CHAPTER TWENTY

The Diets, Preferences, and Overlap of the Primate Community in the Budongo Forest Reserve, Uganda

Effects of Logging on Primate Diets

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INTRODUCTION

The Budongo Forest Reserve in western Uganda forms the northernmost forest of the forests of the Albertine rift (Howard, 1991). Six species of diurnal primate are known to inhabit this forest: eastern chimpanzee *Pan troglodytes schweinfurthii*, black-and-white colobus *Colobus guereza*, redtail monkey *Cercopithecus ascanius*, blue monkey *Cercopithecus mitis*, olive baboon *Papio anubis*, and the vervet monkey *Cercopithecus aethiops*. The latter two species are generally found

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around the edges of the forest and did not form part of this study. Budongo has been Uganda's main forest for timber production and has been logged on a sustainable yield basis since the 1920s up to the present day although there has been much illegal logging in recent years. Research has shown that the forest management practices have changed the forest composition from a forest type dominated by *Cynometra alexandri* to a more mixed forest type where the diversity of tree species is higher (Plumptre, 1996). Plumptre and Reynolds (1994) showed that the densities of the *C. mitis*, *C. ascanius*, and *C. guereza* were significantly higher in logged compartments in the forest while there was no significant difference in the density of *P. troglodytes* between logged and unlogged compartments. This study also showed that *C. mitis* and *C. ascanius* were more abundant in mixed forest. At the time it was hypothesized that the increase in density could be attributed to the greater tree species diversity in the logged areas, particularly of trees bearing fruits edible for primates but the data at the time were not available to test this. Since this paper was produced, data were collected on the diets and food preferences of the primates in Budongo Forest. This hypothesis that variations in primate abundance in Budongo are due to dietary requirements is tested here using analyses of primate diets in different areas of the forest and measures of fruit production.

METHODOLOGY

Study Area

The Budongo Forest Reserve (latitude: 10°37′–20°00′ N; longitude: 31°22′–31°46′ E) covers 793 km^2 of moist semideciduous forest and grassland, 428 km^2 of which is forested (Howard, 1991). The Reserve lies at a mean altitude of 1100 m and is divided into 70 compartments for management purposes. Eight of these compartments were chosen as study sites, two unlogged (N15, K11–13) and six logged (B4, N3, N11, W21, B1, K4) at approximately 10-year intervals since 1950 (for map see Plumptre & Reynolds, 1994). Mean annual rainfall is 1392 mm (1993–1996) and the climate is characterized by a dry season of about 3 months from mid-December to mid-March (Newton-Fisher, 1999a,b,c). Temperatures vary little during the year with the highest maximum values, and lowest minimum values occur in the dry season. Temperatures rarely fall below 12°C at night.

Tree Species Enumeration and Fruit Production

During 1992, five 2-km transects were established in a stratified random manner (Plumptre & Reynolds, 1994) in each of eight compartments (B4, B1, N15, N3, N11, W21, K4, and K11–13). Every 50 m along these transects, all tree species of over 10 cm diameter at breast height (DBH) were identified in 7-m-radius circular plots (Plumptre, 1996) and their DBH at 1.3 m measured following Alder and Synnott (1992). Each plot was assigned one of five forest types: *Cynometra*, *Cynometra*-mixed, mixed, colonizing, and swamp. Every second plot at 100-m intervals was marked, trees numbered, and the measurement points of each tree painted. This enumeration enabled us to calculate the sum of the DBH values for different groups of trees producing different fruit types as a measure of potential fruit availability (see below).

In N15 (unlogged) and N3 (logged in 1950), the painted trees were used to obtain measures of phenology. These measures were concentrated in two sites because of the costs of collecting in all eight sites. Measures of availability of fruit are always fraught with problems and ideally should be based on the biomass of fruits available on the tree. Chapman *et al.* (1992) showed that DBH was a good predictor of fruit abundance (biomass) for particular tree species, and the sum of DBH values across different species have been used as a measure of availability (Chapman & Chapman, 1999). Others have calculated availability as the density of fruiting trees in a habitat (e.g., Sourd & Gautier-Hion, 1986) and some have multiplied tree basal area by a score of fruit production similar to that given above (Dasilva, 1989; Fairgrieve, 1995). Given the finding by Chapman *et al.* (1992), we decided to calculate two measures of availability: (1) the "potential fruit availability" calculated as the sum of the DBH values of trees and (2) the product of the DBH and whether the tree was fruiting or not. The second measure allows a seasonal analysis of fruit availability. To multiply DBH by a fruit score would have overweighted those trees producing much fruit if the correlations found by Chapman *et al.* (1992) also hold for the species in Budongo. We then summed these two measures for trees producing similar fruit types (small and fleshy [<2.5 cm long], large and fleshy [>2.5 cm long], and pods). Although these measures also have weaknesses, they have the advantage that there are fewer problems with interobserver error as only an identification of whether the tree was fruiting is required.

