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Caroline E. G. Tutin, Michel Fernandez, M. Elizabeth Rogers, Elizabeth A. Williamson, William C. McGrew, S. A. Altmann, D. A. T. Southgate, I. Crowe, C. E. G. Tutin, A. Whiten, N. L. Conklin and L. Barrett

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Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon

CAROLINE E. G. TUTIN[1]†, MICHEL FERNANDEZ[1], M. ELIZABETH ROGERS[2], ELIZABETH A. WILLIAMSON[3] AND WILLIAM C. McGREW[3]

[1] *Centre International de Recherches Médicales de Franceville, Gabon; Scottish Primate Research Group, University of Stirling, U.K.*
[2] *Scottish Primate Research Group and Institute of Cell, Animal and Population Biology, University of Edinburgh, U.K.*
[3] *Scottish Primate Research Group and Department of Psychology, University of Stirling, U.K.*

SUMMARY

Comparison of the diets of sympatric gorillas and chimpanzees allows an analysis of niche separation between these two closely related species. Qualitatively, their diets are similar, being dominated by an equally diverse array of fruit species complemented with vegetative plant parts, seeds and insects. Gorillas eat more vegetative plant parts than do chimpanzees, but niche separation is most obvious in periods of fruit scarcity when the two species show different strategies that reduce competition for food. Their abilities to overcome mechanical and physical plant defences appear to differ, as gorillas are able to subsist entirely on abundant vegetative foods. Chimpanzees show social adjustment, foraging alone or in small groups, to reduce intra-specific competition for scarce fruit resources. Thus it seems that subtle physiological differences have far-reaching repercussions, defining potential evolutionary pathways for social organization and allowing sufficient niche separation between species.

1. INTRODUCTION

Foraging profiles describe the ways in which a species searches for food, what foods it selects, and the strategies it uses in competing for food, both with members of its own species and with those of sympatric species with overlapping diets. Complete description of the diets of wild primates is not easy, even in the simplest terms of compiling a qualitative list of species and parts eaten. The number of food items recorded for a species varies both with the duration of study and with habitat. The habitat defines the potential diet of each species, and floristic variation is often so great as to limit inter-site comparisons. Food availability changes seasonally, and dramatic inter-annual variations have been recorded in most long-term studies. However, the distribution of different plant food categories (fruits, leaves, insects, etc.) is consistent within most primate species (Sussman 1987), allowing classification of diet as frugivorous, folivorous or insectivorous. Morphological and physiological adaptations to diet are often clear, and multi-factorial allometric analyses have shown that the dietary class correlates with some physical and social variables (Clutton-Brock & Harvey 1980).

With respect to the African apes, chimpanzees (*Pan troglodytes*) have been classed as frugivores, and gorillas (*Gorilla gorilla*) as folivores. For all populations of chimpanzees studied to date, fruit dominates the diet, both qualitatively in percentage terms of total foods and quantitatively in terms of percentage of feeding time and mass ingested (Hladik 1973; Wrangham 1977). Gorilla diet appears to be determined by the variety of foods available in the habitat, with the proportion of fruit increasing with plant species diversity: lowest in the montane habitat of mountain gorillas, intermediate in disturbed forest habitats and highest in lowland tropical forest (Tutin & Fernandez 1985).

Dietary niche is an important ecological constraint on the evolution of primate social systems (Terborgh 1983; Wrangham 1987), as different foods are dispersed differently in time and space, defining the extent and nature of intra-specific competition for food. Allometric analyses suggest a relation between brain size (relative to body mass) and diet, with frugivores having relatively larger brains (Harvey & Clutton-Brock 1983). Maintaining a frugivorous diet presents huge intellectual challenges of memory and spatial mapping compared with the relative ease of harvesting abundant foliage foods (Milton 1981).

The theory of competitive exclusion predicts clear niche differentiation and differences in foraging profiles between two species as closely related and morphologically similar as the gorilla and chimpanzee. Gorillas and chimpanzees are similar genetically (Sarich 1983), in gut morphology (Chivers & Hladik 1984), craniodental anatomy (Shea 1983), gut passage time (Milton 1984) and longevity, but there are differences in social organization, sexual dimorphism, and intestinal flora and fauna. For example, gorillas have cohesive groups led usually by a single fully adult male, whereas chimpanzees live in large fission–fusion communities.

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† All correspondence to: Dr C. Tutin, C.I.R.M.F., B.P. 769, Franceville, Gabon.

