rather than feeding per se (6,7). Table 1 details information on gorilla ecology presented in the literature after 1962. Diverse nutritional analyses have been done including amino acids, mineral, water content (3); gross energy and protein, crude fibre and digestibility (4). Rarely has an attempt been made to quantify distribution or abundance of foods (2,3,6) or food plant phenology (3).

Considerably less information is available about the feeding of western gorillas. The report of Jones and Sabater Pi on their 16-month survey of primates in Rio Muni includes data on gorilla diet and habitat use (1971; see also Sabater Pi,1977). Merfield (1954,1956) presents his excellent, anecdotal observations of gorilla ecology based on fifteen years of collecting Cameroonian gorillas for museums. Very brief surveys were done in Cameroon by Critchley (1968) in the Takamanda Reserve, and Butzler (1980) in the coast, plateau and Sanga regions.

A major goal of the current study was to examine western gorilla feeding in diverse habitats including cultivated and logged areas. Particular interests in this study were the delineation of diet

TABLE 1

Scope of gorilla ecology studies since 1962

Parameter	Schaller 1963	Casimir & Butenandt 1973	Casimir 1977	Goodall 1977	Fossey 1974	Caro 1976	Elliott 1976	Fossey & Harcourt 1977	Harcourt & Stewart 1978	Watts 1980	Jones & Sabater Pi 1971	Sabater Pi 1977 + +
Diet composition	x		x	x	x			x	x	x	x	x
Feeding techniques	x		x	x				x				
Nutrition	+		x	x								
Food distribution/ abundance quantified		x				x				x		
Food plant phenology quantified			x									
Home range area	x	x		x	x	x	x	x		x	x	
Day travel length	x	x		x			x	x				
Seasonality travel	x	x	x	x	x							
Habitat description	x	x	x	x	x						x	x

+Nutritional analysis for Peucedanum commissioned by Dart is reported in Schaller 1963.

++A comprehensive summary of Sabater Pi's fieldwork 1956-1969.

breadth and diet variability across a range of forest habitats. It was hoped that such dietary information would aid in an assessment of the behavioral flexibility with which gorillas face habitat disturbance. A second interest was to assess the impact which gorillas have on the abundance of their major plant foods. Waser and Homewood (1979) have suggested that renewal rates of food may be the critical variable in the spacing of foragers. The preference of gorillas for certain foods is discussed elsewhere in relation to food chemistry (Calvert, 1985). In the same paper, the food chemistry of mountain gorillas is compared to that of western gorillas. The impact of selective logging on the abundance of food resources of western gorillas is assessed in another paper (Calvert, manuscript).

Systematic study of non-human primates in disturbed habitats has only begun. Wilson and Wilson (e.g. 1975) examined the impact of Indonesian logging on East Bornean primates. More recently, Johns has completed study in West Malaysia on the impact of selective logging on some aspects of primate social structure (1981, 1982A, 1982B). Wild non-human primates have generally been studied remote from human influence, although such settings are increasingly scarce. The effect of habitat disturbance on western gorilla feeding is particularly important because the subspecies is still abundant and a contribution may yet be made to their management and longevity (Webb & Bullock, 1977).

Methods and study site

Research reported here was conducted near Campo on the southern border of the United Republic of Cameroon in coastal forest

(2°0',23'N,10°0',3'E) (See Figure 1). Letouzey (1968) describes forest in this region as low elevation, evergreen forest characterized by a predominance of gregarious species of Caesalpineaceae relatively absent from neighboring Congolese Forest. Richards notes that Cameroonian forest is particularly lacking in epiphytes and abundant in cauliflorous shrubs and trees (1963). Letouzey notes that forest in the immediate vicinity of Campo has a considerable semi-deciduous component due to local rainfall patterns.

The area consists of gently rolling hills punctuated by local streams. Elevation here is approximately 200m. The region forms a portion of the watershed of the Bitande River which eventually joins the Bongola and Ntem Rivers entering the Atlantic Ocean at Campo Beach. The soil is ferralitic latosol. Daily temperatures vary little from 27°C. There are two rainy seasons annually with considerable local variation in the yearly totals. In the town of Campo on the coast, annual rainfall totalled 2571 mm. (May 1976-June 1977). Twenty-six kms. to the east, at Nkoelon where this study occurred, rainfall for the same period was 1575 mm. (61% of Campo rainfall). Figure 2 shows the distribution of rainfall at Nkoelon collected in this study (1976-1977).

The forest in the center of the Campo Reserve included thirteen species of primates: Gorilla gorilla gorilla, Pan troglodytes, Colobus satanas, Cercopithecus erythrotus, Cercopithecus pogonias, Cercopithecus cephus, Cercopithecus nictitans, Cercocebus albigena,

FIGURE 1

Location of this study (+)

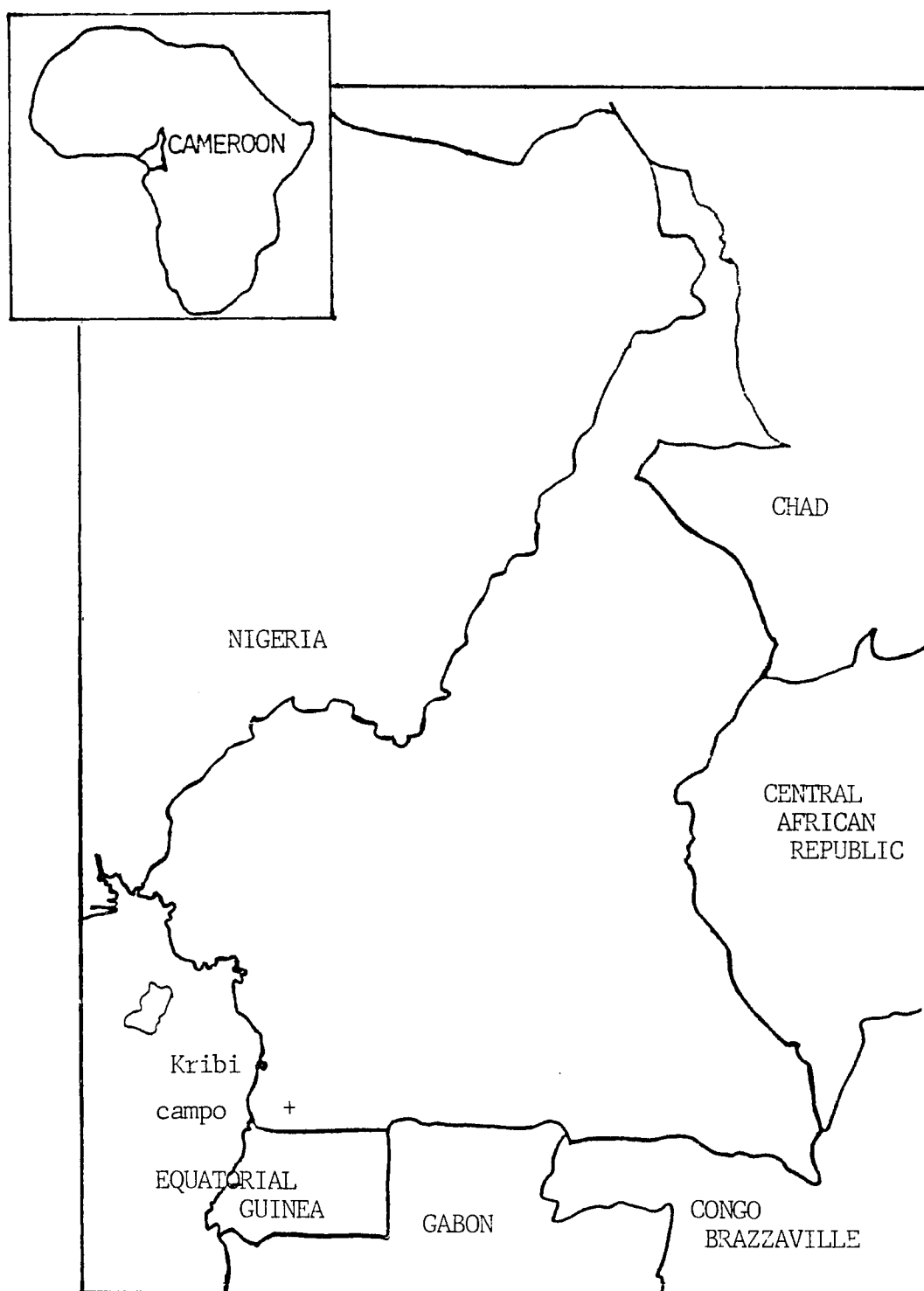
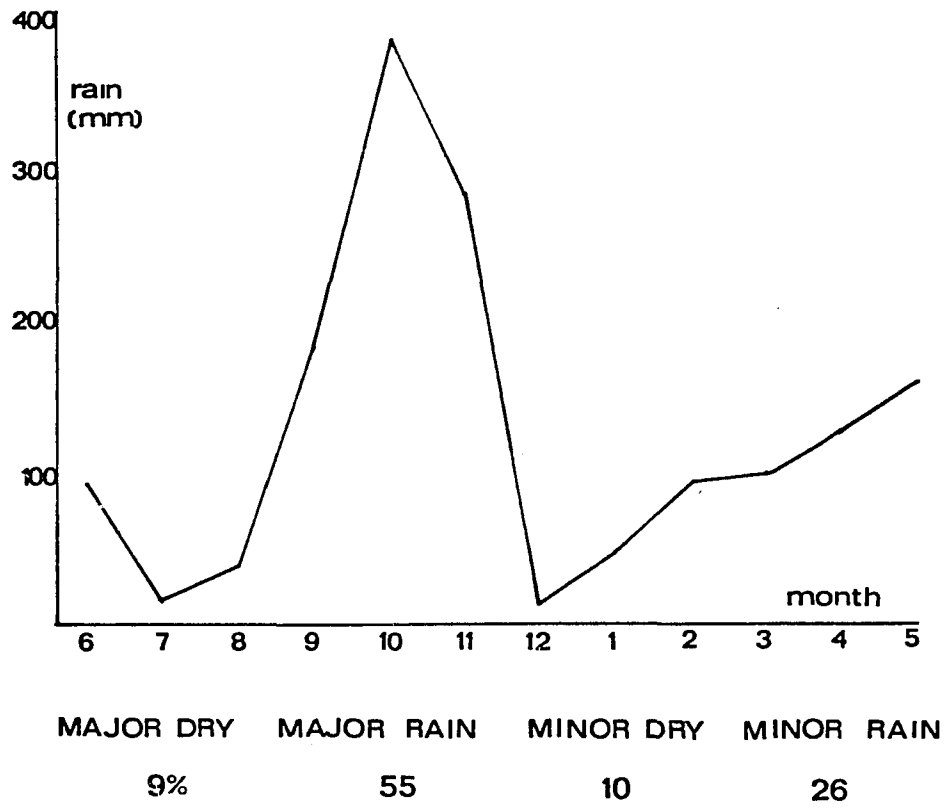


FIGURE 2

Nkoelon rainfall 1976-1977



Cercocebus torquatus, Miopithecus talapoin, Galago sp., Papio sphinx and Homo sapiens. The human component included Bantu agriculturalists and pygmy (Badjele) gatherer-hunters. Other common, large mammals included Syncerus caffer, Potamochoerus porcus porcus, Loxodonta africana cyclotis, Panthera pardus, Felis aurata, Iragelaphus spekei gratus and four species of duiker.

Four areas within 15 kms of Nkoelon village were utilized in this study including fields and logged areas(Figure 3). Crops cultivated at field site 1 were yams, banana, plaintain, cucumber, manioc and peanuts. Bananas and yams were cultivated at field site 2. Logged area 1 was cut in 1971 and roads there were later bulldozed in 1974 and 1976. Logged area 2 was cut in 1968 and has not been cleared subsequently. Small-scale logging occurred outside study areas earlier near the coast. A road network at Campo/Ipono was extended east into the study areas in the mid-1960's. Less than 1% of the Campo region (sensu Bullock, 1980) consisted of fields, villages, roads or logged areas before 1968. Between 1968 and 1977, that figure reached about 10%.

Gorilla feeding was studied in mature and disturbed forest. Emphasis in this study was on feeding patterns characteristic of fields and logged areas. Diverse microhabitats were sampled intensively in these contexts including streams, tree fall gaps, tractor trails, roadsides, tractor parks, recently planted and abandoned fields. Feeding of six gorilla groups and one solitary male is reported here. The size of gorilla groups in my study areas is reported in Table 2. Table 3 summarizes the group size data in the

FIGURE 3

Major study areas

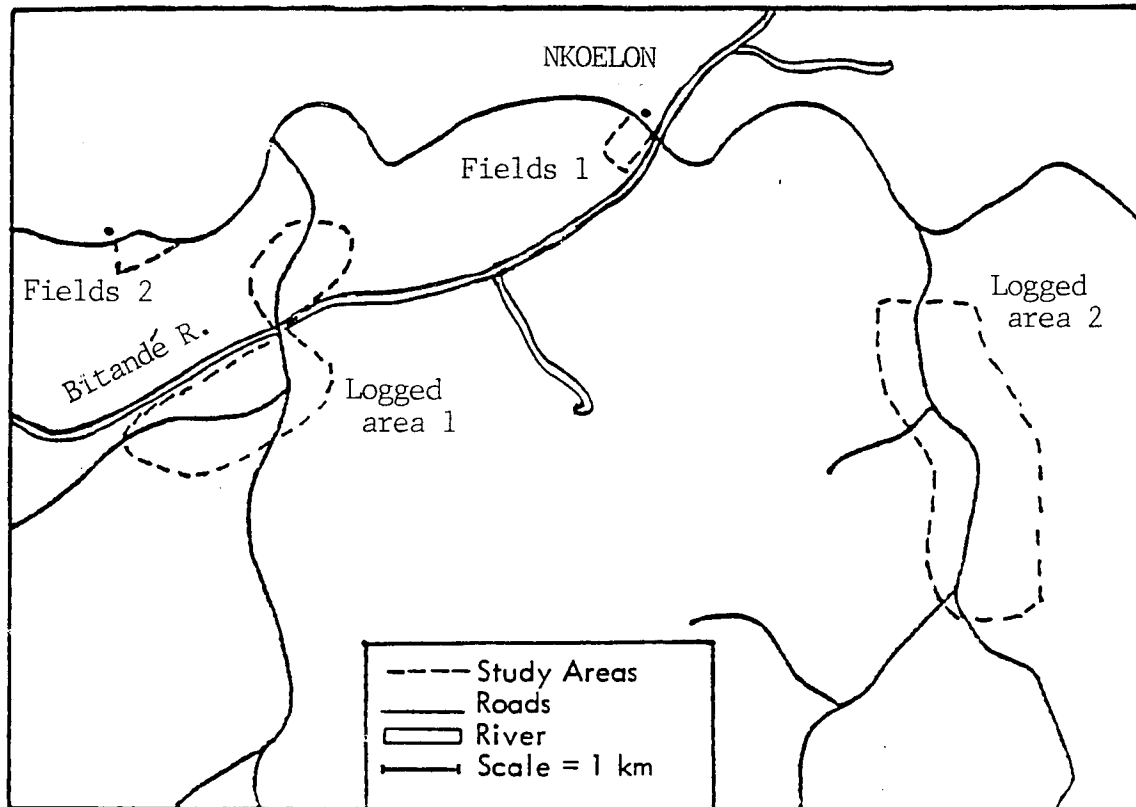


TABLE 2

Size of gorilla groups in my study areas

Area	Group size
Logged area 1	4, 10, 5
Logged area 2	11, (1)
Fields 1	7
Fields 2	11

TABLE 3

Comparisons to other western gorilla groups in the literature

Location ⁺	Reference	Range of Grp. sizes	Number of groups	Mean size	Median size	Solitarious present?
Plateau (Batouri)	Merfield 1954 ⁺⁺	6	1	6	--	--
--	Geddes 1955 ⁺⁺⁺	10	1	10	--	--
Plateau	Merfield and Miller 1956 ⁺⁺⁺	2-10	5	7	9	yes
Nigeria (Obudu)	Critchley 1968	4-6	3	5	5	no
Coast (Mt. Alen/ Abuminzok, Rio Muni)	Jones & Sabater Pi 1971	2-12	13	7	7	yes
Sangha (Moloundou)	Butzler 1980	4-11	4	8	8.5 (9)	yes

⁺Locations are within Cameroon unless otherwise designated. Locations outside parentheses refer to regions of gorilla distribution defined in relation to Groves' morphological classification of the genus Gorilla (1967).

⁺⁺Merfield (1954) mentions two groups (N=2,6). Only the latter is shown here as the former group was mentioned in Merfield and Miller (1956).