Measures of Primate Diet

Feeding Scans from Transects

Five 2-km transects were cut in each of the eight compartments using a stratified random sampling procedure to enable the primates to be censused during 1992 (see Plumptre & Reynolds, 1994). From March 1993 to February 1994 the same transects were walked from 7.30 to 11.00 am. Whenever a primate was seen, the observers watched it (provided it did not react to the presence of the observer by fleeing) and recorded the first food item it was seen to feed upon. Items recorded were young leaves, mature leaves, ripe fruit, unripe fruit, flowers, bark, and arthropods. For groups of primates this involved scans of the group, recording food items of all individuals that could be seen until all of them had been sampled once or until the group spotted the observer and fled. This method will bias the estimation of diets toward food items that are more easily visible. On the other hand it allows many more groups to be sampled and a larger area to be covered so that diets obtained will include a wider range of tree species parts eaten in each compartment.

Preference for certain food types was measured with Manly's alpha (Krebs, 1989) and calculated for fruits and leaves for each tree species consumed. Manly's alpha measures preference taking into account availability (as measured by sum DBH). Rare species are almost always preferred using this index because their availability is low and therefore it is not very meaningful to consider them.

Dawn to Dusk Follows

In compartments N3 (logged) and N15 (unlogged), a total of 17 groups of monkeys were habituated sufficiently to follow them. In both compartments, three groups of *C. mitis* and *C. guereza* as well as three *C. ascanius* groups in N3 and two *C. ascanius* groups in N15 were habituated. Some of the *C. mitis* groups were those followed by Fairgrieve (1995). In N3 the habituation of a *P. troglodytes* community had begun in 1990 and by December 1994 it was sufficiently far advanced that individual chimpanzees could be identified and followed (Newton-Fisher, 1999a,b,c). Only data from complete dawn to dusk follows were used in analyses for the chimpanzee data as individuals were sometimes lost when they left feeding trees and it was felt that diets might be biased if these were included. Primate groups or individual *P. troglodytes* were located at about 16.00 and followed for a period of 48 h from dawn to dusk. Each group of monkeys was followed for 2 days each month from October 1994 to January 1996. Individual *P. troglodytes* were followed on 2 days each week by four observers between December 1994 and December 1996.

Scan samples at 30-min intervals were made for all individuals visible and the following data recorded:

Activity. If feeding, the plant species and part. With habituated monkeys, it was possible to identify parts in more detail than in the study from the transects and so fruit was separated into whole fruit, flesh and seeds (discarding pericarp), and seeds only (discarding surrounding tissue and pericarp).

Dietary Overlap. This was calculated at the two different scales between the same species at different sites and between species at the same site. Horn's overlap index was used as the measure of overlap because it has been shown to have lower bias than other measures (Krebs, 1989). Monte Carlo simulations were made generating random numbers for the dietary intake of plant species and parts (only for those species and parts known to be consumed by the primates) to assess whether the dietary overlap values calculated were significantly higher or lower than might be expected from random sampling. This form of neutral sampling keeps plant parts that are not eaten as zeros but varies the proportion of plant parts that are eaten 100 times to obtain the lowest and highest 5% overlap values. If the true value falls within the lowest or highest five values, it is considered to be significantly different from a random value.

RESULTS

Fruit Availability

It was found that the variation in tree species composition of the forest was greatest between the west and east of Budongo (Plumptre, 1996) so that comparing compartments K11–13 in the east with B4 and B1 in the west was hampered by this effect. This was why it was decided to combine tree species into groups based on their fruit characters (see Methods). Table 1 gives the sum DBH values for the different fruit types for each compartment and also the density of the primates. In most compartments, trees that produce small fleshy fruits were the most abundant.