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Sexual dimorphism is pronounced in gorillas, with mature males weighing twice as much as females, but is less marked in chimpanzees, with adult females weighing about three-quarters as much as adult males (Groves 1970; Wrangham & Smuts 1980). The intestinal flora and fauna are ubiquitous and more diverse in wild gorillas than in chimpanzees (Ashford *et al.* 1990; File *et al.* 1976; Goussard *et al.* 1983).

Meaningful comparison of diet and foraging strategies can best be made by using the same methods to study sympatric populations. This is especially true when the two species are closely related, as the presence of one is likely to influence the other. Here we present seven years of data to compare the diets of sympatric western lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) in tropical rain forest in the Lopé Reserve, Gabon.

2. STUDY SITE AND METHODS

The study area covers approximately 40 km^2 of tropical rain forest in the Lopé Reserve (0° 10′ S, 11° 35′ E) in central Gabon. Chimpanzees and gorillas occur at similar population densities of about one individual per square kilometre. Average annual rainfall is 1536 mm (1984–1990) and the climate is characterized by a three month dry season from mid-June to mid-September.

Research on the gorillas and chimpanzees began in late 1983 and is ongoing. Field procedure involves searching through the forest for gorillas and chimpanzees, or for indirect signs of their presence and activities. At the beginning of the study the apes were unused to humans and usually fled when encountered. By 1988, two groups of gorillas had become partly habituated, but chimpanzees still remain shy and, as visibility is generally poor, observation is limited. Thus, in addition to observation, we use indirect methods to describe diet, systematically collecting fresh faeces and describing feeding remains.

Faecal samples collected in the field are sealed in plastic bags and later weighed and washed in sieves with 1 mm mesh. The particulate remains are examined macroscopically and the contents listed, large seeds counted and small seeds rated on a four-point scale of abundance (abundant, common, few, rare). Non-fruit plant parts (leaves, stems, pith and bark) are represented in faeces by fibre and partly digested fragments of leaves. These cannot be identified to species level macroscopically, so the volume of the categories ‘fibre’ and ‘green leaf fragments’ is assessed with respect to the total mass of the faecal sample and rated on the same four-point abundance scale. We computed a numerical value for the proportion of non-fruit remains in faeces by converting the abundance ratings as follows: abundant = 4; common = 3; few = 2; rare = 1. The combined score of all non-fruit categories gives the ‘foliage score’ and faeces were classed as ‘foliage dominated’ if the foliage score was 4 or more.

Phenological data on leaf, flower and fruit production have been collected monthly since 1984. Initially, data were collected on five individuals of 83 common tree species, but since October 1986 we have monitored ten individuals of each of 60 species of woody plants (56 trees, three shrubs and one liana), the fruit of which is important in the diet of gorillas and chimpanzees. Each tree is examined at the beginning of each month, and the relative quantities of flowers, fruit (immature and ripe) and leaves (flush, mature and senescent) are scored on a ten-point scale.

The data come from seven years of continuous research at Lopé (January 1984–December 1990), during which we have had 653 contacts with gorillas and 791 with chimpanzees. At least eight groups of gorillas and two communities of chimpanzees have been involved.

3. RESULTS

(*a*) *Composition of diet*

Qualitatively, the diets of gorillas and chimpanzees at the Lopé are similar. To date we have identified 142 chimpanzee foods and 203 gorilla foods. Table 1 compares the diet in terms of the different food types eaten. Fruit is the most numerous food class for both apes: gorillas eat fruit of at least 91 species and chimpanzees of at least 96 species. Dietary overlap is extensive; only 4% of gorilla fruits and 7% of chimpanzee fruits are not shared.

Figure 1 compares the diversity of fruit species eaten by gorillas and chimpanzees using data from five randomly selected faecal samples per species per month over a three-year period. The plots are similar with the number of different species of fruit eaten by gorillas equal to, or slightly greater than, those eaten by chimpanzees. Remains of at least one species of fruit were found in 96% of the 4301 gorilla faeces and in 98% of the 1656 chimpanzee faeces analysed over seven years. The mean number of different fruit species per faecal sample was 3.0 (range 0–10) for gorillas and 2.7 (range 0–9) for chimpanzees.

Both gorillas and chimpanzees regularly consume insects. Remains of at least one species of insect were found in 30% of gorilla faeces and 31% of chimpanzee faeces. The species eaten most often by both apes was the weaver ant (*Oecophylla longinoda*), but there was little overlap in the other species eaten. Chimpanzees used tools to obtain two large species of social ants and the honey of *Apis* sp., whereas gorillas ate three or more species of small ants.