⁺⁺⁺These data are from Schaller 1963, Table 20, p.355.

literature. The size of groups in this study was not significantly larger (mean=8) than that of other western groups (mean=7).

Diet and feeding patterns. Each week between May 1976 and August 1977, I visited the four study areas to find recent evidence of gorillas (necessary exceptions were September 16-October 2, 1976; December 19, 1976-January 3, 1977; January 12-February 10, 1977). When more than one area contained recent evidence of gorillas, I collected data in the least commonly used habitats. Once begun, data were collected in an area for 2-3 days continuously. During that period, brief visits to other areas yielded the next focal area.

I observed animals feeding whenever possible making a concerted effort to remain unnoticed by the animals, none of whom were habituated to my presence. Usually I moved along within about 5-10m of a group simultaneously mapping and studying feeding of the previous hour and, as the vegetation permitted, catching glimpses of animals feeding. Notes were taken on species and plant part consumed, units consumed, feeding technique and position, food plants within arms' length (one meter), and foods visible from the location (at gorilla eye level about one meter). Plant parts include fruit, seeds, leaves, petioles, stems, shoots and roots. Units of food refer to the number of a given plant part consumed, e.g. 10 leaves.

The composition of 1400 feeding sites (meals) was enumerated and mapped. Feeding sites indicate spatially and temporally distinct feedings, one or more units of one or more species consumed within a one meter radius, separated from similar events by a distance of about one meter (or more). Nine hundred feeding sites were included

in extensive vegetation analysis. At every sixth (of nine hundred) feeding, vegetation structure and composition were recorded. The abundance of herbs, vines, shrubs/saplings, and trees was indicated at height intervals 0-0.5m, 0.6-2.5, 2.6-10.5, 10.6-20, and ≥ 20 m (similar to Peek et al, 1976). Distances between feeding sites were paced where vegetation density permitted. More often distances were measured with a meter stick or tape. Heights were estimated with a rangefinder. Abundance of growth forms was ranked on a scale of 1-4 where 1=absent, or rare and inconspicuous; 2=occasional, or rare but conspicuous; 3=common uniformly or in patches, and 4=abundant. Plant growth forms include herbs, vines, saplings (≤ 10 cm.diameter bole), and trees (≥ 10 cm. diameter bole). All food plants within arms' reach of an adult gorilla were listed, as were foods visible from gorilla eye level. Evidence of previous use (feeding, beds or feces) was noted, along with its approximate age.

Food plants were identified at the Cameroon National Herbarium and Royal Botanic Gardens, Kew. A second set of plants comprising 36 plant parts of 27 species was dried for chemical analysis. This represents half the diet and includes nearly all frequently consumed items. Two hundred eighty fresh fecal samples were collected and evaluated.

Results

General feeding pattern. Gorilla feeding involves two basic types of areas, and a bimodal travel pattern similar to that documented in other African primates (Struhsaker, 1978; Waser, 1977;

Rudran, 1978). Type A areas are large, dense groves of herbs, vines and saplings characteristic of fields, roadsides, tractor trails, tree fall gaps and streams. Vegetation on the ground is thick and tunnels persist wherever gorillas have passed. Travel in these areas involves short daily trips with frequent turns. Animals are generally at least 3 meters apart with the exception of mother-infant pairs who are together. Typically only a small portion of another gorilla is visible to any nearby gorilla. An individual might walk 1-2 meters, sit down, snap and strip 4-5 long stems of Aframomum hanburyi, consuming the juicy internal pith, discarding the dry paper-like sheath in a pile on the ground. This meal would be followed by another 1-2 meter walk and a similar feeding. Most rest and sleep sites are in or adjacent to Type A areas. A typical travel pattern over several days would involve 2-3 days of intensive feeding in this type A area, followed by a day of travel over a considerable distance through a Type B area. In Type B areas, food resource density and ground cover are relatively sparse. The bulk of the vegetation is in the canopies and boles of mature trees. Travel here may be single-file for the entire group, and involve occasional feedings. Individuals feed along the path briefly, and traverse arcs out from the group's linear path. Such loops are completed by the individual rejoining the linear progression further on. See Figure 4 for comparisons of travel patterns and spacing of feedings in the two types of areas.

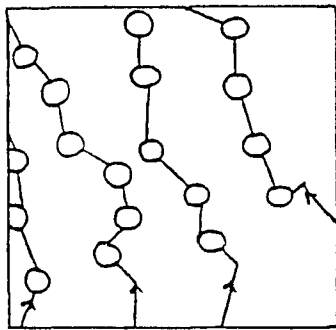
Diet summary. Gorillas eat a wide diversity of plants in this coastal forest. Growth forms in the diet included vines, herbs,

FIGURE 4

Feeding and travel in two habitats

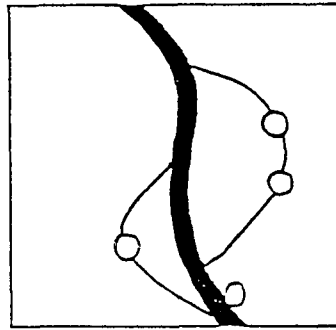
Type A

roadsides, tree fall
gaps, streambanks and
fields



Type B

closed canopy, ground
clear forest



Feeding (o), individual path (-), group path (—)

TABLE 4

Composition of gorilla diet at Campo 5.76-7.77

Family	Species	Plant part consumed (Leaf,Stem,Bark,Shoot=O,Fruit=R)
Araceae		
	<u>Anchomanes difformis</u>	L,S
	<u>Raphidophora africana</u>	L,S
	<u>Rhektophyllum mirabile</u>	L,S
Areaceae		
	<u>Podococcus barteri</u>	S
Commelinaceae		
	<u>Palisota ambigua</u>	L,S,O
Convolvulaceae		
	<u>Ipomoea involucrata</u>	L
Dioscoreaceae		
	<u>Dioscorea praehensilis</u>	L
	<u>Dioscorea sp. (nampenday)</u>	L
Euphorbiaceae		
	<u>Manihot esculenta</u>	S,root
	<u>Uapaca staudtii</u>	R
Humiriaceae		
	<u>Sacoglottis gabonensis</u>	R
Loganiaceae		
	<u>Anthocleista vogelii</u>	L
Marantaceae		
	<u>Halopegia azurea</u>	O
	<u>Haumania danckelmaniana</u>	O
	<u>Hypselodelphys sp.</u>	O,R
	<u>Megaphrynium macrostachyum</u>	O,R
Mimosaceae		
	<u>Tetrapleura tetraptera</u>	R

TABLE 4 (continued)

Family	Species	Plant part consumed (Leaf, Stem, Bark, Shoot=O, Fruit=R)
Moraceae	<u>Musanga cecropioides</u>	L,B,stem cork
Musaceae	<u>Musa</u> sp.	S,O,R
Solanaceae	<u>Solanum torvum</u>	R
Sterculiaceae	<u>Eribroma oblongum</u>	B
Tiliaceae	<u>Grewia coriacea</u>	R
Urticaceae	<u>Urera cameroonensis</u>	L,B
Vitaceae	<u>Cissus petiolata</u>	L
	<u>Cissus</u> sp.	R
Zingiberaceae	<u>Aframomum aulacocarpus</u>	R
	<u>Aframomum citratum</u>	S,O
	<u>Aframomum daniellii</u>	S,O,R
	<u>Aframomum giganteum</u>	S,R
	<u>Aframomum hanburyi</u>	S,O,R
	<u>Aframomum subsericeum</u>	S,O,R
	<u>Costus</u> sp.	S,O,R

Additional species were consumed only once: (Annonaceae) Pachypodanthium sp.(L); (Apocynaceae) Baissea sp.(L); (Arecaceae) Eremospatha sp.(S); (Combretaceae) Terminalia superba(L); (Commelinaceae) Palisota barteri(S); (Fabaceae) Dalbergia sp.(L); (Flacourtiaceae) Caloncoba sp.(R); (Lauraceae) Hypnodaphnis zenkeri(L); (Moraceae) Ficus vogeliana(L); (Myristicaceae) Staudtia stipitata(R); (Passifloraceae) Deidamia clematoides(L); (Poaceae) Guaduella sp.(L); (Rhizophoraceae) Poga oleosa(R); (Tiliaceae) Desplatsia sp.(R); (Urticaceae) Urera oblongifolia(L); (Violaceae) Rinoria sp.(L); (Vitaceae) Cissus cf. dinklagei(L,R); Leea guineensis(R); (Zingiberaceae) Renealmia sp.(S).

saplings and trees. Table 4 details the composition of the diet which includes fifty-one plant species representing forty-one genera and twenty-nine families. (An additional food plant was formally identified after publication of Calvert, 1985.) In addition to thirteen major food plant species, nineteen species are eaten occasionally. Nineteen additional species were eaten only once. Often more than one species was consumed at a single sitting. There was no evidence of animal matter ingested by gorillas either in observations of animals, refuse, stomachs (N=1), or feces (N=280).

Thirteen species (nine genera) of plants are commonly consumed. Five species belong to one genus, Aframomum (Zingiberaceae). Major food plants are characteristic of disturbed situations, whether in widely disturbed areas, or small pockets of disturbance in mature forest. The growth forms include gigantic pioneer herbs (eight), vines (terrestrial and climbing), small trees and a sapling. Table 5 details the relative contributions of the nine genera to the diet including the number of sites where each was consumed and the number of units each contributed to the diet. For the most important plant parts, the total weight is additionally estimated by multiplying the total units consumed times the estimated fresh weight of a unit. Fresh weight includes only the portion of the plant part which is consumed. An estimation of weight is important as frequency/density measures of feeding do not give an accurate indication of bulk ingested (Hladik, 1977; Struhsaker, 1978). Although Musa stems contribute twice as many kilograms as Aframomum stems do to the diet, it seems likely that on most days gorilla stomachs are full of

TABLE 5

Relative contribution of major foods to the diet 5.76-7.77

Family	Food	Part Consumed	Number of Feeding Sites	Units Eaten	Estim. Unit Wt.	Estim. Total g. Eaten
Commelinaceae						
	<u>Palisota ambigua</u>	S	96	190	140 g.	26,600 g.
		O	6	9		
		L	24	46		
Dioscoreaceae						
	<u>Dioscorea</u> sp. (nampenday)	L	42	1,022		
Marantaceae						
	<u>Halopegia azurea</u>	O	18	140		
	<u>Haumania danckelmaniana</u>	O	44	117		
	<u>Hypselodelphys</u> sp.	O	21	187		
		R	1	1		
	<u>Megaphrynium macrostachyum</u>	O	39	87	20	1,740
		R	2	26		
Moraceae						
	<u>Musanga cecropioides</u>	L	91	327	20	6,540
		Bark	6	6		
		Stem cork	4	5		
		S	2	7		

TABLE 5 (continued)

Family	Food	Part Consumed	Number of Feeding Sites	Units Eaten	Estim. Unit Wt.	Estim. Total g. Eaten
Musaceae						
	<u>Musa</u> sp.	S	45	59	7,000	413,000
		O	3	3		
		R	8	149	50	7,450
Zingiberaceae						
	<u>Aframomum aulacocarpus</u>	S	12	25		
		O	1	1		
		R	3	4		
	<u>Aframomum daniellii/</u> <u>hanburyi</u> *	S	346	973	100	97,300
		O	31	72		
		R	169	1,539	10	15,390
	<u>Aframomum giganteum</u>	S	13	19		
		R	101	1,120	15	16,800
	<u>Aframomum subsericeum</u>	S	298	727	90	65,430
		O	38	63		
		R	6	6		

*Aframomum daniellii and A.hanburyi can only be distinguished on the basis of flowers which the former species rarely has. The two species commonly interdigitate in mixed species groves. Thus the feedings are pooled here.

Aframomum stems. The large, heavy Musa stems are ingested on relatively few days while one or more species of Aframomum was consumed at 75% of the feeding sites.

More than one plant part was eaten on 20% of the food species, generally stem and fruit though not necessarily at the same time and place. Parts consumed included leaves, shoots, stems, fruit, bark and roots. The bulk of the diet consisted of stems and shoots. The number of units (e.g. stems) consumed per plant part/species varied considerably (range 1-174). Seventy-five per cent of the feedings were less than five units/plant part/species. Small fruit and leaves were eaten in particularly large numbers. Half the two hundred and eighty fecal samples which were analyzed contained some evidence of fruit consumption, generally tiny seeds.

Diet variability. A number of variables are important in understanding gorilla diet and foraging. These include (1) diet variability, (2) independence of food choices, and (3) impact of gorillas on food resources, among others. Table 6 compares the diets in various habitats and areas. A major difference between fields is the quantity of Dioscorea and Musanga cecropioides consumed. The proportions of Musa and Aframomum are similar in various fields. Logged areas differ in the proportions of Halopegia, Musanga and fruit of Aframomum giganteum. Fields differ from logged habitats in the smaller proportions of Aframomum and the larger proportions of Musa and Dioscorea consumed.

There are differences in the numbers of rare and occasional plants consumed across areas and habitat types. Fields contribute

TABLE 6

Diet variability across areas and habitats

Family	Food	Part Consumed	Number of Units Eaten (e.g. stems)					
			Area			Habitat		
			F1	F2	L1	L2	TF	TL
Commelinaceae								
	<u>Palisota ambigua</u>	S	0	6	10	174	6	184
		O	0	2	0	7	2	7
		L	0	2	0	44	2	44
Dioscoreaceae								
	<u>Dioscorea</u> sp. (nampenday)	L	19	422	0	581	441	581
Marantaceae								
	<u>Halopegia azurea</u>	O	0	0	135	5	0	140
	<u>Haumania danckelmaniana</u>	O	0	1	44	72	1	116
	<u>Hypselodelphys</u> sp.	O	0	0	9	178	0	187
		R	0	0	0	1	0	1
	<u>Megaphrynium macrostachyum</u>	O	0	4	29	54	4	83
		R	0	0	0	26	0	26
Moraceae								
	<u>Musanga cecropioides</u>	L	75	27	82	143	102	225
		Bark	0	1	5	0	1	5
		Stem cork	0	0	5	0	0	5
		Stem	4	0	0	3	4	3

TABLE 6 (continued)

Family	Food	Part Consumed	Number of Units Eaten (e.g. stems)					
			Area				Habitat	
			F1	F2	L1	L2	TF	TL
Musaceae								
	<u>Musa</u> sp.	S	16	43	0	0	59	0
		O	0	3	0	0	3	0
		R	46	103	0	0	149	0
Zingiberaceae								
	<u>Aframomum aulacocarpus</u>	S	0	0	5	20	0	25
		O	0	0	0	1	0	1
		R	0	0	1	3	0	4
	<u>Aframomum daniellii/</u> <u>hanburyi</u>	S	52	186	86	649	238	735
		O	5	1	0	66	6	66
		R	34	150	104	1251	184	1355
	<u>Aframomum giganteum</u>	S	1	1	6	11	2	17
		R	0	0	0	1120	0	1120
	<u>Aframomum subsericeum</u>	S	5	33	86	603	38	689
		O	0	5	0	58	5	58
		R	0	0	0	6	0	6

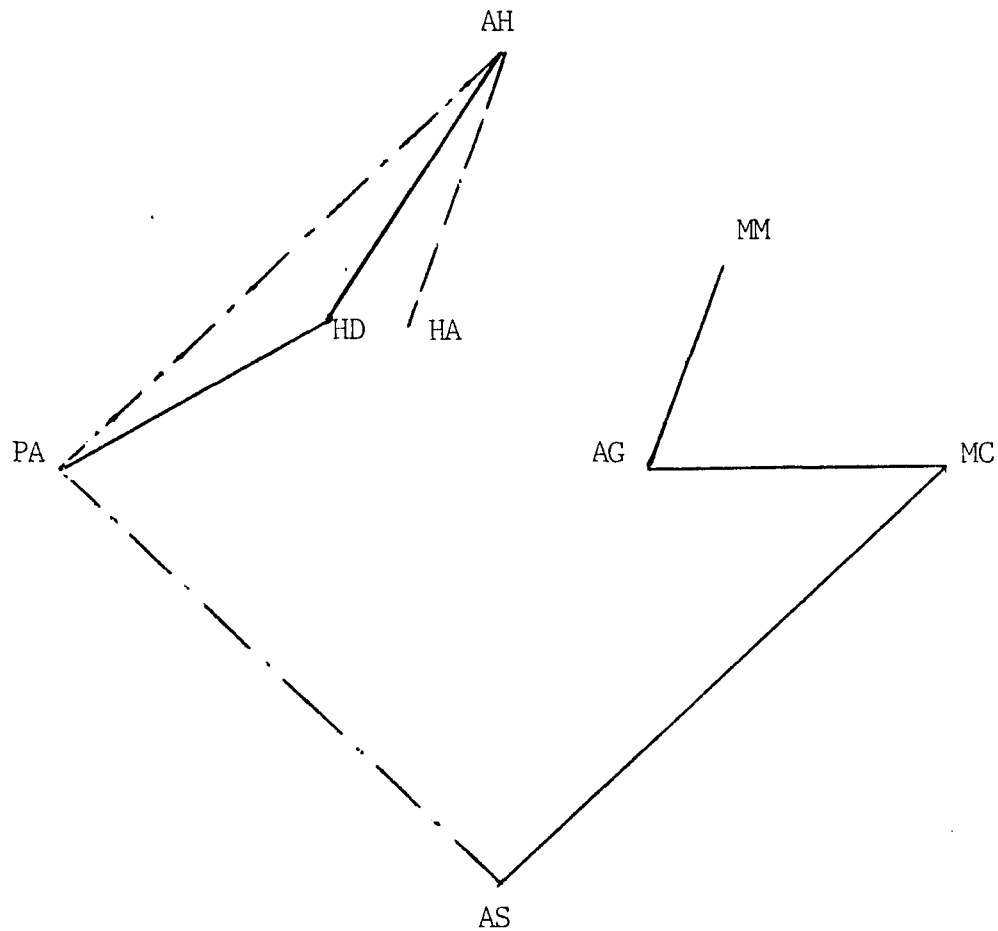
fewer rare and occasional food species than logged areas. There is no noticeable difference between areas of the same habitat type in the number of rare and occasional foods consumed. Fields had the same number of such foods, although the species composition varied considerably.