The results of the phenology analysis for the three fruit categories in compartments N15 and N3 for ripe and unripe fruit showed that trees producing

Table 1. Measures of the potential availability of fruit (sum DBH values) for different fruit types in each compartment per hectare and the density of each primate in each compartment (No. per km^2)

Compartment	N15	K11–13	B4	N3	N11	W21	B1	K4
Year logged	Unlogged	Unlogged	1941–1942	1947–1952	1960	1963–1964	1981–86	1988–1996
Small fleshy fruits	6,060	3,770	4,960	6,440	5,370	4,960	4,560	4,740
Large fleshy fruits	4,330	5,440	4,390	5,120	4,880	3,680	3,580	4,100
Pods	3,810	3,570	3,190	3,740	4,230	3,070	2,600	4,170
Total	**14,200**	**12,780**	**12,540**	**15,300**	**14,480**	**11,710**	**10,700**	**13,010**
C. mitis	31.2	7.7	61.6	57.5	45.1	45.3	86.8	33.2
C. ascanius	12.7	8.9	54.4	38.0	44.3	39.5	63.6	30.6
C. guereza	25.8	26.7	37.1	51.7	46.6	48.9	34.0	49.9
P. troglodytes	0.9	3.0	0.5	1.4	1.5	1.6	1.0	0.9

Census data are from Plumptre and Reynolds (1994).

small fleshy fruits were the most abundant but that production could fluctuate greatly between months and years. This fluctuation between boom and bust periods could be important for primates, with species preferring areas where food supply is relatively constant. In addition the patchiness of food availability will be important (Newton Fisher *et al.*, 2000). If there are areas with lots of fruit and areas with little, then primates will need larger home ranges to find sufficient food over the year and density will consequently be lower. The coefficient of variation (standard deviation and mean) between phenology scores in plots varied over the 4 years from January 1993 to December 1996 but was higher for 91% of months in N15 compared with N3 for small fleshy fruits and 71% of the time for large fleshy fruits. This shows that for much of the time for small fleshy fruits and large fleshy fruits, the variation between plots was greater in N15, the unlogged compartment. Therefore the food supply was more patchily distributed here.

Diets from Transect Scans in Compartments

Diets obtained from the transect scans determined some of the main food plants that provide food for these primates. Primate densities were correlated (Spearman rank correlations) with the sum DBH (potential food available) of the 10 most commonly consumed tree species that were found in all compartments in the forest, but few significant correlations were found (Table 2). *Colobus guereza* was positively correlated with *Celtis durandii*, and *Celtis mitis* and *Cercopithecus ascanius* were negatively correlated with *Cynometra alexandri* (Table 2). *Pan troglodytes* density was only correlated with the sum DBH of trees producing large fleshy fruits. Given the large number of correlations (64) in Table 2, it would be expected that three significant correlations would be obtained by chance (1 in 20 tests at $P = 0.05$). With only eight points to correlate, reducing the probability level to compensate for the number of correlations eliminates almost all pattern because a correlation coefficient of 1.00 is required for $P = 0.001$. Consequently the $P = 0.05$ level is given here to show that some patterns exist and that future work could investigate these further.

Correlations were calculated between the density of the three monkey species and the percentage of pods and fleshy, ripe, and unripe fruit in the diets obtained from scans along transects in each compartment. For *C. ascanius* and *C. mitis* there were significant correlations between the percentage of fleshy fruit (+ve), ripe fruit (+ve), and unripe fruit (−ve) in the diet and primate density. For

Table 2. *R* values and significance of Spearman rank correlations between primate density and (a) sum DBH of tree species and those producing certain fruit types in compartments and (b) percentage scans of food items.

	C. mitis	*C. ascanius*	*C. guereza*	*P. troglodytes*
(a) Tree density				
Cynometra alexandri	−0.93**	−0.82*	−0.14 ns	0.59 ns
Maesopsis eminii	0.71*	0.36 ns	0.52 ns	−0.24 ns
Celtis durandii	0.33 ns	−0.07 ns	0.76*	0.10 ns
Celtis mildbraedii	−0.02 ns	−0.61 ns	0.17 ns	−0.02 ns
Celtis zenkeri	0.52 ns	0.61 ns	0.38 ns	−0.21 ns
Alstonia boonei	0.13 ns	−0.38 ns	0.83*	0.12 ns
Albizia spp.	0.80*	0.88**	0.07 ns	−0.18 ns
Funtumia elastica	0.43 ns	0.21 ns	0.74 ns	0.04 ns
Croton macrostachys	0.79*	0.46 ns	0.60 ns	−0.16 ns
Ficus spp.	0.68 ns	0.31 ns	0.26 ns	−0.35 ns
Small fleshy fruits	0.24 ns	−0.07 ns	0.21 ns	−0.05 ns
Large fleshy fruits	−0.31 ns	−0.25 ns	−0.12 ns	0.88**
Pods	0.57 ns	0.46 ns	0.62 ns	0.04 ns
(b) Dietary scans				
Ripe fruit	0.74*	0.86*	0.19 ns	NA
Unripe fruit	−0.90**	−0.93**	−0.24 ns	NA
Fleshy fruit	0.74*	0.82*	0.29 ns	NA
Pods	−0.88**	−0.54 ns	−0.26 ns	NA