(*b*) *Seasonal variation in diet*

The range of ripe fruit available to the apes at Lopé varied considerably over the annual cycle. Figure 2 shows the average number of species in the phenology sample (total $n = 60$, including 53 species eaten by gorillas and 57 by chimpanzees) bearing ripe fruit in each month over a four-year period (October 1986–September 1990). Few (4–7) species in the phenology sample bear ripe fruit during the long dry season from June to August, and the maximum diversity of fruit (16–19 species) is available from November to January.

Table 2 shows how three measures of diet vary over

Table 1. *Comparison of diets of gorillas and chimpanzees at Lopé*

	gorilla		chimpanzee	
category of food	number of species eaten	percentage of total	number of species eaten	percentage of total
fruit	91	44.8	96	67.6
young leaves	27	13.3	14	9.9
mature leaves	22	10.8	2	1.4
immature seeds	11	5.4	4	2.8
ripe seeds	10	4.9	6	4.2
pith	17	8.4	3	2.1
bark	9	4.4	1	0.7
flowers	3	1.5	3	2.1
miscellaneous[a]	8	3.9	2	1.4
insects	5	2.5	8	5.6
mammals	0	0.0	3	2.1
total	203	99.9	142	99.9

[a] Includes roots, galls and fungi.

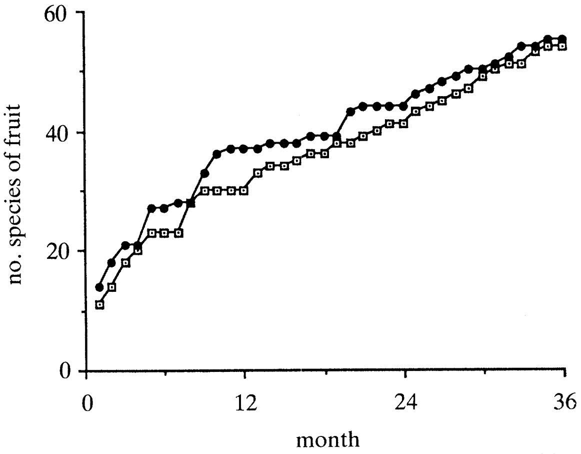

Figure 1. Cumulative number of fruit species recorded in five faecal samples per month (squares, chimpanzee; circles, gorilla).

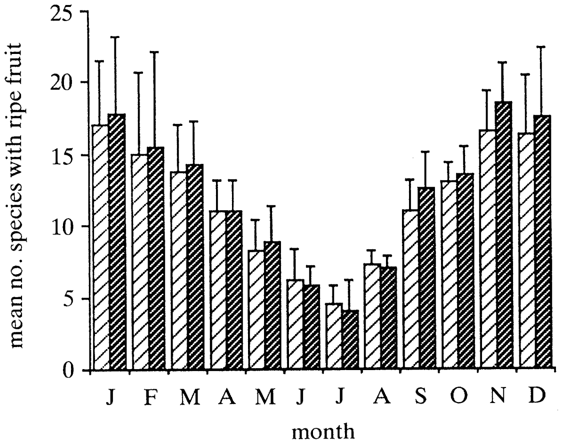

Figure 2. Phenology data: mean number of species with ripe fruit eaten by gorillas (light shading) and by chimpanzees (bold shading), 1986–1990.

the year. The mean number of different fruit species found per faecal sample reflects the diversity of the fruit diet: for gorillas, the maximum of 4.2 fell in January and the minimum of 1.6 in July; for chimpanzees, the maximum of 3.2 was recorded in March and April and the minimum of 1.5 was in July. The annual variation correlates positively with that of the fruit phenology data, reaching significance for gorillas (Spearman Rank Correlation, $r_s = 0.61$, $n = 12$, $p < 0.05$) but not for chimpanzees ($r_s = 0.55$, $n = 12$, $p = 0.06$). Although data from faecal analysis allow quantification of the diversity of the fruit part of the diet, they do not easily allow estimation of the absolute quantities of fruit ingested. Instead, we used foliage scores (see §2) to compare the relative amounts of non-fruit foods in faecal samples. Foliage scores for gorillas were consistently higher than those for chimpanzees, but annual variation was similar, with maximum values during the long dry season, June to August. Annual variation in the mean number of different fruit species recorded in the total monthly sample of faeces was much less marked, but minimum values for both gorillas and chimpanzees fell in June. Gorillas ate a wider variety of fruit than chimpanzees in eight months of the year.

The frequency of insectivory showed no significant correlation with the diversity of fruit eaten or with foliage scores, but chimpanzees did eat most insects in the first two months of the long dry season when their foliage scores were highest and fruit diet least diverse.