Independence of food choices. The nature of interspecific food selection was explored by examining the distribution of major food plants (N=8). An initial focus was the probability of any two food species co-occurring. The strength of food plant associations was assessed by stratified random transects (on which 724 one meter radius plots were located) through the study area. The presence/absence of each species in all plots was assessed relative to the presence/absence of all other major food plants. Chi-square tests of association fell into several constellations as shown in Figure 5. The choice of one food species does to some degree influence subsequent choices given these links in the spatial distribution of foods. Associations among food species are presumably related to ecological gradients although the critical variable(s) is often illusive. Candidates include soil moisture, soil nutrients, slope, drainage, light availability, canopy cover, soil compaction and root crowding. The distribution of major foods in relation to these factors is explored in another paper (Calvert, manuscript).

Impact of foraging on food resources. There are several other ways in which food selection at a given time influences later opportunities. Foragers generally affect the environment by reducing

FIGURE 5

Food plant associations (χ^2)



Food species include *Aframomum hanburyi* (AH), *A. giganteum* (AG), *A. subsericeum* (AS), *Halopegia azurea* (HA), *Haumania danckelmaniana* (HD), *Megaphrynium macrostachyum* (MM), *Musanga cecropioides* (MC) and *Palisota ambigua* (PA). Chi-square tests of association between species pairs (df=1) are statistically significant at levels of ≤ 0.001 (-), ≤ 0.01 (--) or ≤ 0.05 (-.-) for N=724 plots.

the rate of capture, "resource depression" (Charnov et al, 1976). The characteristics of the prey (birth or germination, growth and immigration rates) are important to the type and magnitude of depression. For example, the growth of some weeds may be stimulated by revisiting and cropping of herbivores. The specific impact of the forager on the prey will depend in part on the degree of exclusivity the forager obtains. The production of "sustained yields" by foragers depends on exclusivity and where resources are widely shared, a maximal initial yield at the expense of later yields may be preferable (Charnov, 1973 in Pyke et al, 1977).

What impact do gorillas have on their resources? Bullock (1978) recorded the regeneration of 45 banana plants (clones) for 6 months following gorilla feeding in my study areas. The maximal regeneration in the first month was 65% of clones. After 6 months, the number of stems was increased 253% of the number consumed. Fruit production was delayed by the foraging and regeneration period.

Although Aframomum groves were not similarly measured following gorilla feeding here, relevant data were collected. In a 12-month demography study of three species of Aframomum in my study areas, Bullock noted an average emergence rate for new shoots of 1/10 old shoots/month; in groves which were manually thinned (simulating gorilla foraging) the emergence rate reached 9/10 old shoots/month (1981). The gorilla pattern of feeding on 2-3 stems at more than 1 meter intervals very likely increases considerably the emergence rate of shoots. It is interesting that gorilla groups commonly revisit a specific grove within 3-4 days and then abandon the grove for a

minimum of a month. The average daily growth rate of Aframomum hanburyi, for example, is 5 cm. (Bullock, 1981) and the smallest shoots eaten by gorillas are about .5m. Within 30 days of intense feeding (spaced over 3-4 days), it is very likely that a high percentage of old shoots will have produced young shoots (in vegetative reproduction along the rhizomes). Further, many of those new shoots will have reached the minimum size class consumed by gorillas.

Discussion and conclusions

Comparison to other gorilla studies. Group sizes in this study (N=6, mean=8, median=8.5) were insignificantly different from other western groups reported in the literature. Group size for western gorillas is only somewhat smaller (mean and median=7) than comparable figures for eastern gorillas (median=9). The range of variation in group size is, however, much larger in eastern (2-37) than western groups (2-12) (Harcourt et al, 1981).

Diet breadth and substance. The diet consists of 51 species of herbs, vines, trees and saplings, thirteen of which constitute the bulk of the diet. Half the feces examined contained some evidence of fruit consumption but feces never consisted primarily of fruit refuse.

Feeding pattern. Western gorillas were found to have a bimodal travel pattern similar to that documented for other African primates. Travel in areas of high resource density involved much turning, intensive feeding and considerable inter-individual distance. Travel

in areas of low resource density involved longer directional, often single-file progression with relatively few feedings. Travel and feeding patterns vary between mature and disturbed forest. Fossey (1974) and Caro (1976) reported travel variation across forest types for mountain gorillas. Schaller (1963) suggested one factor which may facilitate gorilla travel in multiple forest types. Several major foods e.g. Aframomum and Palisota occur in both lowland and mountain forest. The wide habitat breadth of giant herbs in Cameroon may also facilitate gorilla travel in mature and disturbed forests (Calvert, manuscript).

Covich (1976:244) suggests that "individual consumers optimize distances traveled in terms of their probability of finding specific combination of multiple resources while minimizing exposure time to predators." The hypothetical mechanism by which this is accomplished has been described by Tinbergen (in Wiens 1976) as "area restricted search", whereby feeding is focused in the vicinity of the most recent successful capture. Animals "meander" until appropriate prey are encountered and subsequently turn at a higher rate effectively increasing the duration of their presence in the immediate area (Pyke et al, 1977). Altmann (1974) notes that when large clumps can be detected and between clump travel minimized, animals may reduce the risk of peninsular walks where the return trip is wasted.

Independence of food choices. Interspecific food choices made by gorillas are highly interdependent. Food plant species are often highly associated with other food species. The role of these

associations is not clear. Root and Feeny (see Wiens, 1976) independently suggested that early successional plant populations interdigitating in local areas may benefit by "associational resistance" to some herbivores' foraging, trampling, burrowing and dung deposition. Combined plant defenses may enjoy efficacy greater than the sum of the parts. However, such defense may be mitigated by the greater visibility of such associations to predators. Presumably the benefit of such association is largest where predator meal size is limited per encounter.

Impact of gorillas on food resources. The ability of gorillas to control resource growth by their use patterns is limited by the degree of their diet exclusivity. None of the 13 major foods in my study area is consumed exclusively by gorillas. Opportunistic observation of other mammals in my study shows dietary overlap between gorillas and talapoins, mandrills, chimpanzees, porcupines, elephants and humans. Extensive dietary overlap is not unusual for African forest primates (Struhsaker, 1978; Gautier-Hion et al, 1980). However, most of the important gorilla foods (Aframomum hanburyi/daniellii/subsericeum stems, Musa stems and Musanga cecropioides stems and leaves) are infrequently consumed by others. Struhsaker (1978) noted a comparable pattern among Kibale primates where the commonest foods are rarely shared. The ability of gorillas to control resource growth by their use patterns is not then precluded by the degree of dietary overlap with other mammals.

Gorillas do stimulate regeneration of some food species by their foraging techniques and visitation patterns. Banana stems increased

253% of the number consumed (Bullock, 1978). Simulated gorilla foraging on three species of Aframomum demonstrated a marked increase in shoot production (Bullock, 1981). The gorilla pattern of abandoning Aframomum groves after 3-4 days for about a month is advantageous in allowing new shoots thereby produced to reach the minimal edible size class of .5m. The gorilla foraging pattern is reminiscent of bird flocks studied by Cody (1974). Cody hypothesized that flocks act as "return time regulators", effectively staggering visits to specific areas while foods regenerate to a visitable quality.

The diet and feeding pattern delineated in this paper raise several questions which are addressed elsewhere (Calvert, 1985; Calvert, manuscript). To what degree is the diet selection of gorillas influenced by food chemistry including nutrients, digestibility and digestion-inhibitors? How does the food chemistry of western gorillas compare to that of mountain gorillas? Why does the diet of western gorillas contain so much more fruit, stems and shoots than that of mountain gorillas? In what ways do logging and cultivation impact the abundance and diversity of gorilla foods at Campo? Delineation of the diet in the current paper, however, is a necessary foundation for subsequent consideration of all these interesting questions.

Acknowledgements

This study was funded by World Wildlife Fund, the National Geographic Society, the New York Zoological Society and the

L.S.B.Leakey Foundation. Fieldwork in Cameroon was sponsored by ONAREST with the assistance of the Ministries of Agriculture and Tourism. M.Bihlong of the National Herbarium in Cameroon and Dr. F.N.Hepper of the Royal Botanic Gardens, Kew, generously provided plant identifications. P.Maké, S.Bullock, G.Schroeder, E.Ngi, and the late N.Nguui were extremely helpful in the field. The manuscript has profited from the reading and suggestions of: D.Lindburg, S.Strum, S.Ripley, J.Sauer, G.Bartholomew, J.Birdsell and S.Bullock. I would like to acknowledge diverse assistance from: J.Hill, D.Ela, E.Batoku, A. & V.Balinga, J.Baumer, J.Travis, R.Ippen, C.Jones, D.Harding, S.Gartlan, B.Campbell, J.Eckstrom, A.Herbert, D.Agee, A. Forsythe and B. Corre. Particular thanks are due to Robert Hinde for suggesting this area of research and to Martha Coolidge and the late Harold Coolidge whose considerable encouragement was critical to the project's development.

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Food Selection by Western Gorillas (G.g.gorilla)
in Relation to Food Chemistry

Summary

Samples of stems, leaves, shoots and fruit (N=36) from lowland, African rain forest are analyzed for nutrients, digestibility and digestion-inhibiting substances. Plants from which the samples are drawn are all important in the diet of western gorillas, large generalist herbivores in coastal Cameroon. Many of the plants are common in the early succession following disturbance to the forest. Analysis of food chemistry in relation to food preference indicates that lignin, digestibility and crude protein are the most significant factors in food selection for western gorillas at this site. Food chemistry of western gorillas is compared to food chemistry of mountain gorillas in the montane forest of East Africa. Foliage consumed by western gorillas contains more condensed tannin than does foliage consumed by mountain gorillas. The greater content of condensed tannin in the leaves consumed by western gorillas is related to the greater representation of woody plants in the western diet.

Introduction

A rich theoretical and empirical literature has developed about foraging strategies based on studies of birds, rodents, reptiles and invertebrates. In the theory of optimal diets which was developed in the 1960's, the benefit of food was widely taken to be its energy value or caloric intake per unit cost, that is, time, distance traveled or some other index of energy expenditure. In the mid 1970's, predictions about food selection were re-evaluated in the

case of large, generalist herbivores, suggesting that nutritional value, nutrient balancing and toxin minimization might be more relevant interpretations of food value than caloric intake for herbivores (Westoby, 1974; Pulliam, 1975). Studies of food selection mechanisms in herbivores have focused on true ruminants whose enlarged sacculated stomachs facilitate fermentation and the breakdown of cell walls in foods (Arnold & Hill, 1972). In this study I examine the nutritional benefits as well as the costs of fiber, tannins and phenols in the food of a large, non-ruminant herbivore, the western gorilla. It is the largest living primate and is regarded as the most herbivorous of the hominoids. The basis of gorilla food choice remains to be explained, although two attempts have been made in Zaire to correlate diet with nutrient composition. Casimir (1975) tried to explain diet in terms of amino acids, mineral and water content. Goodall (1977) used gross energy and protein, crude fiber and an estimate of digestibility. In 1974, I began a study of western gorilla diet in Cameroon. I was particularly interested to see if diet could be explained in terms of food costs, particularly those costs generated by digestibility-reducing substances such as simple phenols, hydrolyzable and condensed tannins. In another paper, I have summarized the diet of gorillas in Cameroon (ms.).

Gorilla diet includes species of vines (23%), herbs (38%), saplings (24%) and trees (15%). There was no evidence of animal matter being eaten by gorillas either in observations of feeding, refuse of meals, contents of stomachs (N=1), or feces. The diet

included fifty species of plants (and sixty-nine plant parts) representing forty genera and twenty-nine families. Of the thirteen major species of food plants, five belonged to one genus, Aframomum. At least one species of Aframomum was consumed at 75% of the feeding sites. Plant parts eaten included leaves, stems, fruit, bark, shoots and roots. Half of the two hundred and eighty fecal samples which were analyzed contained at least some evidence of fruit consumption. Stems and shoots constitute more than half of the diet. Since the initial paper summarizing gorilla diet in my study area, the chemical content of foods has been analyzed; those results are presented here.

One aim in this paper was to explain why gorillas consume so many shoots and stems. Gorillas are the only primates known for whom stems and shoots constitute the bulk of the diet. Little is known nutritionally about stems consumed by primates--whether undifferentiated stem tissue or unerupted shoots still encased by stems. Most of the attention in primate food selection studies has focused instead on differences between immature and mature leaves (Hladik, 1978; Milton, 1979; Oates et al, 1980; McKey, 1979; Wrangham & Waterman, 1981), or on differences between fruit and leaves (Hladik et al, 1971; Nagy & Milton, 1979; Milton, 1977, 1980). A range of predictions relate plant maturation to increased fiber content, decreased digestibility, decreased protein and increased chemical defenses. It is not yet clear how stems and shoots of herbs fit into these predictions. We would expect relatively short-lived, early successional herbs to have different strategies of growth, defense, resource allocation and storage than do large trees in mature forest

(Cates & Orians, 1975; Odum, 1969). A related interest was to compare analyses of food chemistry of western gorillas to food chemistry of mountain gorillas in Rwanda (Waterman et al, 1983). Studies of food chemistry in other closely related primate pairs suggests that there may be significant dietary differences in forests with divergent profiles of nutrients and secondary chemistry (McKey et al, 1978).

Methods

Western gorillas were studied at Campo, Cameroon, West Africa (2°23'N, 10°3'E) for 15 months (May 1976-July 1977). Techniques and procedures used in the field are described elsewhere (Calvert, ms.). Gorilla feeding was studied in both mature and disturbed forest at an elevation of about 200 m. The study area consists of gently rolling hills of ferrallitic latosol. There are two rainy seasons annually. Total annual rainfall measured during this study at Nkoelon was about 5 feet (1976-77). Letouzey (1968) describes Biafran forest as low elevation, evergreen forest with a high water table, characterized by a predominance of gregarious species of Caesalpineaceae. The forest included thirteen species of primates: Colobus satanas, Cercocebus albigena, Cercocebus torquatus, Papio sphinx, Pan troglodytes, Miopithecus talapoin, Cercopithecus erythrotus, Cercopithecus pogonias, Cercopithecus cephus, Cercopithecus nictitans, Galago sp. and humans. Major agents of disturbance to the forest are: French logging efforts, Bantu slash and burn agriculture and elephants. Emphasis in this study was on feeding patterns characteristic of

fields and logged areas. Diverse habitats which were sampled intensively included: streams, tree fall gaps, tractor trails, roadsides, tractor parks, recently planted and abandoned fields. The feeding of six, unhabituated groups of gorillas and one solitary male is reported here.

The composition of 1400 feeding sites (meals) was enumerated and mapped. Feeding sites indicated spatially and temporally distinct feedings, i.e., one or more units of one or more species consumed within a one meter radius, separated from similar events by a distance of at least one meter. At feedings, all food plants within the arms' reach of an adult gorilla were listed, as were all foods visible from the eye level of an adult gorilla. At nine hundred feedings sites analysis of vegetation was also done.