* $P < 0.05$. ** $P < 0.01$. NA = not able to calculate.

C. mitis the correlation between density and pods consumed was also significant (−ve) at $P = 0.01$ (Table 2). There were no significant correlations for these measurements and *C. guereza* density. It was not possible to obtain a measure of *P. troglodytes* diets in the eight compartments because sightings were too few.

Table 3 summarizes the preferences for the three monkey species in each compartment for the most common trees (top 15 species in each compartment) where a preference was shown. This table shows the importance of *Celtis durandii* in the diets of all these three primates with a preference shown for its fruit (and leaves in the case of the *C. guereza*) in almost all compartments. This is despite the fact that it is an abundant tree species in most areas and availability values are high. It is interesting to note, however, that many species may be preferred in some compartments but not others.

Diets from Dawn to Dusk Follows

Figures 1 through 7 show the percentage of scans of different plant parts consumed by primates in N15 (unlogged) and N3 (logged) throughout the year.

Table 3. Dietary preferences for each monkey species in each compartment

Tree	Part	N15	K11–13	B4	N3	N11	W21	B1	K4
No. of scans		450	50	332	823	362	576	393	192
C. mitis									
Aningeria altissima	Fruit	+							
Alstonia boonei	Leaf							+	
Albizia spp.	Leaf		+	+	+		+	+	+
Bosqueia phoberos	Fruit				+			+	
Broussonetia papyrifera	Fruit				+				
	Leaf								
Chrysophylum albidum	Fruit					+	+		+
	Leaf							+	+
Celtis durandii	Fruit	+	+	+	+	+	+	+	+
Celtis zenkeri	Fruit								+
Cleistopholis patens	Fruit						+		
Cordia millenii	Fruit							+	
C. alexandri	Leaf				+			+	
Erythrophleum suaveolens	Fruit								
	Leaf	+			+			+	
Ficus exasperata	Fruit				+			+	
Ficus sur	Fruit					+			
Funtumia elastica	Fruit		+				+	+	+
Maesopsis eminii	Fruit							+	+
Morus lactea	Fruit								
	Leaf								
Tapura fischeri	Fruit							+	+
C. ascanius									
Aningeria altissima	Fruit								
Alstonia boonei	Leaf								
Albizia spp.	Leaf			+	+		+	+	
Bosqueia phoberos	Fruit				+		+		
Broussonetia papyrifera	Fruit				+				
	Leaf				+				
Chrysophylum albidum	Fruit		+	+		+	+	+	
	Leaf	+		+	+	+	+		
Celtis durandii	Fruit	+	+		+	+	+	+	
Celtis zenkeri	Fruit	+							
Cleistopholis patens	Fruit	+				+	+		
Cordia millenii	Fruit								
Cynometra alexandri	Fruit								
	Leaf	+			+				
Erythrophleum suaveolens	Fruit								+
	Leaf								+
Ficus exasperata	Fruit				+			+	
Ficus sur	Fruit				+	+			
Funtumia elastica	Fruit	+							
Maesopsis eminii	Fruit	+				+			+

(*Cont.*)

Table 3. *(Continued)*

Tree	Part	N15	K11–13	B4	N3	N11	W21	B1	K4
C. guereza									
Aningeria altissima	Fruit			+					
Alstonia boonei	Leaf	+	+	+	+	+	+	+	+
Albizia spp.	Leaf				+			+	
Bosqueia phoberos	Fruit			+					
Broussonetia papyrifera	Fruit								
	Leaf								
Chrysophylum albidum	Fruit		+		+		+	+	
	Leaf							+	
Celtis durandii	Fruit	+	+	+	+	+	+	+	+
	Leaf	+	+	+	+	+	+	+	+
Celtis zenkeri	Fruit								
	Leaf					+			
Cleistopholis patens	Fruit					+	+		
Cynometra alexandri	Fruit				+	+		+	
	Leaf			+	+	+	+	+	+
Erythrophleum suaveolens	Fruit		+					+	
	Leaf								+
Ficus exasperata	Fruit				+				
Ficus sur	Fruit				+			+	
Funtumia elastica	Fruit								
Holoptelea grandis	Leaf	+		+		+	+		
Maesopsis eminii	Fruit			+	+	+	+	+	
	Leaf	+		+	+				