(*c*) *Inter-annual variation*

Inter-annual variation in fruit food diversity was considerable. No clear correlation emerged between fruit abundance and rainfall, and it is probable that differences in plant productivity were caused by a number of factors, including inherent species-specific, non-annual rhythms, insect attacks, and climate. Figure 3 compares the number of species in the phenology sample with fruit eaten by gorillas that had ripe fruit in 1987–1988 and 1989–1990, respectively the 'worst' and 'best' fruit years since expanded data collection began in October 1986 (see §2). Data are presented from August to July, as the climatic break of the long dry season appears to affect productivity rhythms over the ensuing 12 months.

Figure 3 shows that in five months of the 'good' fruit

Table 2. *Seasonal variation in chimpanzee and gorilla diet*

	mean fruit species per faecal sample		mean foliage score		total fruit species eaten per month	
month	chimpanzee	gorilla	chimpanzee	gorilla	chimpanzee	gorilla
January	2.9	4.4	2.6	4.5	12.3	17.6
February	3.1	4.2	2.8	4.1	11.2	17.6
March	3.2	3.3	2.5	4.7	10.3	15.0
April	3.2	3.0	3.2	5.9	13.2	11.0
May	2.5	3.3	3.0	5.3	10.7	10.2
June	1.7	2.0	5.0	6.7	9.3	8.9
July	1.5	1.6	5.4	7.5	10.0	11.7
August	2.5	2.4	4.5	7.2	14.5	14.3
September	2.1	2.8	3.0	6.3	12.0	17.6
October	3.1	3.6	2.6	5.7	12.8	17.3
November	2.7	2.6	2.6	6.0	10.8	15.0
December	2.3	2.7	2.8	6.0	11.4	14.0

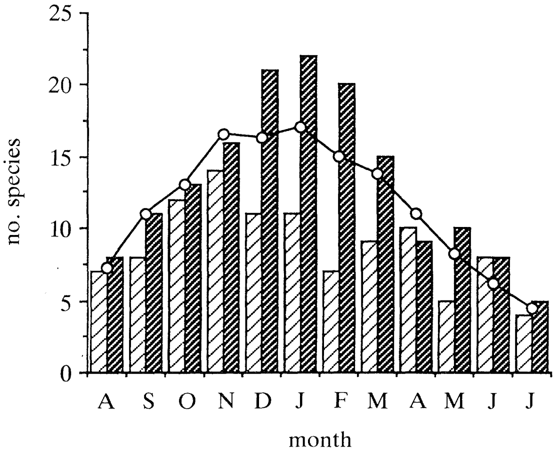

Figure 3. Number of species bearing ripe fruit eaten by gorillas (light shading, 1987–1988; bold shading, 1989–1990; circles, 5-year mean).

year, 1989–1990, fruit diversity was at least twice as great as in the 'bad' fruit year, 1987–1988, in which fruit diversity was low in December–May but not in October–November, a period when production is relatively constant (see figure 2, standard deviations). The plant phenology sample includes all of the major ape foods, except the oil palm, *Elaeis guineensis* (as the fruits are hidden from view), but does not take account of the density of the various tree species in the study area. The phenology data record only fruit diversity, not absolute abundance, but there was a significant negative correlation between the diversity of ripe fruit in the phenology sample each month and the average monthly foliage score from faeces over the two years (for gorillas, $r_s = -0.631$, $n = 24$, $p < 0.001$; for chimpanzees, $r_s = -0.641$, $n = 24$, $p < 0.001$), suggesting that the number of phenology species with ripe fruit does reflect differences in overall abundance of fruit foods.

Table 3 compares the diets of gorillas and chimpanzees in the 'bad' fruit year and the 'good' fruit year. The differences in the average number of different species of fruit per faecal sample are greater between years than between species. The comparison of foliage scores shows a similar general result but the relation is not as clear-cut. Chimpanzees only showed high foliage scores when fruit diversity was very low: in the dry season (July–August) and in five additional months in the 'bad' fruit year. Gorillas showed low average foliage scores (< 4) in only five of the 24 months (January–May 1990). In three of these months, diversity of ripe fruit was high (> 15 species) but this was not the case in April–May. Also, foliage scores were not low in November–December 1989 when fruit diversity was high (see figure 3). The percentage of faeces per month that were 'foliage dominated' (see §2) show that gorillas consume more foliage than chimpanzees, both species eat more foliage when fruit is scarce, and when fruit is abundant, gorillas continue to eat relatively large amounts of foliage.