The plants were identified by the Cameroon National Herbarium and the Royal Botanic Gardens, Kew. A second set of plants comprising 36 parts of 27 species was dried for chemical analyses. These species represented half of the gorillas' diet at Nkoelon and included nearly all the items eaten frequently. The specimens were carefully selected to be comparable to those eaten by gorillas. Samples were dried at 32-49°C in boxes or in an oven with an open door until 100 g. of a constant dry weight was accumulated per part/species. Most of the nutrient analyses were performed at the Dept. of Animal Science, Michigan State University ; the pepsin-cellulase digestibility, total phenols and condensed tannin analyses were performed by the University of Strathclyde, Scotland.

Samples were ground twice in a Wiley Mill through a screen with 2 mm. openings. A subsample was placed in an alundum thimble and dried to a constant weight in a vacuum oven (18 hrs, 65°C, vacuum of 740 mm Hg). The dried subsample was then extracted with anhydrous diethyl ether in a Goldfish apparatus for 3 hr. The residue was ashed overnight in a muffle furnace at 650°C. Crude protein was determined using a modification of the kjeldahl procedure (Horowitz, 1980). The samples were digested with H₂SO₄ using K₂SO₄ to raise the boiling temperature, CuSO₄ as a catalyst and H₂O₂ as an oxidant in the final stages of digestion. Nitrogen was determined spectrophotometrically after nesslerization, and crude protein was estimated by multiplying nitrogen values by 6.25. Neutral detergent fiber, acid detergent fiber and acid detergent lignin determinations were made according to Goering and Van Soest (1970). A residual fraction of nonstructural carbohydrates presumed to be largely starch and sugar, was estimated by subtracting the concentrations (dry basis) of crude protein, ether extract, ash and neutral detergent fiber from 100. Calcium, magnesium, iron, copper, zinc and manganese concentrations were determined after nitric and perchloric acid digestion, by atomic absorption spectrophotometry. Phosphorus was analyzed by the ammonium molybdate procedure (Gomori, 1942). Selenium concentrations were found by the spectrophotofluorometric procedure of Whetter and Ullrey (1978). The pepsin-cellulase assay for digestibility was performed on powdered plant material according to the method of Choo et al (1981). This assay of digestibility (CDIG) has been used on stems, leaves and seeds (Oates et al, 1980;

Choo et al, 1981; Waterman et al, 1980, 1983; McKey et al, 1981). The utility of the assay for shoots and fruit is evaluated in the discussion section. Assays for total phenols (TP) and condensed tannin (CT) were performed on extracts prepared with 50% aqueous ethanol and methanol respectively; assays were measured against the same standards as employed in Gartlan et al (1980). The concentration of condensed tannin was expressed in terms of quebracho tannin and total phenolics (which will include both condensed and hydrolyzable tannins and simple phenols) in terms of tannic acid. On all assays duplicates were run for each sample and these gave good agreement. Mean values in the text include all replicated tests, and are given as percentage or parts per million (ppm) of dry matter. The dry matter values reported were derived by adjusting the preliminary dry matter values to a completely dry basis as determined in the vacuum oven .

Results

Table 1 presents the dry matter values (DM) as well as the results of assays of food plants for crude protein (CP), gross energy (GE), ash, crude fat, nonstructural carbohydrate (Ncarbo), fiber fractions (acid detergent fiber=ADF, neutral detergent fiber=NDF and acid detergent lignin=LIG), in vitro pepsin-cellulase digestibility (CDIG), total phenols (TP) and condensed tannin (CT). Table 2 presents the results of assays for calcium (Ca), magnesium (Mg), phosphorus (P), potassium (K), iron (Fe), copper (Cu), zinc (Zn), manganese (Mn), sodium (Na) and selenium (Se). Variables in Tables 1

TABLE 1

Nutrient, fiber and toxin content of gorilla foods at Campo 1977

Food	Part Consumed	DM	CP	GE	Ash	Fat	NDF	ADF	Lig	CDIG	TP	CT
Araceae												
<u>Anchomanes difformis</u>	S	6.2	7.1	3.99	7.3	4.2	34.7	36.8	6.3	81.3	1.93	0
	L	15.6	32.2	4.83	5.0	13.5	21.3	22.6	6.2	76.4	1.70	0
Arecaceae												
<u>Podococcus barteri</u>	S	22.9	5.6	4.21	5.1	1.6	72.2	59.9	34.6	25.4	1.22	0
Commelinaceae												
<u>Palisota ambigua</u>	S-immature	8.9	10.3	3.39	9.9	1.7	66.9	55.8	10.3	37.1	.71	0
	O	7.6	10.3	3.95	9.0	2.1	63.3	53.9	14.8	38.9	1.38	0
<u>Palisota barteri</u>	S	27.0	14.0	2.95	17.5	1.4	40.7	24.4	3.2	55.2	.82	0
Dioscoreaceae												
<u>Dioscorea</u> sp. (ngohn)	L	17.0	18.1	4.75	5.1	3.3	47.5	45.3	19.8	45.9	5.62	8.18
(nahmpenday)	L	20.9	14.2	4.25	9.1	3.1	44.3	41.3	14.0	60.1	3.36	0
Euphorbiaceae												
<u>Manihot esculenta</u>	R	35.2	3.0	3.90	1.3	.7	43.0	6.0	2.1	31.8	.34	0
Fabaceae												
<u>Dalbergia</u> sp.	L	34.7	14.7	5.08	1.4	1.6	72.6	58.0	26.5	23.4	3.25	0
Humiriaceae												
<u>Sacoglottis gabonensis</u>	F-entire	22.7	2.5	4.27	1.5	4.0	58.4	59.1	44.5	40.3	1.16	0
Loganiaceae												
<u>Anthocleista vogelii</u>	L	21.7	11.3	4.90	2.2	4.1	42.8	37.5	13.8	55.5	2.51	0
Marantaceae												
<u>Halopegia azurea</u>	O	10.5	8.4	3.39	14.3	3.4	71.1	52.0	7.9	45.4	1.25	0
<u>Haumania danckelmaniana</u>	O	14.3	16.5	4.10	7.6	3.8	78.5	48.4	10.2	35.4	1.51	0
<u>Hypselodelphys</u> sp.	O	12.6	13.8	4.15	10.0	3.2	80.4	54.1	14.5	47.3	.57	0
<u>Megaphrynium macrostachyum</u>	O	10.2	10.5	4.26	8.3	2.4	72.6	51.6	9.1	47.2	1.62	0
Ubinosaceae												
<u>Tetrapleura tetraptera</u>	F	45.8	4.5	4.62	1.5	1.5	55.2	51.9	25.3	33.2	5.59	5.54

TABLE 1 (continued)

Nutrient, fiber and toxin content of gorilla foods at Campo 1977

Food	Part Consumed	DM	CP	GE	Ash	Fat	NDF	ADF	Lig	CDIG	TP	CT
Moraceae												
<u>Musanga cecropioides</u>	L-mature	29.0	15.9	4.59	6.6	5.8	44.9	45.6	26.0	29.2	10.29	19.11
	S-cork	37.4	1.7	5.78	1.4	2.9	70.3	72.5	30.6	4.6	2.91	2.92
	L-immature	21.3	13.2	4.62	5.8	2.7	41.8	49.3	29.3	25.3	11.39	24.20
	B	23.7	4.7	4.12	5.4	1.1	68.5	70.8	20.2	21.4	3.08	7.38
	Trunk-woody	34.2	1.5	4.61	1.3	2.1	89.7	81.1	20.0	3.5	.79	0
Musaceae												
<u>Musa paradisiaca</u>	F-pulp	31.4	4.1	4.09	2.6	.8	82.3	10.2	6.2	17.9	.33	0
	S-core	3.2	11.3	4.09	11.6	7.1	37.8	26.8	4.0	70.5	1.71	0
Solanaceae												
<u>Solanum</u> sp.	F	23.0	13.8	5.19	4.0	5.8	55.1	48.1	25.4	45.0	2.04	0
Sterculiaceae												
<u>Eribroma oblonga</u>	B	35.0	7.1	3.46	3.1	.5	81.9	72.2	22.4	29.1	.66	0
Tiliaceae												
<u>Desplatsia</u> sp.	F	38.8	3.7	4.61	2.0	1.9	59.6	66.5	33.0	20.5	2.60	9.13
<u>Grewia coriacea</u>	F	33.3	4.2	4.49	2.8	2.1	68.7	60.5	43.0	27.4	1.33	0
Vitaceae												
<u>Cissus petiolata</u>	L	20.5	12.9	4.37	7.7	1.9	53.2	41.0	19.9	44.5	5.42	6.57
Zingiberaceae												
<u>Aframomum daniellii</u>	S	11.2	3.5	3.73	10.9	2.6	55.6	38.1	6.1	36.3	.95	0
<u>Aframomum giganteum</u>	S	5.4	5.5	3.57	17.5	4.4	52.9	38.7	5.5	47.3	.73	0
<u>Aframomum hanburyi</u>	S	9.7	2.6	3.81	11.0	4.4	62.7	43.5	8.3	39.9	1.30	0
	F-mature	30.0	6.6	4.81	4.7	12.3	71.0	30.7	22.6	17.4	2.37	0
	F-immature	15.3	10.4	5.22	4.8	20.9	66.4	31.1	14.9	25.7	1.92	1.11
<u>Aframomum subsericeum</u>	S	10.0	3.6	4.04	9.0	5.7	61.6	45.9	9.0	35.3	1.40	2.23
<u>Costus</u> sp.	S	5.1	8.9	3.52	12.6	1.6	59.2	45.7	7.1	44.9	.93	0

DM=dry matter, CP=crude protein, GE=gross energy, Fat=ether extract, NDF=neutral detergent fiber, ADF=acid detergent fiber, Lig=lignin, CDIG=pepsin-cellulase digestibility, TP=total phenols, CT=condensed tannin. CP,GE,Ash,Fat, CDIG and fiber values as %dry matter. GE values as kcal/g. Plant parts consumed include leaf(L), stem(S), shoot(O), fruit(F), bark(B) and root(R). Badjele pygmy names of food species are in parentheses.

TABLE 2

Mineral content of gorilla foods at Campo 1975-77

Food	Part Consumed	Ca	Mg	P	K	Fe	Cu	Zn	Mn	Na	Se
Araceae											
<u>Anchomanes difformis</u>	S	0.67	.07	.15	4.5	102	2	48	187	165	.04
	L	0.48	.19	.34	3.0	530	6	95	430	70	.13
Arecaceae											
<u>Podococcus barteri</u>	S	0.34	.30	.15	1.8	96	16	110	130	70	.13
Commelinaceae											
<u>Palisota ambigua</u>	S-immature	0.75	.22	.07	6.4	54	14	20	1700	185	.04
	O	0.63	.27	.13	4.7	90	13	25	1200	160	.03
<u>Palisota barteri</u>	S	4.58	.50	.07	8.4	40	8	59	540	270	.04
Dioscoreaceae											
<u>Dioscorea</u> sp. (ngohn)	L	1.16	.24	.16	2.5	100	15	33	280	120	.13
(nahmpenday)	L	2.40	.50	.14	1.1	630	10	22	190	140	.13
Euphorbiaceae											
<u>Manihot esculenta</u>	R	0.11	.04	.07	1.0	37	4	14	0	70	.05
Fabaceae											
<u>Dalbergia</u> sp.	L	0.24	.09	.13	1.2	56	7	5	240	40	.16
Humiriaceae											
<u>Sacoglottis gabonensis</u>	F-entire	0.08	.11	.05	1.5	74	5	6	28	510	.03
Loganiaceae											
<u>Anthocleista vogelii</u>	L	0.55	.11	.15	1.1	73	23	36	430	630	.24
Marantaceae											
<u>Halopegia azurea</u>	O	0.31	.38	.16	2.7	120	10	68	380	380	.05
<u>Haumania danckelmaniana</u>	O	0.19	.13	.27	1.9	73	22	47	260	80	.18
<u>Hypselodelphys</u> sp.	O	0.38	.25	.32	3.8	87	17	57	470	115	.09
<u>Megaphrynium macrostachyum</u>	O	0.46	.28	.20	2.0	97	8	43	450	40	.05
Mimosaceae											
<u>Tetrapleura tetraptera</u>	F	1.20	.22	.27	3.5	1200	33	22	90	80	.03

TABLE 2 (continued)

Mineral content of gorilla foods at Campo 1975-77

Food	Part Consumed	Ca	Mg	P	K	Fe	Cu	Zn	Mn	Na	Se
Moraceae											
<u>Musanga cecropioides</u>	L-mature	2.00	.56	.15	1.1	368	15	27	163	125	.14
	S-cork	2.02	.15	.00	.3	53	5	8	115	110	.09
	L-immature	1.02	.34	.23	1.2	160	18	25	94	50	.10
	B	1.15	.20	.05	2.3	160	6	13	190	120	.15
	Trunk-woody	.29	.09	.02	.8	45	9	14	9	100	.06
Musaceae											
<u>Musa paradisiaca</u>	F-pulp	.03	.09	.09	.1	13	5	8	4	30	.05
	S-core	.33	.28	.18	6.0	110	8	28	200	40	.06
Solanaceae											
<u>Solanum</u> sp.	F	.55	.26	.35	2.4	64	18	19	28	85	.03
Sterculiaceae											
<u>Eribroma oblonga</u>	B	1.31	.04	.08	1.0	51	6	8	120	50	.05
Tiliaceae											
<u>Desplatsia</u> sp.	F	.14	.06	.06	1.6	24	8	6	30	30	.06
<u>Grewia coriacea</u>	F	.50	.17	.10	1.7	22	9	11	180	100	.03
Vitaceae											
<u>Cissus petiolata</u>	L	2.88	.46	.15	2.2	275	19	36	445	255	.11
Zingiberaceae											
<u>Aframomum daniellii</u>	S	.58	.54	.10	5.6	96	11	73	530	240	.02
<u>Aframomum giganteum</u>	S	1.18	.98	.14	6.2	120	7	170	490	95	.08
<u>Aframomum hanburyi</u>	S	.58	.38	.08	4.3	72	11	73	283	187	.06
	F-mature	.15	.21	.21	1.2	168	11	302	390	40	.05
	F-immature	.13	.14	.25	2.5	83	10	48	370	80	.04
<u>Aframomum subericeum</u>	S	.41	.22	.07	3.8	78	8	83	607	277	.03
<u>Costus</u> sp.	S	.26	.07	.13	8.1	77	8	110	450	70	.06

TABLE 2 (continued)

Plant parts include leaf(L),stem(S),shoot(O),fruit(F),bark(B) and root(R). Badjele pygmy names of food species are in parentheses. Ca, Mg, P and K values as % DM; Fe, Cu, Zn, Mn, Na and Se as PPM. Ca=calcium, Mg=magnesium, P=phosphorus, K=potassium, Fe=iron, Cu=copper, Zn=zinc, Mn=manganese, Na=sodium and Se=selenium.

and 2 whose distribution varied significantly from normal ($p \leq .05$) received either a square root (for mild skew) or a natural log transformation (for considerable skew) prior to statistical analyses.

I. Composition of important plant parts. One of the first tasks in analyzing the nutrient results was to describe differences among the plant parts which were important in the gorillas' diet.

Brown-Forsythe F^* tests (Brown & Forsythe, 1974) revealed significant differences among plant parts in crude protein, gross energy, ash, nonstructural carbohydrate, neutral detergent fiber, lignin, dry matter and total phenols ($p \leq .05$). In Table 3 the geometric mean, coefficient of variation of raw scores and results of F^* tests are presented for each of twelve assays. For each of the eight variables in which plant part groups varied significantly, Welch t^* tests were done on all possible pairs of plant parts e.g. pith versus leaves. Table 4 indicates the significant results of the pair-wise t^* tests (Brown & Forsythe, 1974).

Relative to other plant parts, leaves are high in protein, gross energy, fat, nonstructural carbohydrates, total phenols and condensed tannin. Leaves differ most from shoots (in gross energy, nonstructural carbohydrate, neutral detergent fiber, dry matter and total phenols) and are the least distinct from fruit (only protein differs significantly).