Only those tree species which were relatively abundant in all compartments and where a preference was shown are listed. Preferences were calculated using Manly's alpha and the sum DBH values were used as a measure of availability. The values of alpha are not given because they are dependent on the number of food items and hence are not comparable between compartments. + = preference.

These show that for most months there was more ripe fruit and more fruit in general being eaten in N3. Table 4 lists the 10 most commonly eaten food items for each species in each compartment and gives the total number of items eaten. The top 10 items constitute between 43 and 55% of the total diet for the monkey species while for *P. troglodytes* they form 70.7% of the diet. In Table 5, preference calculations (Manly's alpha) are given for the same species as in Table 3. These two tables show good agreement, which gives support to the method used on the transects as a way of collecting data on diets over a larger area.

Colobines are usually considered to be folivores or seed eaters (Davies & Oates, 1994; Davies *et al.*, 1999), but in Budongo Forest fruit eating (including ripe, unripe, and seeds) could form over 50% of the diet, and averaged 25.6% in N15 (Figure 3) and 36.3% in N3 (Figure 6). In N3 the four most abundantly eaten food items by *C. guereza* were fruit (Table 4). Seeds formed about

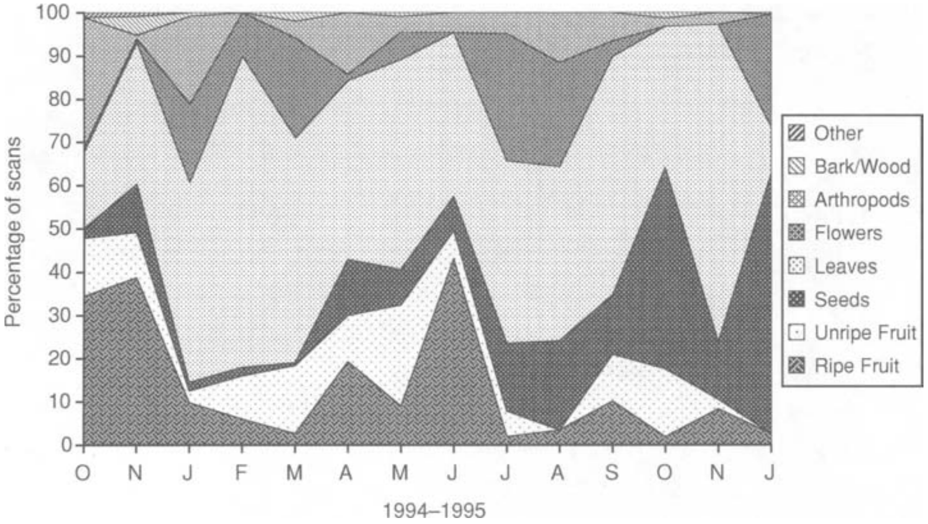

Figure 1. The diets of the *Cercopithecus ascanius* groups in compartment N15, unlogged. These diets are calculated from dawn-to-dusk follows of groups and averaged for the species.