(*d*) *Diet during periods of fruit scarcity*

During the three month dry season at the Lopé, gorillas eat large quantities of vegetative foods, some of which (leaves and bark of the large tree *Chlorophora excelsa*, and pith and young leaves of two species of herbs, *Marantochloa* spp.) are permanently available but are usually ignored. Chimpanzees increase their consumption of the fruit of *Elaeis guineensis* and of the pith and young leaves of herbaceous plants (Zingiberaceae and Marantaceae). Chimpanzees eat *Elaeis* fruit throughout the year (22 months out of 24 in the two years) but gorillas never eat it. *Duboscia macrocarpa* fruit are also available throughout the year as trees fruit asynchronously. Gorillas eat *Duboscia* fruit regularly (21 out of 24 months) but chimpanzees consume it only when other fruit is scarce (the dry season every year, and in April and May 1988).

In periods of fruit scarcity during 'bad' years, gorillas and chimpanzees both increase consumption of pith and young leaves of Zingiberaceae and Marantaceae and the fruit of *Duboscia*, but other foods, especially immature and ripe seeds of a range of species, are also eaten in large quantities. Gorillas eat *Chlorophora* and *Marantochloa* only rarely at such times, suggesting that these dry season keystone foods are the least preferred and eaten only when all other foods are unavailable.

Table 3. *Comparison of ape diets in a 'bad' (1987–1988) and a 'good' (1989–1990) fruit year*

	mean fruit spp. per faecal sample				mean foliage score				percentage of foliage dominated			
	chimpanzee		gorilla		chimpanzee		gorilla		chimpanzee		gorilla	
month	bad	good	bad	good	bad	good	bad	good	bad	good	bad	good
August	2.1	2.5	1.6	2.2	5.0	4.9	7.3	7.3	75	77	100	100
September	1.6	2.5	2.2	3.3	4.0	2.0	6.1	6.8	60	16	100	98
October	2.8	3.9	3.0	4.6	2.7	2.4	6.1	5.2	36	22	100	87
November	1.8	4.4	2.1	3.0	2.5	2.6	6.1	5.3	20	40	96	91
December	2.1	2.7	2.6	2.6	2.6	2.6	5.9	5.4	33	36	100	91
January	3.3	2.5	3.8	5.1	1.8	3.2	4.4	3.5	28	50	71	49
February	3.0	3.0	3.4	4.8	3.0	3.3	5.5	3.1	35	50	92	47
March	2.1	3.4	1.6	3.6	4.7	1.4	7.4	3.1	42	17	100	45
April	1.8	3.7	0.8	3.4	5.3	1.9	7.5	3.9	100	13	100	53
May	1.4	2.6	1.2	3.4	5.9	1.6	7.1	4.0	89	21	100	57
June	0.7	2.0	0.3	2.7	7.2	2.5	7.6	5.3	100	34	100	73
July	1.6	1.3	1.7	1.5	6.0	5.7	7.5	7.3	100	80	100	100

4. DISCUSSION

The diets of the two species of ape at Lopé are generally similar, being numerically dominated by fruit, with leaves as the second most important part (table 1). Although the fruit diet is similar, the diversity of fruit consumption by gorillas at Lopé somewhat exceeds that of chimpanzees (figure 1, table 2), showing that this population of lowland gorillas cannot accurately be described as folivorous. Both gorillas and chimpanzees at Lopé are generalized, opportunistic frugivores, but neither species subsists entirely on fruit. Insects are eaten at similar frequencies, and vegetative plant parts such as leaves and pith are eaten regularly, but in larger quantities by gorillas than by chimpanzees (table 2). When fruit is scarce, during the dry season each year and for longer periods in some years (figures 2 and 3), both chimpanzees and gorillas increase their foliage intake, but both continue to find a surprising diversity of fruit (table 3).

The fruits eaten by apes at Lopé are diverse in terms of size, colour and chemistry, but it is instructive to look in more detail at the few species of fruit that are eaten exclusively, or in much greater quantities, by one of the two species of ape. There are seven important fruit foods of chimpanzees that are not eaten by gorillas at Lopé: five of these, including *Elaeis*, have an 'oily' flesh high in lipids (Rogers *et al.* 1990). Fruit and seeds eaten by gorillas at Lopé are relatively low in lipids, suggesting a general avoidance of foods with high lipid content (Rogers *et al.* 1990). The small number of species of mature leaves eaten by chimpanzees (table 1) suggests general avoidance of foods with high fibre content or with secondary compounds such as tannins and phenolics.