Shoots are high in protein, ash, digestibility and water content. While they are also high for two of the fiber indices, they are the lowest in total phenols, and are also low in lignin. Shoots are the only plant part for which no measureable condensed tannin was

TABLE 3

Comparison of content across plant parts: geometric mean, coefficient of variation, F* tests

Assay	Leaves N=8		Shoots N=5		Stem N=11		Fruit N=8		F*	p
	\bar{x}	c.v.								
% CP	16.6	(.40)	11.9	(.27)	6.7	(.59)	6.3	(.63)	10.4	<.001
GE(kcal/g)	4.7	(.06)	4.0	(.09)	3.7	(.10)	4.7	(.09)	16.8	.001
% Ash	5.3	(.48)	9.8	(.27)	10.4	(.46)	3.0	(.46)	11.7	.001
% Fat	4.5	(.86)	3.0	(.23)	3.4	(.56)	6.2	(1.14)	.2	NS
% NCarbo	27.5	(.33)	4.9	(1.3)	23.6	(.41)	20.4	(.69)	5.7	<.01
% NDF	46.1	(.31)	73.2	(.09)	55.9	(.23)	64.6	(.15)	6.3	<.01
% ADF	42.6	(.24)	52.0	(.04)	44.4	(.32)	44.8	(.43)	.6	NS
% Lig	19.4	(.40)	11.3	(.28)	11.3	(.95)	26.9	(.49)	6.0	<.01
% CDIG	45.0	(.41)	42.8	(.13)	43.4	(.48)	28.4	(.36)	2.1	NS
% DM	22.6	(.28)	11.0	(.23)	13.4	(.82)	30.0	(.32)	10.9	<.001
TP	5.4	(.66)	1.3	(.33)	1.3	(.50)	2.2	(.72)	8.4	<.001
CT	7.3	(1.3)	0	(0)	.5	(2.3)	2.0	(1.8)	-	-

TABLE 3 (continued)

All data are presented on a dry matter basis. CP=crude protein, GE=gross energy, Fat=ether extract, NCarbo=non-structural carbohydrate, DM=dry matter, NDF=neutral detergent fiber, ADF=acid detergent fiber, Lig=lignin, CDIG=pepsin-cellulase digestibility, TP=total phenols, CT=condensed tannin. Brown-Forsythe F* tests use N=32. Samples of woody trunk (N=1), bark(N=2) and root (N=1) were insufficient to include here. An F* test was not computed on CT, measureable amounts of which were absent from most samples. C.v. is based on raw scores; F* is calculated on transformed scores.

TABLE 4

Differences among plant parts in Welch t tests (Bonferroni significance levels)

Assay	<u>Plant parts</u>					
	S vs O	S vs L	S vs F	O vs L	O vs F	L vs F
CP	t= -3.10 ⁺	-4.46 ⁺⁺	.17	-1.86	3.30 ⁺	4.65 ⁺⁺
GE	-1.25	-6.41 ⁺⁺⁺	-5.17 ⁺⁺⁺	-3.88 ⁺	-3.32 ⁺	.07
Ash	-0	2.60	4.89	3.10	6.29	2.13
Fat	.09	- .67	- .46	- .82	- .53	-0
NCarbo	4.62 ⁺⁺	- .91	.57	-5.33 ⁺⁺	-2.72	1.22
NDF	-3.35 ⁺	1.48	-1.79	3.95 ⁺	2.00	2.87
ADF	-1.74	.32	- .05	2.51	1.06	- .29
Lig	-1.01	-2.57	-3.17 ⁺	-2.19	-2.90	- .95
CDIG	- .30	- .30	1.73	- .09	3.32 ⁺	2.22
DM	.25	-2.77	-3.83 ⁺⁺	-4.96 ⁺⁺	-5.80 ⁺⁺⁺	-1.79
TP	.06	-4.85 ⁺⁺	-1.07	-4.39 ⁺⁺	-1.02	2.62

$P < .05 = +$, $P < .01 = ++$, $P < .001 = +++$. Plant parts: leaves (N=8)=L, shoots (N=5)=O, fruit (N=8)=F and stems (N=11)=S.

found in any sample. Shoots are the least different from stems and the most different from leaves and fruit (albeit along different axes.)

Stems are high in water, nonstructural carbohydrates and ash but very low in protein and gross energy. Perhaps importantly, stems are very low in lignin, total phenols and condensed tannin. Stems are the most distinct from fruit and the least distinct from shoots.

Fruits are high in gross energy and fat but low in protein. They are low in water and very high in lignin. Fruits have measureable condensed tannin and total phenols. The digestibility of fruit appears relatively low but this might be an artifact of the pepsin-cellulase assay. Fruits are the most like leaves and the least like shoots. The most significant distinctions among consumed plant parts are between shoots and leaves/fruit, not as one might have expected, between leaves, stems, shoots on the one hand, and fruit on the other.

II. The relationship of food chemistry to food preference. The second goal of the data analysis was to delineate the relationship of food preference to food content. For these purposes a systematically selected subset of the 1400 feeding records was used (N=139). This subset included feedings on 13 of the original 36 plant parts whose chemistry was analyzed. The index used to define food preference was the number of feeding sites at which a food was consumed over the number of sites at which a food was present. The values were then grouped into the most and least preferred foods. Welch t^* tests were performed on the two groups in relation to CP, GE, DM, Ash, Fat, NDF,

ADF, LIG, TP, Ncarbo and CDIG. As shown in Table 5, lignin was the only independent variable significantly related to preference in the t^* tests ($p \leq .05$). Highly preferred foods were lower in lignin content than were less preferred foods. Fat, dry matter and digestibility approached significance. Highly preferred foods contain more fat, water and were more digestible than were less preferred foods.

A stepwise linear regression on arms' reach preference (ungrouped) was subsequently performed using the same 10 independent variables. The stepwise regression indicates that only digestibility and crude protein were important in understanding preference in this sample ($N=13$, adjusted $R = .66$, $p \leq .01$, $s.e.=.18$). Digestibility is much more important in food preference than is crude protein as judged from the F-to-remove levels of 23 and 9.2 respectively. One question which this analysis raises is to what degree lignin, digestibility and crude protein are interrelated.

III. Comparisons to chemistry of mountain gorilla foods.

Mountain gorillas also consume leaves and stems and the chemistry of their diet has recently been analyzed (Waterman et al, 1983). There are some striking differences in comparable plant parts between the mountain gorilla foods from Rwanda (MGR) analyzed by Waterman et al and the western gorilla foods from Cameroon (WGC) reported in this paper (Table 6).

Leaves. A much higher percent of leaves in the WGC sample contained condensed tannins than did the leaves in the MGR diet. Also, when condensed tannins were present in leaves eaten by western

TABLE 5

Differences between high and low preference groups (ARPREF) in Welch t tests

Assay	Low preference (N=8) \bar{x}	High preference (N=5) \bar{x}	W t	Sig
CP	2.4	1.9	1.30	NS
GE	4.2	4.2	- .24	NS
Ash	2.6	2.8	- .50	NS
Fat	.9	1.5	-2.12	NS
NCarbo	16.2	23.5	- .97	NS
DM	4.4	3.2	2.20	NS
NDF	4.1	4.0	.83	NS
ADF	45.6	41.0	.66	NS
Lig	2.8	2.1	2.21	<.05
CDIG	5.8	7.0	-2.02	NS
TP	.6	.5	.06	NS

TABLE 6

Comparison of leaves and stems from diets of western gorillas in Cameroon (WGC) and mountain gorillas in Rwanda (MGR): geometric means and Welch t tests

<u>Western gorilla diet - Cameroon</u>				
<u>Assay</u>	<u>leaves (N=8)</u>	<u>stems (N=11)</u>	<u>Wt*</u>	<u>p**</u>
DM	22.6	13.4	-2.77	<.01
CDIG	45.0	43.4	- .30	NS
CP	16.6	6.7	-4.46	<.001
TP	5.4	1.3	-4.85	<.001
CT	7.3	.5	-	-
ADF	42.6	44.4	.32	NS
<u>Mountain gorilla diet - Rwanda***</u>				
<u>Assay</u>	<u>leaves (N=21)</u>	<u>stems (N=12)</u>	<u>Wt*</u>	<u>p</u>
DM****	16.7	15.8	- .34	NS
CDIG	56.5	41.1	-2.38	<.05
CP	15.5	6.2	-8.58	<.001
TP	5.0	2.0	-3.56	<.01
CT	1.1	.7	.77	NS
ADF	35.5	49.3	3.87	<.001

TABLE 6 (continued)

*Welch t tests were performed on transformed data. **P values are not at Bonferroni levels as in Table 4. ***From Waterman et al, 1983. ****Values for %H₂O from Waterman et al, 1983 were converted to %dry matter.

gorillas, they occurred in larger amounts than in leaves eaten by mountain gorillas. The average value for condensed tannin in the WGC sample was 14.5 (N=4) but the average value for the MGR sample was 7.6 (N=3). Leaves eaten by western gorillas in Cameroon contain more digestion-inhibitors than leaves eaten by mountain gorillas. Leaves in the WGC sample contained more dry matter, condensed tannin and acid detergent fiber. It was not surprising then that leaves in the WGC sample were less digestible than those in the MGR sample. Leaves from the two areas are roughly comparable in crude protein and total phenol levels.

Stems. Condensed tannin was rare in stems from both samples. Stems eaten by western gorillas in Cameroon are roughly comparable to stems consumed by mountain gorillas in Rwanda. In the WGC sample, stems are somewhat juicier, more digestible and contain slightly less acid detergent fiber. Crude protein and total phenol levels are comparable.

Discussion

I. Puzzles in food choice and the utility of chemical analyses.

Analyses of food chemistry aided in explaining some local problems in the gorillas' food choices which were enigmatic in the field. Five of those problems are sketched here. A) Mature leaves of Musanga cecropioides are preferred over immature leaves. One might have expected the younger leaves to be higher in nutritional value and lower in fiber/digestibility costs. In Musanga, however, immature leaves are relatively lower in protein, gross energy, digestibility

and higher in lignin than mature leaves. B) Only the central core of banana stems, about half the diameter, was consumed. I could not understand why the outer layers of the stem were discarded as it appeared uniform in consistency except for the outermost sheath. Relative to the outer, discarded portion of the stem, however, the central core is higher in protein and gross energy, and is twice as digestible. The appeal of the central core is apparently not countered by its having 4.6 times the total phenolic content of the entire stem. Both values (.37 and 1.71) are below the mean value (\bar{x} =2.4) for total phenols in my sample (N=36). C) Banana fruits are often available where banana trunks are brought down, but the fruit is rarely consumed. Banana fruit (Musa sapientium L. var. Gros Michel) has been reported to contain phenolic compounds including tannins (Barnell & Barnell, 1945; Goldstein & Swain, 1963). Immature fruit in my study (M.paradisiaca) does contain total phenols (simple phenols/condensed and or hydrolysable tannins) but stem core contains more (TP=.33 and 1.71 respectively). So the presence of phenols in immature fruit does not explain why immature fruit is often ignored by gorillas. Fruit is however much less digestible than stem core and also much lower in protein and fat content. (The low CDIG value of 17.9 for Musa is unlikely an artifact of the CDIG assay since its fat content (.8) is extremely low.) D) Another problem which analyses of plant chemistry helped to understand is the gorillas' preference for mature versus immature Aframomum fruit. By almost every index, immature fruit is of higher nutritional quality: more protein, gross energy and less fiber. And immature fruit is commonly

available within arms' reach of mature fruit. Why then is mature fruit consumed in a 3:2 ratio to immature fruit? Both mature and immature fruit contain total phenols (2.37 and 1.92 respectively). In mature fruit the total phenolic content varies seasonally (2.76 in October, 1.97 in July). Both levels of total phenols are low or average relative to other foods ($x=2.41$). In addition to total phenols, however, immature fruit contains condensed tannin; mature fruit does not. Condensed tannin is rare in gorilla foods. Only 10 of 36 samples have any measureable condensed tannin. Immature Aframomum fruit has the lowest condensed tannin content of any of the 10 samples which contain condensed tannin, but that may be sufficient to mitigate against its frequent consumption. According to Swain (1979), a condensed tannin level of about 2.00 is sufficient to deter feeding. Such a decline in tannin content with fruit ripening has been reported in other plant species (Goldstein & Swain, 1963). Presumably the presence of condensed tannin in immature fruit aids in defending the plant against insects and herbivores at least until the seed is viable. If gorilla distribution of viable Aframomum seeds is important to Aframomum dispersal, waiting to consume mature fruit and viable seeds may be the best long term investment for gorillas as well. Massive consumption of immature fruits by gorillas might reduce the distribution of Aframomum plants if their reproduction is greatly dependent on seed dispersal rather than on vegetative means. This genus is capable of both methods of reproduction and their relative importance is unknown (Bullock, 1981). E) One problem which is not well explained by analyses of plant chemistry is the gorillas'

preference for particular species of Aframomum. Species of Aframomum commonly interdigitate in mixed-species groves including Aframomum subsericeum, A.hanburyi and A.giganteum. Stems of the last of these three species are the least preferred and rarely consumed. This seemed paradoxical to me because one stem of A.giganteum provides nearly twice the volume of food as that for either of the other two species, but preparation costs are only slightly greater. Also, A.giganteum has a higher protein content, higher average digestibility and lower lignin content. Two possible explanations come to mind but neither is totally satisfying. The three species are all relatively low in protein and lignin so these differences among the species are probably not meaningful when selecting among Aframomum stems. More meaningful differences might be 1) the absolutely high fat content of A.subsericeum and 2) the wide range of digestibility of A.giganteum (27.1-67.4 versus 34.5-46.1 in A.hanburyi or 31.4-39.6 in A.subsericeum). Gorillas may avoid A.giganteum stems because of the minimal levels of digestibility which it sometimes attains. They may select A.subsericeum stems for their high fat content.

Thus, with the exception of the problem in understanding why gorillas consume so few stems of A.giganteum, the analyses of food chemistry were useful in elucidating puzzles of gorillas' food selection. It was still unclear, however, as to why gorillas were selecting such large quantities of stems and shoots relative to other plant parts.

II. Relative importance of stems and shoots in the diet. Shoots are high in protein as are the most preferred stems e.g. Musa. Stems in general are high in nonstructural carbohydrates. The major difference between stems/shoots and other plant parts, however, is the former's low lignin content. The most commonly consumed stems such as Aframomum are even lower in lignin than are stems on the average. Stems and shoots are also high in water content and moderately to extremely digestible. It seems therefore that it is the relatively low cost of digesting stems and shoots, as well as their protein and nonstructural carbohydrate content which makes them important in the gorillas' diet.

III. Relative importance of fruit in the diet. In all reports to date, western gorillas consume more fruit than do their eastern counterparts (Calvert, ms.; Butzler, 1980; Jones & Sabater Pi, 1971; Tutin & Fernandez, 1982). This may have to do with a relative scarcity of appropriate fruits in montane forest, or conversely, the scarcity of appropriate leaves in lowland forest. One cannot test this proposition with the available data. Yet even if western lowland forests have a greater abundance of appropriate fruit, that alone would not explain why gorillas consume it. What is there about fruit in western lowland forests which is distinct nutritionally from other plant parts consumed by gorillas there?

Two obvious benefits of fruit consumed in Cameroon were their high gross energy and fat contents relative to other plant parts. The most commonly consumed fruits (mature Aframomum hanburyi) had three times the average fat value of less commonly consumed fruits.

The importance of fruit in the diets of primates has been discussed elsewhere primarily as a source of nonstructural carbohydrates (Milton, 1977). However, fats have twice the energy value of nonstructural carbohydrates (Maynard et al, 1979). Fats also carry some fat-soluble vitamins and aid in vitamin absorption. So fats should be considered in evaluating the significance of fruit in primate diets. Only the abundance of digestion-inhibitors such as phenols/tannins suggest why fruit is not more important in western gorilla diet. The idea that fruits contain considerable digestion-inhibiting compounds is counter-intuitive. Mature fruit flesh is expected to contain few such compounds (Hladik, 1975). Many of the fruits eaten by gorillas in this study, however, are very woody and atypical of fleshy fruits consumed by other primates. The gorillas powerful chewing musculature and dentition enable them to eat some fruits which would probably not be useful to most primates.

IV. Utility of the pepsin-cellulase assay for digestibility of fruits and shoots. The pepsin-cellulase assay (CDIG) used in this study has previously been used on samples of leaves, seeds and stems (Oates et al, 1980; Waterman et al, 1980, 1983; McKey et al, 1981; Choo et al, 1981). At first glance the use of this assay on fruits, particularly, may seem unwarranted in this paper since fruits may contain much fat. Choo et al (1981) have suggested that the CDIG assay may be inappropriate on samples containing a high fat content as the CDIG assay is relatively insensitive to fats. A general examination of the relationship of fat to CDIG in my samples may be useful in assessing the utility of this assay in this study. A) The

assumption that fruit as a group contains significantly more fat than other plant parts is not supported by these data. Welch t^* tests indicate that there are no significant differences in fat content between fruit and other plant parts (Table 4). This result lends support to the idea mentioned earlier that fruits consumed by gorillas in this study are indeed atypical of fruit in general.

B) The relationship of fat to CDIG is graphed in Figure 1 with different symbols for each plant part. The correlation is insignificant (see Table 7) but several interesting things are apparent in the graph. Two fruits and one leaf had very high fat contents and their CDIG values may be disproportionately low as an artifact of the pepsin-cellulase assay for digestibility. The three samples are of fruit (mature and immature) of Aframomum hanburyi and of leaves of Anchomanes difformis. The Anchomanes leaves are very digestible even by the fat-insensitive pepsin-cellulase assay. The two samples of Aframomum fruit, however, show rather poor digestibility. It is here that I would most expect higher digestibility with a rumen liquor assay for digestibility. Because both Aframomum fruit samples are highly preferred foods, I would expect digestibility to be even more important than it already is in Welch t^* tests between high/low ARPREF groups (Table 5) and in the stepwise linear regression on ARPREF (Results II). Digestibility approaches significance in the t^* tests and is significant in the regression even with the CDIG assay however. On balance then the costs of using the fat insensitive CDIG assay do not appear to outweigh its benefits in terms of efficiency and standardizability.

FIGURE 1

Relationship of fat to digestibility among various plant parts at Campo. Plant parts include fruit(F), stem(S), shoot(O), leaf(L), root(R) and bark(B) (N=36, $r=.266$)

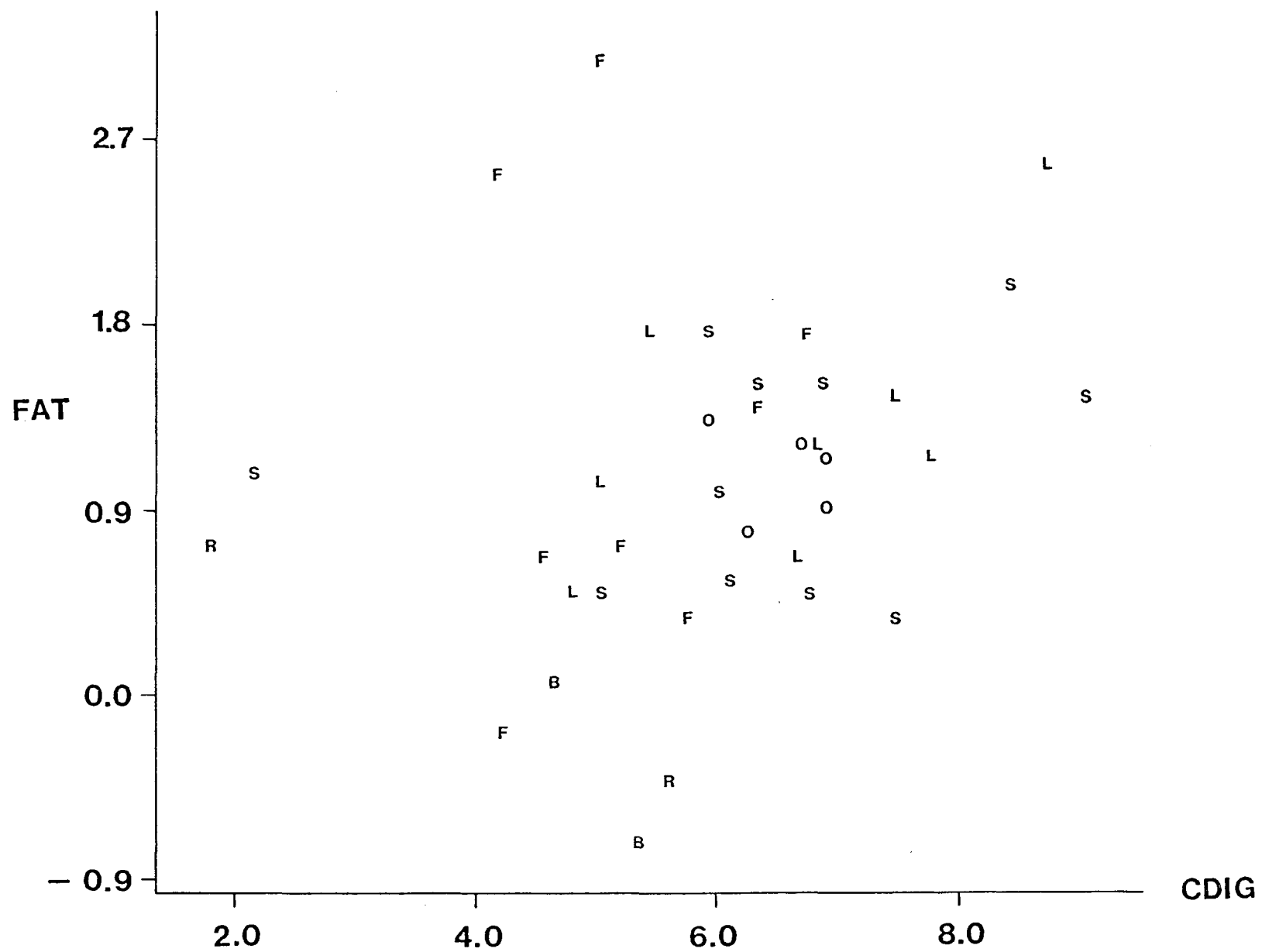


TABLE 7

Pearson correlations among nutrient, fiber and toxin assays

	CP	GE	Ash	Fat	NCarbo	DM	NDF	ADF	LIG	CDIG
CP	--									
GE	.22	--								
Ash	.36*	-.58***	--							
Fat	.29	.44**	.20	--						
NCarbo	-.11	.04	-.20	-.09	--					
DM	-.28	.34*	-.77***	-.38*	.12	--				
NDF	-.43**	-.10	-.16	-.34*	-.72***	.21	--			
ADF	-.30	.03	-.24	-.23	-.30	.22	.54***	--		
Lig	-.11	.52***	-.54***	.02	-.14	.50**	.37*	.71***	--	
CDIG	.60***	-.15	.55***	.27	.32	-.62***	-.66***	-.47**	-.48**	--
TP	.33*	.53***	-.14	.31	.27	.19	-.30	.21	.53***	-.01

*p <0.05, **p <0.01, ***p <0.001 (df=34). CP=crude protein, GE=gross energy, Fat=ether extract, NCarbo=non-structural carbohydrate, DM=dry matter, NDF=neutral detergent fiber, ADF=acid detergent fiber, LIG=lignin, CDIG=pepsin-cellulase digestibility, TP=total phenols.

Rumen liquor assays vary considerably and are difficult to standardize. Use of the rumen liquor assay in my study would probably have only enhanced the relationships which are already apparent between digestibility and preference. One of the reasons that the CDIG assay creates so few problems in my study in spite of having widened its use to include fruit and shoot samples, may be that my samples are not particularly high in fat content. The CDIG assay might still be inappropriate on samples with a high fat content as Choo et al (1981) have suggested. (Waterman reports that a new assay for digestibility has been developed in his laboratory which is efficient, standardizable and is not insensitive to samples of high fat content.)

V. Comparison to chemistry of mountain gorilla foods.

Proportions of leaves/stems in the diet. There are striking differences between leaves consumed by western gorillas and those consumed by mountain gorillas. Stems from the two samples are more similar. Differences in leaf content between the two areas might help explain the relative proportions of leaves/stem consumed in the two areas.

A) In Rwanda (MGR) the leaves and stems do not differ significantly in CT or DM. They are, however, very different in CP, CDIG, TP and ADF. Leaves are more digestible, contain more protein and less acid detergent fiber. The only way in which leaves here are less appealing than stems as a group is that they contain more total phenols. This last difference may be unimportant since the mean values in total phenols for both leaves and stems are rather low.

One might expect then that the diet of mountain gorillas would contain more leaves than stems if our sample of 33 is typical of foods there.

B) In Cameroon (WGC) leaves and stems do not differ significantly in CDIG or ADF. They are quite different however in DM, CP, TP and CT. Leaves are drier and have more total phenols and condensed tannin. However, leaves also have a higher CP content. In the Cameroonian sample then leaves are appealing for high protein levels (as they are in Rwanda), but digestion-inhibiting factors e.g. CT, TP, and a higher proportion of dry matter make the cost of processing them higher relative to stems, than is the case in Rwanda. In Cameroon one would expect the diet to contain relatively fewer leaves and/or more stems than in Rwanda given the mixed appeal of Cameroonian leaves. That foliage in Cameroon has relatively higher costs than in Rwanda also suggests a possible advantage to the inclusion of fruit in the western diet.

C) The explanation for the greater defense of Cameroonian foliage relative to Rwandese foliage is not obvious. Ostensibly mountain and western gorilla diets are both drawn primarily from the herbaceous strata of the forest. However, closer examination of the growth form from which samples are drawn is instructive. 95% of the MGR leaf samples (vs. 63% of the WGC samples) come from herbs, vines, shrubs, sedges and ferns. 5% of the MGR leaf samples (vs. 37% of the WGC samples) come from woody plants. The woody plants consist of one tree parasite in the MGR sample and immature and mature leaves of a young sapling in the WGC sample. In the course of forest succession

this sapling, Musanga cecropioides, becomes a large tree. In both the MGR and WGR samples, leaves from the few woody plants contribute all of the extremely high values for condensed tannin.

Several factors contribute to the higher average value for condensed tannin in the WGR foliage. The woody plants from which WGR leaves derive have even higher tannin contents than the woody plants of the MGR sample. Secondly, leaf samples from woody plants are more common in the western diet. This pattern of the woodier plants containing more condensed tannin or leuco-anthocyanins than herbaceous plants do is well documented in the literature (e.g. Bate-Smith, 1956). Within plant families woodier species contain more leuco-anthocyanins. Among plant families, those with a woodier tendency seem to contain more leuco-anthocyanin.

VI. Generalizability of these results. Two cautionary notes should be considered in any attempt to generalize from the results of this study. 1) True protein content of tissue is probably overestimated because crude protein is based on an analysis of total nitrogen (Hansen, 1970). This may impact the absolute values for protein but should not impact the relative amounts. 2) Within-item variability in food chemistry is not accounted for in this study. Results for most items were based on 3 or fewer samples. Local variability with light and soil conditions as well as seasonal variation within-items may be considerable.

Keeping these two cautions in mind then, what can be said of gorilla food selection using the arms' reach index of preference? Preference here is best understood as a function of digestibility,

lignin and crude protein. More preferred foods contained less lignin, more protein and were more digestible than less preferred foods. Lignin, crude protein and digestibility may not act independently.

Is this appearance of lignin, digestibility and crude protein as the most significant factors in food selection of gorillas consistent with predictions in the literature? Given the lack of rumination in gorillas, it is not surprising that digestibility is critical in food choice. Large generalist, non-ruminant herbivores are limited by the time they can hold food in the gut for digestion, so any improvement in the digestibility of foods should be quite beneficial. Westoby and Pulliam's idea that calorie maximization is not adequate to explain food selection appears to hold true for gorillas. The very significant positive correlations between gross energy and lignin/total phenols (Table 7) observed in this and other studies make it even less likely that gross energy will suffice as a single factor explanation of herbivore food choice. Lignin and total phenols are known impediments to digestion. Even the level of tannin does not predict gorilla food choice as a single factor explanation suggested by Harborne (1977). Finally, it is not surprising that crude protein is significant in food selection of gorillas given the relative lack of animal matter which gorillas ingest.

It is not yet clear to what degree results of this study will generalize to other groups of western gorillas. All western gorilla groups studied thus far are consistently more frugivorous than eastern gorillas. However, both the species composition of the diet

and the proportions of various plant parts in the diet may vary considerably. The relative costs and benefits of various plant parts in the diet may vary considerably for example with soil fertility. The digestion-inhibiting defenses of leaves might be reduced in other locations, as was noted in the mountain gorilla diet in Rwanda. The proportions of leaves might therefore be increased relative to the proportions of stems/shoots seen in this study. It is likely, however, that lignin, digestibility and crude protein will continue to be significant factors in gorilla food choice given the anatomical similarities of the genus throughout its range.

Acknowledgements

The field study was funded by World Wildlife Fund, the National Geographic Society, the New York Zoological Society and the L.S.B. Leakey Foundation. Fieldwork in Cameroon was sponsored by ONAREST with the assistance of the Ministry of Agriculture. M. Bihlong of the National Herbarium in Cameroon and Dr. F.N. Hepper of the Royal Botanic Gardens, Kew, generously provided plant identifications. P. Maké, S. Bullock, G. Schroeder, E. Ngi, and the late N. Nguu were helpful in collecting plant samples in the field. Nutritional analyses were funded by the L.S.B. Leakey Foundation and completed in the Department of Animal Science at Michigan State University. The following individuals performed nutritional analyses: P. Ku, P. Whetter, L. Green and R. Barbiers. Analysis of digestibility, condensed tannin and total phenols were performed by P.G. Waterman at the University of Strathclyde, Scotland under

N.E.R.C. grant #GR3/3455. The manuscript profited from the reading and suggestions of: D.Lindburg, P.G.Waterman, R.W.Wrangham, D.E.Ullrey and W.McGrew. I would also like to acknowledge diverse assistance from: J.Hill, C.Yale, L.Youkeles, A.Forsythe, J.Baumer, G.Binney, B.Corre, B.Campbell, R. Ippen, J. Travis, A. and V. Balinga, E.Batoku, D.McKey, M.Jarvik, D.Harding, S.Gartlan, A.Herbert, P.Robinson and D.Agee. Particular thanks are due to Harold and Martha Coolidge whose considerable encouragement was critical to the project's development.

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Received May 30, 1984

Factors Affecting the Food Resources of Western Gorillas:

Selective Logging, Subsistence Farming, Elephants

Summary

In Cameroon gorillas consume plants from mature forest, subsistence farms and forest which has been selectively logged. One factor of possible importance in gorilla food selection is the distribution of major food resources. In 759 plots (1 m. radius), data were collected on vegetation structure and composition including the abundance of 8 major gorilla food plants. Plots were located in fields, mature forest and forest logged 3,4 and 6 years earlier. Several habitats were sampled for each logged area e.g. tractor trails, tree fall gaps and roadsides. Logged and cultivated areas exceed mature forest in the number of plots of high resource abundance. Comparison of logged areas to fields indicates that trails and gaps (all years) have greater abundance of foods than do roads or fields. Abundance of most foods decreases from the third to the sixth year after logging. The variation in food abundance on trails and gaps increases from year 3 to year 6. Patterns of differential food abundance do not seem well explained by the size or the commonness of habitats alone. The absence of trees above 26m. seems to be one of the best structural predictors of high food abundance. The impact of logging and cultivation on gorillas is evaluated in an evolutionary context and compared to the long-standing relationship of elephants and gorillas. Large-bodied, North American mammals such as moose, white-tailed deer and black-tailed deer are discussed as models for patterns observed in this study of lowland gorillas in disturbed habitats.

Introduction

Most studies of the impact of logging on animal populations have dealt with large-bodied mammals in temperate climates. In North America, white-tailed deer, black-tailed deer and moose have long been studied in relation to logging practices (Dasmann & Hines, ms.; Leopold, 1933; Bennett et al, 1980; Cowan et al, 1950; Einarson, 1946; Peek et al, 1976). Logging increases food resource abundance and ground cover for all three species. Heterogeneous mixtures of mature forest and disturbed forest produce maximal densities of deer and moose. Dasmann et al showed that densities of black-tailed deer increase rapidly the first 5 years after logging to seven times unlogged values. Between 6-10 years, the population peaks at three times values for years 1-5. After 10 years, the population declines and between years 21-50 mature forest returns. The population decline after 10 years is accompanied by a decline in the abundance of food plants (pers. comm.).

Wild non-human primates have generally been studied remote from human influence, although such settings are increasingly scarce. Some descriptive accounts of human interaction with non-human primates do, however, appear in the literature (Dunnett et al, 1970; Bernstein et al, 1976; Suzuki, 1971; Chivers, 1972; Daugherty, 1972; MacKinnon, 1971; Bermant & Lindburg, 1975; Whitmore, 1975; Harcourt, 1979). Wilson and Wilson (1975) were the first to systematically examine the **impact** of Indonesian logging on East Bornean primates. Their censuses showed that many species continued to exist in forest

with limited, selective logging 8-12 trees/ha. The densities of several primate species remained about the same between unlogged and lightly logged areas. Other authors have documented primate migration away from logging activities (Martin & Asibey, 1979; MacKinnon, 1971; Petter & Peyrieras, 1974).

More recently, Johns (1981, 1982A, 1982B) has completed a study in West Malaysia on the impact of selective logging on some aspects of primate social structure. Johns showed that selective logging may increase infant mortality in lar gibbons and banded langurs. Recovery of pre-logging group structure was said to take 5-6 years. Selective logging also had short term effects on ranging and dietary patterns. More fruit was eaten before logging and more leaves were consumed afterwards. Tree species logged did not feature prominently in the diets of any of the primates which Johns studied. Dietary flexibility and diversity might be even more important in Ghanaian red colobus and diana monkeys for whom logged species do constitute a major portion of the diet as described by Asibey (1978). In summary then, there is some evidence that selective logging has some impact on the ranging patterns, diet, and infant mortality of at least some primates.