Studies of frugivorous communities elsewhere suggest that dietary divergence is highest when preferred food (succulent fruit) is scarce, and that niche separation is clear only at such times (Gautier–Hion & Gautier 1979; Terborgh 1983). Terborgh (1986) suggested that frugivorous vertebrates survive periods of fruit scarcity by relying on a few plant foods that either produce fruit outwith the community peak (e.g. figs), or have long-lasting, protected fruit (e.g. palms). These keystone resources are exploited in a specialized way by different members of the frugivore community, reducing inter-specific competition for food.

The diets of gorillas and chimpanzees differ when preferred foods are scarce, with each species of ape having some exclusive keystone resources whilst sharing others. Diet during the dry season at Lopé shows only minor inter-annual variation. By definition, keystone resources must be available in significant quantities when succulent fruit is scarce. This is true of mature leaves, pith, and bark of common species, but young leaves, fruit, and seeds can only be dependable keystone foods if produced continuously on a community basis, as is the case for fruit of *Duboscia* and *Elaeis* and young leaves of *Chlorophora* at Lopé (C. E. G. Tutin, unpublished data).

Plant chemistry is also relevant to niche separation. Fibre and phenolics help to protect plants from herbivores as they decrease digestibility (Freeland & Janzen 1974), but fibrous foods can provide energy if the cellulose can be digested (Gaulin & Konner 1977). The entodiniomorph ciliates, ubiquitous in faeces of lowland gorillas in Gabon (Goussard *et al.* 1983), are symbiotic cellulose digesters (Collet *et al.* 1984). Chimpanzees also have ciliates, but they are less frequent in faecal samples (75% of samples compared with 100% for gorillas) and less diverse (two species for chimpanzees, at least four for gorillas) (Imai *et al.* 1991; File *et al.* 1976). Gorillas can survive on a totally folivorous diet but it appears that chimpanzees cannot, as, whereas foliage intake increases when fruit is scarce, they continue to eat more fruit than gorillas during the dry season (table 3). It is not clear why gorillas avoid high-lipid foods, or how they cope with foods with high tannin content.

Food choice is complex, and although the chemical and mechanical properties of plants and the morphological and physiological adaptations of herbivores have significant roles, other, often subtle, factors are also involved. Some social insects are accessible only if tools are used, and are eaten by chimpanzees but not gorillas. Another example is the keystone resource of gorillas, the aquatic herbs (*Marantochloa* spp.) that grow in marshes and along the banks of streams: gorillas harvest the pith and young leaves of these plants while wading in water up to 50 cm deep. Chimpanzees may not eat *Marantochloa* because they have a strong dislike of water, crossing even shallow streams through overhead trees or on bridges. However, explanations for other instances of dietary variance are less clear. Strong preferences for certain fruits also exist, which explains why foliage scores are not consistently related to fruit diversity (figure 3, table 3). When *Dialium* fruit are abundant they dominate the diets of both apes, perhaps because both the sugary mesocarp and some seeds are eaten, providing a balance of nutrients rarely available at a single feeding site. Although often rich in protein, seeds can be small, and lengthy processing is needed to remove them selectively. This may explain why seeds are largely ignored except when fruit is scarce.

If the key to niche separation of the sympatric gorillas and chimpanzees at Lopé is the ability of gorillas to survive lengthy periods of fruit scarcity on an almost entirely folivorous diet, there are important repercussions. Non-reproductive parts of both woody and herbaceous plants are widely available, both in space and time, compared with fruit. Abundant food is available for a group of gorillas both in a *Marantochloa* marsh and the crown of a flushing *Chlorophora*, but the number of ripe fruit on a single *Elaeis* is very limited. Thus within-species feeding competition for keystone resources is likely to be low for gorillas and high for chimpanzees. Chimpanzees make a social adjustment and forage alone, or in small subgroups, when fruit is scarce (Wrangham 1977), whereas gorillas always forage in the company of conspecifics. The degree of intra-specific competition for food, particularly between adult females, is thought to have been a major selective force on the evolution of ape social systems (Wrangham 1979, 1987). Data from Lopé support this but emphasize that, in tropical forest habitats, competition for preferred food is only critical for a minority of the time (see also Gautier–Hion & Gautier 1979; Terborgh 1983). A high overall degree of dietary overlap is to be expected between closely related species that share physical adaptations, such as craniodental anatomy and gut morphology. Gorillas and chimpanzees are remarkably similar in these respects (Chivers & Hladik 1984; Milton 1984; Shea 1983), but the difference in body size could be important in allowing greater consumption of fibre by gorillas.

Apes have large brains, and the challenge of finding and exploiting keystone food resources, as well as keeping track of widely dispersed fruit foods, may have been an important selective pressure in the evolution of intelligence. Regular shortages of preferred foods affect most, if not all, populations of frugivores, and must provide a powerful stimulus for innovative and inventive behaviours. Chimpanzee tool-use gives access to otherwise inaccessible foods, and many tool-use behaviours show cultural variation (Nishida 1987). The kernels of large, well-protected nuts provide a high-quality food, but the essential tool-use technology exists in only some of the chimpanzee populations with access to the resource. Chimpanzees at Lopé do not crack nuts with tools, but if they did, intra-specific feeding competition during the dry season might be reduced, because if *Elaeis* kernels were exploited as well as the flesh, more food would be available.

The fission–fusion social organization of chimpanzees allows rapid adjustment to different levels of food abundance and responds to individual needs and preferences (Wrangham 1979). Living in groups conveys advantages such as reducing the threat of predation (Alexander 1973), if the obstacle of competing for food with conspecifics can be overcome. Predation may not be a constant threat for gorillas and chimpanzees but can assume importance in some habitats (Tutin *et al.* 1981) or on rare occasions (Tsukahara & Nishida 1990), and the risk is likely to be greater for lone individuals (Hiraiwa–Hasegawa *et al.* 1986). Silverback gorillas systematically protect group members from perceived threats whereas chimpanzee males do not (Tutin & Fernandez 1990). Female gorillas have a greater reproductive potential than chimpanzees (earlier age at first birth and shorter inter-birth interval), and this may be a result of living in a closed group (Tutin 1990). Perhaps the social adjustment of chimpanzees to food availability has disadvantages, if foraging alone when fruit is scarce either increases the risk of predation or increases the costs of maternal investment as male protection is not available.

In a complex frugivorous community, competition for preferred food occurs not only within, but also between, species. Of eight species of diurnal primate at Lopé, seven are frugivorous. Clear examples of competition for food are few, but the outcome appears to be determined by relative numbers rather than body size. Thus, although data are scarce, it seems possible that being a member of a group may provide an advantage in inter-specific competition for fruit sources, especially during periods of overall fruit scarcity.

The highly frugivorous diet of gorillas at Lopé shows the genus *Gorilla* has dietary flexibility, but even when fruit is abundant they continue to eat some foliage. Whether this is related to maintaining their complex gut flora and fauna, larger body size, a result of group living, or a combination of these factors, it is a feature that appears to differentiate them from chimpanzees. Detailed behavioural data on the gorillas and chimpanzees at Lopé are needed to quantify levels of intra- and inter-specific competition for food, and to assess the reproductive success of the two species. Continued study of the sympatric apes at Lopé should also shed light on the advantages and disadvantages of the different foraging strategies that were open to our hominoid and hominid ancestors.

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Discussion

S. A. Altmann (*Department of Ecology and Evolution, University of Chicago, Illinois, U.S.A.*). The fact that the gorillas in this forest do not eat the fruit of oil palms is puzzling, as these fruits are nutritious and are eaten by chimpanzees. The oil from the fleshy mesocarp contains high levels of beta carotene and other carotenoid compounds. The composition of the fruits is very variable, with a range of about 37 300–128 700 μg beta carotene or its equivalent per 100 g oil (Leung 1968). If provitamin A is very abundant in the gorilla's diet from other sources, or if these primates are particularly sensitive to carotenoids, their intake may border on hypervitaminosis and thereby condition them against oil palm fruit.

Reference

Leung, W. W. 1968 *Food composition table for use in Africa.* (306 pages.) FAO and USDHEW.

D. A. T. Southgate (*Institute of Food Research, Norwich, U.K.*). Professor Altmann raised the issue of possible effects of excessive carotene intakes. In humans excessive intake does not produce vitamin A toxic effects: the subject merely looks jaundiced from the high circulating levels of carotenoids.

The avoidance of fatty foods by gorillas creates a need to consume a very large bulk of food and appears a rather unusual foraging strategy.

M. E. Rogers. When the authors talk about avoidance of fatty fruits, they are referring to very high fat content of 20–76 % dry mass. When it is suggested that gorillas eat some fatty foods in other studies (Calvert 1985), much lower fat levels were being referred to.

Reference

Calvert, J. J. 1985 Food selection by western gorillas (*G. g. gorilla*) in relation to food chemistry. *Oecologia* **65**, 236–246.