In an 18-month study of western gorillas in Cameroon, West Africa, I explored the impact of cultivation and selective logging on gorilla diet and food distribution. Schaller had suggested on the basis of a 6 month survey in East Africa, that gorillas adjust local foraging to take advantage of temporarily favorable conditions created by cultivation, human habitation and mining (1963). Schaller

found gorillas scarce where villages were 3 or fewer years of age, and in mature forest (1963). Harcourt (1979) found gorillas scarce in the immediate vicinity of loggers. The impact of human cultivation, habitation, mining and logging on gorillas has, however, never been systematically explored before.

In this study gorilla feeding was recorded in both mature and disturbed forest. The focus of the current study is the impact of disturbance to the forest on the abundance and diversity of major food resources utilized by gorillas. The time scale examined is 3-6 years after logging. The ultimate causes of changes in food resource abundance during succession must relate to differential moisture, nutrients, light and space--the critical resources for plant growth and reproduction. The proximate factors in changing food abundance during succession are of greater interest here: scale, frequency and duration of disturbance, soil compaction, shading from other plants, drainage, time elapsed since disturbance. Cultivation and selective logging create many types of disturbance (e.g. roads, trails, tree fall gaps, logging parks) in which such proximate factors vary widely. By studying these diverse habitats, the proximate mechanisms of changing abundance of gorilla foods may be elucidated.

In two previous papers I summarized the diet of gorillas in this area of Cameroon (Calvert,ms.) and the relationship of food selection to food chemistry particularly nutrients, digestibility and digestion-inhibitors(Calvert, 1985). Gorilla diet includes vines, herbs, saplings and trees. The diet includes fifty-one plant species (and sixty-nine plant parts) representing forty-one genera and

twenty-nine families. Plant parts consumed included leaves, stems, fruit, bark, shoots and roots. Half the two hundred and eighty fecal samples which were analyzed contained at least some evidence of fruit consumption. Fruit appears to be an important source of fat and thus of energy. The bulk of the diet consists of stems and shoots which seem desirable for their protein and nonstructural carbohydrate content as well as their relative digestibility. No single nutritional variable seems to explain gorilla food choice. High crude protein and digestibility as well as low lignin content are all important.

Methods

Western gorillas were studied 40 kms. east of Campo, Cameroon, West Africa ($2^{\circ}23'N, 10^{\circ}3'E$) for 15 months (May 1976-July 1977). The study area consists of gently rolling hills of ferrallitic latosol, punctuated by local streams at an elevation of about 200 meters. Daily temperatures vary little about $27^{\circ}C$. There are two rainy seasons annually with considerable local variation in the yearly totals. Total annual rainfall measured during this study at Nkoelon was about 5 feet (1976-77). Letouzey (1968) describes forest in this region as low elevation, evergreen forest characterized by a predominance of Lophira alata and gregarious species of Caesalpineaceae relatively absent from neighboring Congolese forest. Richards notes that Cameroonian forest is particularly lacking in epiphytes and abundant in the number of cauliflorous trees (1963). Bullock describes the Campo forest as relatively high with a canopy

at 30-40m (1980). He also indicates that some trees are deciduous but not synchronously so, such that the forest does not have a deciduous aspect (pers. comm.) The forest included thirteen species of primates: gorilla, colobus, 2 species of mangabey, mandrill, chimpanzee, talapoin, 4 species of Cercopithecus, galago and humans. Major agents of disturbance to the forest are: French logging efforts, Bantu slash and burn agriculture and elephants. Less than 1% of the Campo region consisted of fields, villages, roads or logged areas before 1968. Between 1968 and 1971, that figure reached about 10%.

Local agriculture consists entirely of single-family shifting cultivation. Fields are most often located abutting a roadside or the village, contiguous with other fields. Since villages here are composed of lines of mud and thatch homes along dirt roads, this results in long, narrow strips of fields along roads, with much greater depth of fields immediately adjacent to homes. Commonly some large trees are left standing. The undergrowth is burned in field clearing and then the ground is hoed. Many large boles remain on the ground creating a patchwork of small plots which are plantable. Major crops are manioc and banana (sweet and plaintain). Secondary crops include: peanuts, yams, peppers. Manioc is the staple in the diet. Fields directly adjacent to homes seem to remain in use, although the crops vary. Fields are weeded soon after planting until seedlings or suckers are established. Thereafter giant weeds and eventually large shrubs become dense about banana trunks whose fruit continues to be harvested for several years.

Selective logging has gone on sporadically in the Campo area since 1950. Consistent, intensive effort began in 1969 with the installation of the current company, La Forestière de Campo. Thirty-four species are logged but 38% of the trees extracted are Lophira alata (Ochnaceae)(Bullock, pers. comm.). Actual cutting in a given 5 km. diameter generally takes no more than one year after which the area is abandoned with the exception of roads used as access to other areas. Access roads are cleared about every two years; major arteries are regraded annually.

Bullock (1980) estimated the total areas of direct disturbance due to logging (not including logging parks) in the Campo subdistrict of littoral Cameroon (47,407 ha.) at 8.4% of the region. In his review of the impact of logging on local forest, Bullock indicated that tree fall gaps where a single tree was felled averaged .04 ha. with 5.2 neighboring trees >25m and 6.2 trees 15-25m high dead or felled as a result. Tractor trails generally resulted in less compaction than roads, with two deep furrows created by tractor treads, separated by a high ridge. Where trails met access roads, logging parks were used as staging areas.

In order to analyze the impact of logging on food distribution, a stratified sample was constructed of 3 areas in which various amounts of time (3-6 yrs.) had elapsed since logging. Within each area 3 comparable habitats were sampled: tractor trails, roadsides and tree fall gaps. In each of the 3 areas, roads were cut several months prior to the beginning of extraction which produced gaps and trails so the time elapsed from logging e.g. 4 years is an average

time across the 3 habitats (gaps, trails and roads) in a particular area. One meter radius plots were placed systematically in these habitats (483 plots). Three habitats in which logging had not occurred were also sampled: fields (N=83), stream banks (N=63) and mature forest (N=130).

This plot size approximating the average distance accessible to a seated, feeding gorilla seemed the appropriate area for sampling accepted or ignored foods (Calvert ms.), so a similar plot size was sampled to establish resource abundance. Each 1 meter radius plot was sampled for: the abundance of 8 major food plants, noted on a scale of 1-4, where 1=absent or inconspicuous; 2=occasional, or rare but conspicuous; 3=common either uniformly or in patches; 4=abundant. Vegetation structure and composition were noted in heights and growth forms (vines, herbs, saplings, trees). Notes were also taken on ground slope; height, composition and cover of the various canopies (estimated visually following reliability tests with a rangefinder); meters to the road (paced); evidence of gorilla use (beds, feedings, feces), and evidence of human use (trails, logging, cultivation, and traplines).

Results

Habitats. In the Campo Reserve gorillas feed in both mature and secondary forest. A diversity of secondary habitats are used including: fields, stream banks and three habitats associated with logging: tree fall gaps, roadsides and tractor trails. Six major habitats are compared in terms of their average size, % of local area

and typical ground features (Table 1). These 6 habitats also probably differ in patterns of soil moisture, soil drainage, canopy cover and light availability. Figure 1 shows a diagram of logging habitats. Important foods in the gorilla diet are characteristic of one or more of these 6 habitats (Table 2). For example, Aframomum giganteum is present on 27% of roadside plots. Food plant species range from the rare Halopegia azurea to the ubiquitous Haumania danckelmaniana.

Food abundance index. The index of food abundance used in this paper sums the 2, 3 & 4 values across all 8 foods and assigns that value to the particular case. Abundance thus measured varies considerably among habitat types as might have been anticipated from Table 2. Abundance varies from 0-11 with a median value of 2 (N=759). In the subsequent analyses, food abundance is classified into none, low (≤ 4) and high (≥ 4) groups unless otherwise indicated.

Food abundance in various habitats. Given the distribution of individual food species among habitats (Table 2) how did the index of food abundance vary accordingly? A chi-square test of the relationship between habitat and food abundance groups appears in Table 3. Trails and gaps are clearly superior to other habitats in terms of plots with high abundance levels (48% of trails, 46% of gaps). High abundance plots are less common on roads and in fields (34 and 33% respectively). The appeal of various habitats might alternatively be evaluated as areas which dependably have some (vs. high abundance only) gorilla foods (i.e. either high or low abundance plots). The ranking of habitats on this axis begins similarly with

TABLE 1

Characteristics of disturbed habitats

Habitat	Average size	% of Campo subdistrict (47,407 ha.)	Ground features
fields in cultivation	diverse 1-3 ha.	--	soil enriched briefly with ash from burning
roadsides	29 m. wide	2.6%	central 9m. compacted; bulldozer mounding and drainage to sides of 9m. roadbed
tree fall gaps	400m ² =average	4.2%	diverse
tractor trails	3 m. wide	1.5%	moderate compaction; mounding in center; drainage to sides of central mound

Average size of habitats and % of Campo subdistrict (2°15'N., 10°E.) are taken from Bullock (1980).

FIGURE 1

Habitats created by logging (30 m.)

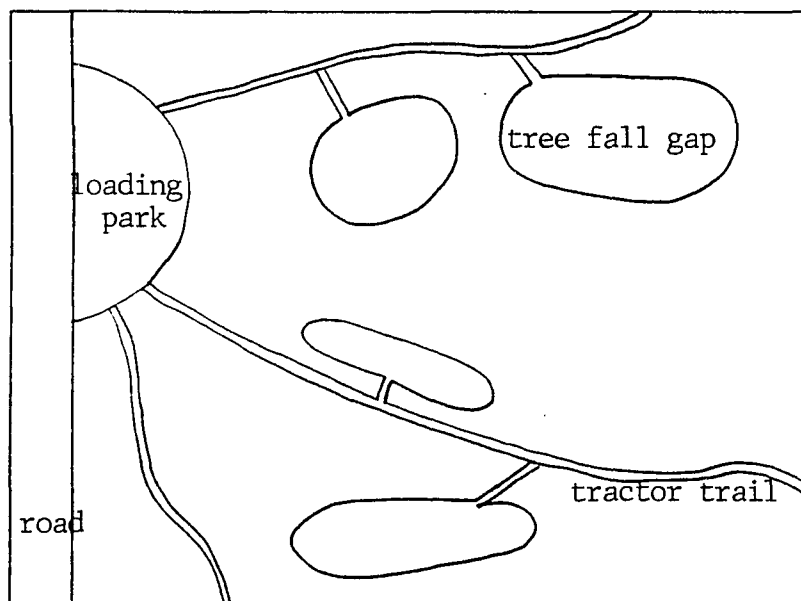


TABLE 2

Frequency of major food species in various habitats

Food	Mature Forest	Fields	Tree Fall Gaps	Tractor Trails	Roads	Stream Banks
<u>Commelinaceae</u>						
<u>Palisota ambigua</u>	15%	12	23	33	8	10
<u>Marantaceae</u>						
<u>Halopegia azurea</u>	0	2	4	11	2	35
<u>Haumania danckelmaniana</u>	67	19	75	48	16	35
<u>Megaphrynium macrostachyum</u>	2	5	12	9	4	2
<u>Moraceae</u>						
<u>Musanga cecropioides</u>	0	19	1	1	8	0
<u>Zingiberaceae</u>						
<u>Aframomum giganteum</u>	0	8	5	13	27	0
<u>Aframomum hanburyi</u>	0	16	4	10	21	0
<u>Aframomum subsericeum</u>	2	24	18	34	33	0
N of plots/habitat:	130	83	171	162	150	63

TABLE 3

Presence of food abundance groups in various habitats

<u>Habitats</u>	<u>Food abundance groups</u>		
	<u>no</u>	<u>low</u>	<u>high</u>
mature forest	39	71	20
fields	31	25	27
tree fall gaps	25	68	78
tractor trails	32	52	78
roadsides	33	66	51
stream banks	39	19	5
N plots/group	199	301	259

N=759, $\chi^2=103.4$, df=10, $p<0$.

gaps (85%), trails (80%) and roads(78%). However 70% of plots in mature forest have some gorilla foods making that habitat possibly preferable to gorillas (as insurance against food absence) to fields (63%) and streams (38%).

Factors in food abundance. Of considerable interest were the possible factors which might be related to the abundance of gorilla foods. The relationship between food abundance and time elapsed since logging is explored in Table 4. The frequencies of various foods within a particular habitat vary considerably with time elapsed since disturbance. Only two of the foods increase in frequency from year 3 to year 6. Most foods decrease from year 3. For example, Aframomum giganteum is present in 28% of plots in year 3 but only appears in 3% of plots in year 6 after logging on tractor trails.

In order to further evaluate the trends of decreasing food abundance with time elapsed since logging, the coefficients of variation of abundance were compared by habitat type and years elapsed since logging (Table 5). Data in Table 5 indicate that variation in food abundance increases steadily from year 3 to year 6 in both tractor trails and gaps. Abundance reaches its highest variability in this study in trails after the 6th year.

One possible factor in the changing abundance of foods with time is the change of vegetation structure and growth form associated with forest succession. Could food abundance be predicted using various facets of vegetation structure and growth form? Kruskal-Wallis H tests were performed on the 3-way groupings of food abundance using 12 features of vegetation structure and growth form as independent

TABLE 4

Presence of major foods on tractor trails
in relation to time since logging

<u>Foods</u>	<u>Time elapsed since logging</u>		
	<u>three yrs.</u>	<u>four</u>	<u>six</u>
Afgi	15	4	2
Afha	7	1	8
Afsu	28	19	8
Hada	36	26	16
Muce	1	1	0
Mema	7	8	1
Paam	14	19	21
N plots/year=	53	51	58

Acronyms for food species represent the first two letters of the generic and specific epithets. Halopegia azurea is not included in this table as it did not occur on tractor trails.

TABLE 5

Variation in abundance of gorilla foods related to time elapsed since logging (coefficient of variation of raw scores)

<u>Habitats</u>	<u>Time</u>		
	<u>three yrs.</u>	<u>four</u>	<u>six</u>
tractor trails (N=162)	.52	.75	.99
tree fall gaps (N=171)	.48	.57	.74

variables in the one-way analysis of variance (N=759). The 12 variables used were: vines (.5-2.5m, 2.6-10m), herbs (.5-2.5m, 2.6-10m), shrubs (.5-2.5m, 2.6-10m) and trees (2.6-10m, 11-26m, >26m). Means and Kruskal-Wallis H scores are presented in Table 6. The highly significant differences among abundance groups in terms of vines and herbs below 10m. are to expected (and ignored) since the major foods are described by those categories of vegetation structure. Of greater interest are the relationships between abundance and the shrub and tree layers. Food abundance decreases significantly with the presence of trees above 26m.

The preceding analysis includes plots from many different habitats. Next I tested the same proposition within a more homogeneous habitat (tractor trails, N=162). H tests were thus performed on a 3-way grouping of food abundance using the same 12 independent variables (Table 7). On tractor trails, food abundance groups are best predicted by shrubs .5-2.5m and trees above 26m. High abundance of foods on trails is associated with the absence of shrubs .5-2.6m and trees above 26m.

Where the food abundance groups vary significantly in vegetation structure/growth forms, the patterns of relationship (ANOVA) on trails resemble those for the pooled sample. Some differences between the results of Tables 6 and 7 were to be expected, however. Table 7 is based on a much reduced sample size and so some effects visible in the pooled sample might not attain significance on trails alone. For example, herbs below .5m appear to have the same trend in

TABLE 6

The relative importance of vegetation structure and growth form to the abundance of major food plants across habitats (N=759 plots): means and Kruskal-Wallis H tests

Vegetation	<u>Food abundance</u>			H	p
	no	low	high		
vine <.5m	1.5	1.4	1.5	3.7	<.16
herb <.5m	1.9	1.7	1.7	8.9	.01
shrub <.5m	1.2	1.2	1.2	.6	.76
vine .5-2.5m	1.5	2.0	2.1	62.0	.00
herb .5-2.5m	1.4	1.6	2.1	89.8	.00
shrub .5-2.5m	1.6	1.5	1.4	2.2	.33
vine 2.6-10m	1.3	1.4	1.6	9.5	.01
herb 2.6-10m	1.0	1.1	1.3	44.9	.00
shrub 2.6-10m	1.9	1.9	2.0	.5	.78
tree 2.6-10m	1.8	1.7	1.5	5.6	.06
tree 11-26m	2.0	1.8	1.8	3.0	.22
tree >26m	1.6	1.7	1.4	19.0	.00
<hr/>					
	N= 199	301	259		

TABLE 7

The relative importance of vegetation structure/growth form to the abundance of major foods on tractor trails (N=162): means and Kruskal-Wallis H tests

Vegetation measures	<u>Food abundance groups</u>			H score	p
	no		high		
vine <.5m	1.2	1.5	1.5	5.2	<.07
herb <.5m	2.2	2.2	1.9	3.5	.17
shrub <.5m	1.2	1.4	1.3	3.6	.17
vine .5-2.5m	1.3	1.7	1.9	11.4	.003
herb .5-2.5m	1.9	1.8	2.3	10.1	.007
shrub .5-2.5m	1.8	1.9	1.5	10.7	.005
vine 2.6-10m	1.3	1.2	1.4	2.0	.37
herb 2.6-10m	1.0	1.0	1.4	17.5	.000
shrub 2.6-10m	1.9	1.7	2.0	4.1	.13
tree 2.6-10m	1.4	1.7	1.7	1.5	.48
tree 11-26m	2.4	2.1	2.3	1.5	.48
tree >26m	2.2	2.3	1.6	12.7	.002

group means in both tables, but only attain significance in the larger sample of Table 6. Other differences between the two tables may be attributable to the fact that only some of the food species are common in any particular habitat. Since the major foods include different growth forms at various height classes, the "independent" variables which describe them will vary accordingly. Also habitats vary considerably in both the nature of the physical disturbance and the scale of the canopy break (Table 1) so the pivotal factors causing greater or lesser food abundance may vary between habitat types. For example, if fields are cleared of all trees over 26m in height, that variable will not discriminate between fields of low and high abundance of gorilla foods. Within trails, however, some of which do have large trees, the variable may discriminate clearly between levels of food abundance.

Discussion

Why do gaps and trails have greater food abundance than other habitats? Whitmore(1978:643) says of establishment that "different species are successful in gaps of different size." The mechanism by which gap size may affect establishment is difficult to assess given the number of microclimatic factors potentially related to gap size. The light regime may be in part a function of gap size (Hartshorn,1980). Also air temperature, ground temperature and humidity may vary with gap size(Denslow,1980). Daily fluctuations in temperature may be more severe in larger gaps as the forest in general dampens the effects of temperature and radiation .

(Cruiziat,1966). Also, habitats under consideration in this study vary not only in microclimatic factors related to gap size but in soil compaction, mounding, drainage and nutrients. These habitats are distinct packages of environmental gradients. However, an interesting pattern emerges when comparing the success of species in various habitats. Table 2 demonstrates that different food species are successful in different habitats. Half of the major food species are most successful in either trails or gaps. Trails and gaps are the second most successful habitats for two additional species. In contrast to streams and forests, where only 4 of the foods occur, trails and gaps do at least occasionally contain all 8 foods. Species which are most successful in habitats as diverse as streams, mature forest, fields and roadsides can all at least marginally survive on trails and gaps. It seems that whatever the specific package of environmental gradients in which these foods succeed best, the trail-gap packages are adequate for subsistence. What are the factors about gaps and trails which encourage high abundance of gorilla foods?

Food abundance in relation to forest structure. The inverse relationship of food abundance to trees above 26m in Table 6 is noteworthy. Early in succession the relative absence of trees above 26m allows much light to reach below 26m and the herbs and vines eaten by gorillas abound. Later, as the trees grow higher and canopies become fuller, light availability below 26m is reduced and the herb/vine layer below 10m declines. This pattern agrees with the findings of Denslow (1978) and Schaller (1963).

Generalizability of these results. Several cautionary notes should be considered in any attempt to generalize from the results of this study. 1) It was assumed that the study plots were homogeneous before disturbance. In this study however we cannot rule out the possibility that site differences which are not elucidated (e.g. soil composition or forest heterogeneity prior to logging and cultivation) might better explain observed patterns of gorilla food abundance than logging and cultivation do. 2) Discussions of the relationship between food abundance and time elapsed since logging are limited by the nature of the variable time. Its predictive utility is important but vegetation change cannot be explained by correlations with time. Time here isn't a causal variable but shorthand for a variety of factors which proximately/ultimately cause vegetation to regenerate. 3) The representativeness of the diet needs to be assessed in order to interpret the results of this study. Several of these points are discussed further.

Representativeness of the major food species. The finding that food abundance decreases with time elapsed since logging cannot be interpreted without an evaluation of the representativeness of the major food species. If, for example, major foods only occurred in extremely disturbed habitats, their relative decrease with forest maturation following disturbance would be meaningless. Examination of Table 2 indicates, however, that the major foods exist in a broad range of habitats in both mature and disturbed forest.

There is a related problem about the delineation of the diet which merits attention. Gorilla diet was delineated (Calvert, ms.)

in large part from two areas in which either 4 or 6 years had elapsed since logging. One might thus anticipate food abundance based on a diet so delineated to increase from year 3 to years 4 and 6 in a given habitat. In fact the reverse finding was observed. Food abundance decreases from year 3. It seems therefore that the determination of major foods largely from areas logged 4 and 6 years previously did not bias the major result of this study: that food abundance decreases with time elapsed from disturbance after year 3.

Predictions. It seems likely that the general trends of gorilla food abundance observed in this study will hold for similar habitats elsewhere. For example, I predict that 1) large scale disturbances in tropical forest (gaps, fields, trails, roads) will all have an immediate, short-term drop in food abundance as these habitats are created from mature forest. Some foods are actually removed in the creation of large-scale disturbance and other species might require e.g. less light intensity than the new disturbance allows. 2) In subsequent years food abundance will increase followed by a decrease beginning in the fifth or sixth year. Such a decrease in abundance would continue slowly as the forest matures and the canopy(ies) closes. The greatest change in food abundance would be in the first four years after disturbance.

These predictions and trends are certainly independent of the climax, stable end point assumptions of e.g. Clements (1916). These predictions are also supported in part by findings in other areas. Denslow (1978) found in her study of succession of Columbian fields that the rate of change decreases with increasing time since

disturbance. Williams et al (1969) also noticed the most rapid changes in succession occurred early on.

Comparisons to other studies of primates in disturbed forest.

There is some difference of opinion in the literature about the impact of selective logging on the food resource distribution and abundance of primates. Chivers(1972,1974) predicted that selective logging at low levels of extraction would not greatly decrease food availability on a permanent basis. He suggested that a rapid depression of food availability immediately following logging would be followed by an increase in young leaves and fruit. He did not think that a limited forest disturbance of this nature would necessarily be detrimental to primates. Johns(1982A) by contrast suggests that colonizing plant species do not produce fruits eaten by primates and leaves of colonizers are much higher in secondary compounds. Therefore, he concludes that logged forest is significantly less attractive than unlogged forest for primates.

In my study, none of the trees extracted in logging efforts constitute major foods for gorillas. In fact Bullock's list of species extracted at Campo (pers.comm.) includes only one species ever eaten by gorillas in this study (bark of Eribroma oblongum, see Calvert,ms.). Initially logging causes a rapid, short-term depression in food abundance at Campo, as Chivers predicted. At Campo, at least some logged habitats (roads, trails and gaps) as well as some fields soon exceed mature forest sites in the frequency of plots of high food abundance (Table 3). Both logging and to a lesser degree cultivation can be said to increase the availability of foods

for gorillas at least for several years. Contrary to Johns' finding, colonizing plant species at Campo do produce fruits eaten by primates e.g. Aframomum, Musanga cecropioides etc. According to the results of my study, logged and cultivated areas would have to be considered preferable to mature forest as gorilla habitat. In fact, some combination of mature and secondary forest probably provides the optimal food availability for gorillas. The sheer diversity of mature forest must be important to gorillas both for seasonally available, large sources of fruit, and for a seed-stocking source for secondary patches constantly being created by elephants, windfalls etc.

The pattern of gorillas using mostly secondary forest adjacent patches of mature forest ("forest edge" sensu Einarson, 1946) is not without precedent in the literature on mammals. In North America, moose (Cowan et al, 1950; Peek et al, 1976), black tailed deer (Einarson, 1946; Dasmann & Hines, ms.) and white tailed deer (Bennett et al, 1980) all seem to have a similar pattern of habitat use, albeit in temperate (vs. tropical) forests. Cowan et al indicate that mature forest supports moose only to the degree that lake shores, streams and other clearings avail (1950). Disturbance of mature forest to stimulate growth and abundance of early successional foods increases the size of the population for these 3 North American mammals. Einarson (1946) first implicated the role of light availability in raising the protein content of early successional shrubs and trees over that available in mature forest. Actually the use of secondary and mature forest by these 3 species appears to be a

function of 1) increased protein availability in early successional food species and 2) the protective concealment of adjacent mature forest. Burning improves the nutritional value of foods more than logging but both treatments are preferable to mature forest (Einarson, 1946).

Gorillas at Campo and elsewhere may also be feeding primarily in early successional habitats in order to avail themselves of higher quality food. Nutrients, digestibility and digestion-inhibiting substances were analyzed for 36 parts of 27 food species eaten at Campo (Calvert, 1985). However foods were not sampled in the same way as Einarson's (same 5 foods sampled from multiple areas in one season). Thus no direct comparison of the two data sets is possible. However, analyses of food content of gorillas at Campo does demonstrate that high crude protein and digestibility as well as low lignin content are the most significant factors in food selection.

Comparisons to other studies of gorillas in disturbed forest.

How do the findings of this study compare to other studies of gorillas? The current study is the only one in which gorillas have been studied in logged areas. However gorillas have been studied albeit briefly near fields. Schaller (1963:44) noted that, "nearly all major food plants of gorillas...grow most abundantly in cultivated fields and young secondary forest, but only thinly scattered or not at all in primary forest." Schaller describes early succession in fields as follows. Within 2-4 years Musa yields to Musanga cecropioides, Aframomum, Megaphrynium, Costus and Marantochloa. Within 5 years Musanga has become dominant at about

40'. This pattern of field succession is based on his survey work with George Emlen in Zaire and Rwanda from 1959-60 which included qualitative description of stands cultivated in different years. Most of the cultivation observed by Schaller and Emlen consisted of small, family farms which often include crops consumed by gorillas. There are thousands of miles between the westernmost point of the Schaller-Emlen survey and the Cameroonian forest but the pattern of early succession seems very similar as it impacts the major foods of gorillas (many of which are the same at the generic level). In contrast, large-scale commercial cultivation of e.g. Pyrethrum in Rwanda introduced recently may have quite a different impact on foods resources of gorillas as well as on the pattern of early field succession. The use of commercial fertilizers, extensive weeding, shorter (or nonexistent) fallow periods and the absence of crops edible by gorillas may preclude the increased abundance of giant herbs so important in gorilla diets while seriously reducing the montane forest habitat available to gorillas (Harcourt & Curry-Lindahl, 1978; Harcourt & Fossey, 1981).

Overall impact of logging. Unfortunately the impact of logging and cultivation on gorillas cannot be confined to shifting levels of food abundance. As has been noted in the literature, cultivation and particularly logging are often accompanied by an increase of firearms and wire traps with which gorillas among others are caught/killed (Gartlan, 1975; Wilson & Johns, 1982). At Campo the build-up of logging activities and a related cash economy has resulted in a significant increase in the number of firearms. Also, affluent

Cameroonians often loan firearms to pygmies in exchange for most of the meat. This practice is particularly troublesome and effective. The visibility of hunting to outsiders varies. At Campo, gorillas are only temporarily protected from favored prey status by the presence (decreasing) of larger prey, elephants (21 of whom are known to have been killed in the Campo Reserve during the period of this study, 4.76-7.77). Two gorillas were shot at Campo during a preliminary visit to the site in 1974.

Logging is reported to have yet another impact on primates. Gartlan(1975) and Wilson & Johns(1982) suggest that logging results in expansion of shifting cultivation along newly opened roads. At Campo most of the workers in the logging company were housed in two large camps about 30kms. apart. Wives of these immigrant workers did some slash and burn cultivation in addition to commercial enterprises. It was expected that those fields would be abandoned when the camps were closed. There was no evidence at Campo that the presence of new roads even temporarily increased farm establishment by local Bantu however. Thus, apart from a temporary increase in workers' farms, logging did not increase the amount of cultivation at Campo. In forest with greater human population density, more fertile soil and/or large fields of cash crops, the impact of road development associated with logging might be very different.

The significance of forest disturbance for gorillas: history and prehistory. In lowland rain forest at Campo habitats used extensively by gorillas included a break in the forest canopy which allowed considerable light to reach the ground stimulating growth and

high abundance of giant herbs and vines. Schaller and Emlen were the first to suggest physiognomic similarities between lowland and montane gorilla habitats (1963). They noted that all habitats were damp, lush, providing an abundance of ground level vegetation including vines, leaves, bark, pith and some fruit (1963). The best gorilla habitats were seen as having the "rankest herb stratum" (Emlen & Schaller, 1960:47). Where cultivation and human habitation did not avail appropriate herbaceous strata, gorillas used open valleys and river courses (Schaller, 1963). At high elevation, such light intensity at ground levels is afforded by extreme ground slope and the relatively short, low-branched structure of trees. (See Fossey 1974 and Schaller 1963 for descriptions of montane vegetation used by gorillas). Throughout gorilla range at low elevation (<1500m) such pockets are associated with humans, elephants and waterways as at Campo.

Gorilla interface with human and elephant-related disturbances is probably long-standing. Human habitation in equatorial Africa is documented from the Pliocene (Howell,1978). Agricultural efforts are known from 1000 B.P. (Flenley,1979) and likely as early as 3000 B.P. (Clark,1962). Logging, beyond field clearing and village establishment dates from the late 19th century in the Congo Basin (Flenley,1979).

For thousands of years there have been other mammalian agents of disturbance to gorilla habitat, most importantly elephants. Extensive gorilla-elephant sympatry is probably long-standing, possibly as early as the late Miocene appearance of the Elephantinae in East

Africa (Maglio,1973). Three species of fossil great apes (Dryopithecines) span the period 14-22 mya in the East African Miocene, after which there is an abrupt discontinuity in the fossil record until the recent appearance of the genus Gorilla (LeGros Clark & Leakey,1951). The largest of the three fossil species, Proconsul proconsul major (Andrews,1976), is the most likely gorilla ancestor (Simons & Pilbeam,1965). East African Miocene sites containing this species are thought to have been lowland rain forest (Andrews & VanCouvering, 1975). Contemporary elephant genera (Loxodonta and Elephas) are major agents of habitat change where they have been studied (Buechner & Dawkins,1961; Laws,1970; Mueller-Dombois,1972) although the magnitude of recent elephant damage is exacerbated by artificially high population densities associated with human-enforced habitat boundaries which restrict seasonal migrations.

It seems likely that humans and elephants both stimulate the growth of gorilla food resources today even as elephants have probably been doing since the late Miocene. However, the patch size of logged areas and some crops under cultivation e.g. Musa assuredly constitutes a scale of habitat improvement for gorillas unattributable to elephants now or in the past. Unfortunately the corrolaries of modern cultivation and particularly logging (increased prevalence of firearms/traps) do not bode well for the continued presence of gorillas or elephants in central African forest without greatly increased control of hunting and trapping. Western gorillas may momentarily be protected by the larger prey size of elephants whom hunters prefer to kill, but that kind of protection will not

last long at the rate at which elephants are being eaten in African forests.

Acknowledgements

The field study was funded by World Wildlife Fund, the National Geographic Society, the New York Zoological Society and the L.S.B. Leakey Foundation. Fieldwork in Cameroon was sponsored by ONAREST with the assistance of the Ministry of Agriculture. M. Bihlong of the National Herbarium in Cameroon and Dr. F.N. Hepper of the Royal Botanic Gardens, Kew, generously provided plant identifications. P. Maké, S. Bullock, G. Schroeder, E. Ngi, and the late N. Ngui were helpful in collecting plant samples in the field. Analyses of food chemistry were funded by the L.S.B. Leakey Foundation and completed in the Department of Animal Science at Michigan State University and in the Phytochemistry Laboratory at the University of Strathclyde, Scotland (N.E.R.C. grant #GR3/3455). The manuscript profited greatly from the reading and suggestions of: J. Sauer and S. Strum. I would also like to acknowledge diverse assistance from: J. Hill, C. Yale, L. Youkeles, A. Forsythe, J. Baumer, B. Corre, B. Campbell, D. Lindburg, R. Ippen, J. Travis, A. and V. Balinga, E. Batoku, D. Harding, S. Gartlan, and A. Herbert. Particular thanks are due to Martha Coolidge and the late Harold Coolidge whose considerable encouragement was critical to the project's development.

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