I. Crowe (*23 Lockhart Close, Dunstable, Bedfordshire, U.K.*). Why do gorillas continue to eat leaves when other favoured foods are available?

M. E. Rogers. Leaves are high-protein foods, and this must be important as both fruit and pith are low in protein. Also, gorillas choose leaf foods from common herbaceous plants that have low levels of digestion inhibitors (total phenols and tannins). It may be desirable from the point of view of digestion to mix high- and low-tannin foods at all times.

I. Crowe. Dr Foley has suggested that climatic changes in Africa (i.e. long dry seasons) affected early hominid diets. I suggest a similar factor might explain the extinction of *Australopithecus boisei* and similar sub-species, given that *A. boisei* was probably a folivore subject to the same dietary constraints: unable to risk diversifying too much, being dependent upon maintaining a high leaf content in its diet, to avoid destroying the gut flora and fauna.

C. E. G. Tutin. The parallel between sympatric hominids and the sympatric apes at Lopé is interesting. Our data show that gorillas at Lopé can subsist on a predominantly folivorous diet, and are dependent on an abundant supply of leaf foods during the annual dry season. Sufficient leaf foods are available throughout the year in equatorial regions and it seems likely that this resource defines the geographical range of the large-bodied *Gorilla*. Chimpanzees can subsist in habitats with a prolonged dry season which are dominated by deciduous vegetation.

A. Whiten (*Scottish Primate Research Group, University of St Andrews, U.K.*). The authors have undertaken very extensive analyses of the chemical composition of gorilla (and chimpanzee?) foods. Do these allow the authors to make comparisons with norms of composition in the diets of different populations of baboons such as Whiten *et al.* (this symposium) show in table 5, or is such comparison defeated by the observational constraints on recording intake?

M. E. Rogers. Observational constraints have certainly prevented the ranking of food items by proportion of total intake, or of feeding time; but they can be ranked by frequency of occurrence on trails and in faeces. By using these data we can provide a mean diet composition for Lopé gorillas. We do not have comparable data for chimpanzees at Lopé.

S. A. Altmann. To what extent are the primates the authors have studied responsible for dispersing the seeds of the plants on which they feed? The faeces of Amboseli baboons contain intact seeds of *Acacia tortilis* and *Balanites aegyptica*, sometimes deposited, complete with fertilizer, at considerable distances from the source plant.

C. E. G. Tutin. Both gorillas and chimpanzees at Lopé disperse the intact seeds of most of their fruit foods. Gorillas disperse seeds of at least 65 species (Tutin *et al.* 1991). The large gut size of both species of ape and their wide ranging makes them seed dispersers 'par excellence', and they undoubtedly play an important role in the dynamics and regeneration patterns of their tropical forrest habitats.

Reference

Tutin, C. E. G., Williamson, E. A., Rogers, M. E. & Fernandez, M. 1991 A case study of a plant–animal relationship: *Cola lizae* and lowland gorillas in the Lopé Reserve, Gabon. *J. trop. Ecol.* **7**, 181–199.

N. L. Conklin (*Department of Anthropology, Harvard University, Cambridge, Massachusetts, U.S.A.*). Chimps are definitely seed dispersers. We are hoping to study the details of seed dispersion by chimps in Kibale in the near future.

L. Barrett (*Department of Anthropology, University College London, U.K.*). There have been several reports, notably by Richard Wrangham, which suggest that chimpanzees at Gombe seek out the leaves of certain plant species, e.g. *Aspilia* spp., specifically for their pharmacological effects, and it is known that, although the baboons at Amboseli avoid the fruits of *Solanum incanum* (which contain high levels of the alkaloid, solanin), those at Laikipia regularly eat the unripe fruits of this species, possibly for 'medical' purposes. Has this phenomenon been noted among the apes at Kibale and Lopé? More generally, how prevalent or important is the selection of plant species for pharmacological, rather than nutritional, purposes among monkeys and apes?

M. E. Rogers. Gorillas eat a lot of ginger (African ginger, *Aframomum* spp.). Commercial ginger (*Zingiber officinale*), which is an Asiatic species, has antihelminthic properties so, if *Aframomum* does also, then gorillas may be regularly consuming a plant with medicinal properties. *Aframomum* certainly contains terpenes. I am not suggesting that they eat it selectively for medicinal reasons, just that they eat so much of it anyway, it may well have therapeutic effects in terms of their parasite load.

N. L. Conklin. The phenomenon is currently being studied in Kibale, but it is too early to say more than that. The topic is reviewed by Goodall & Wrangham (1989).

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