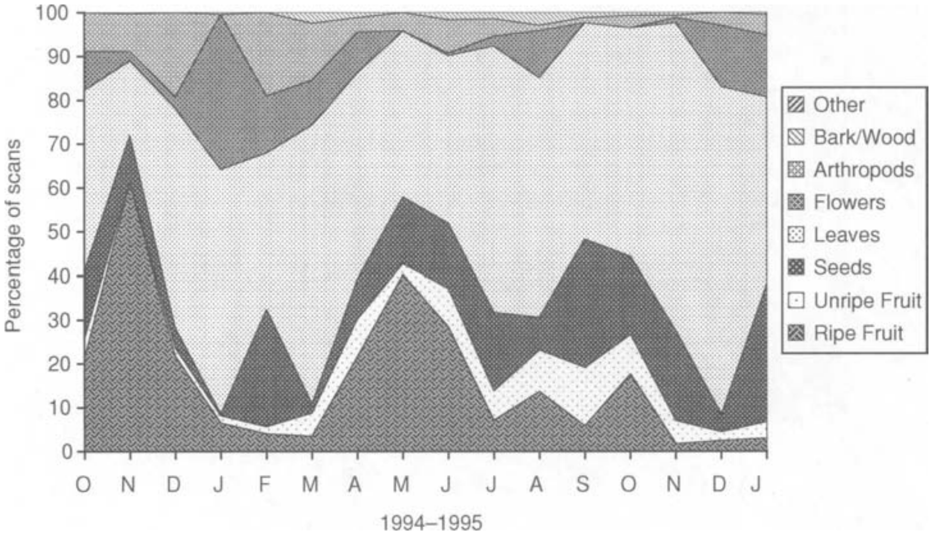

Figure 2. The diets of the *Cercopithecus mitis* groups in compartment N15, unlogged. These diets are calculated from dawn-to-dusk follows of groups and averaged for the species.

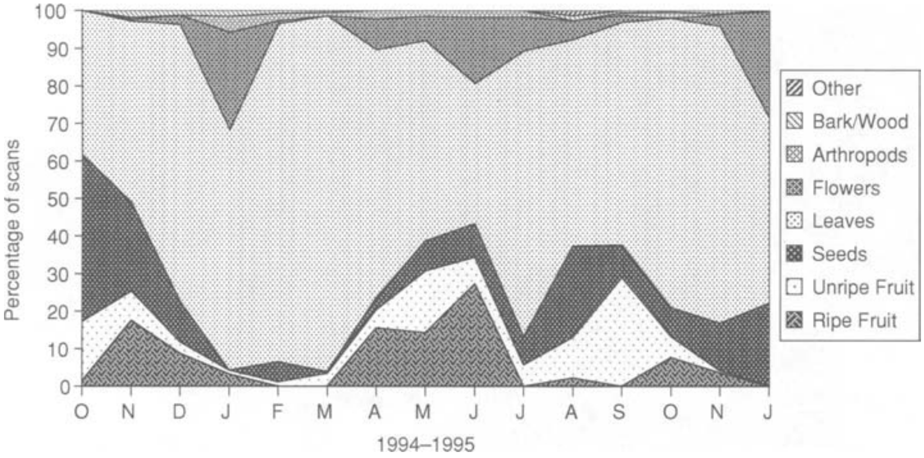

Figure 3. The diets of the *Colobus guereza* groups in compartment N15, unlogged. These diets are calculated from dawn-to-dusk follows of groups and averaged for the species.

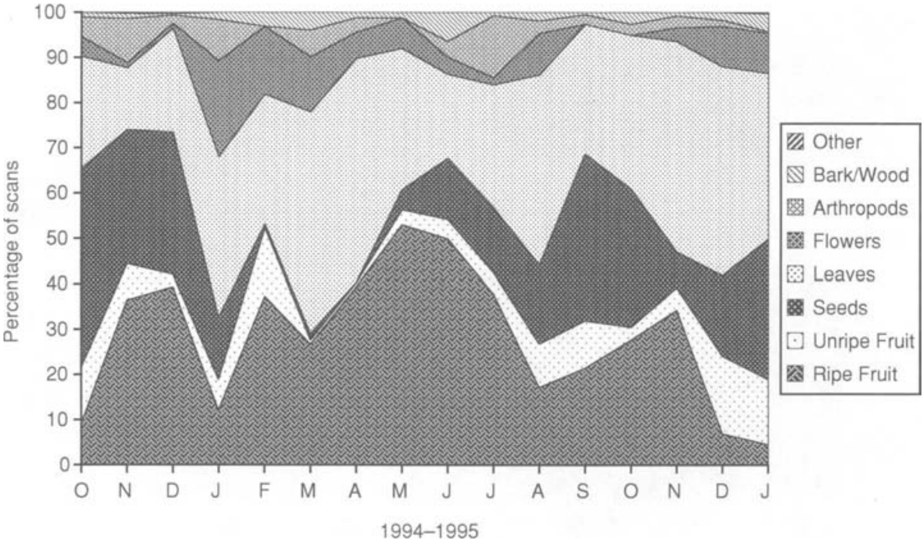

Figure 4. The diets of the *Cercopithecus ascanius* groups in compartment N3, logged. These diets are calculated from dawn-to-dusk follows of groups and averaged for the species.

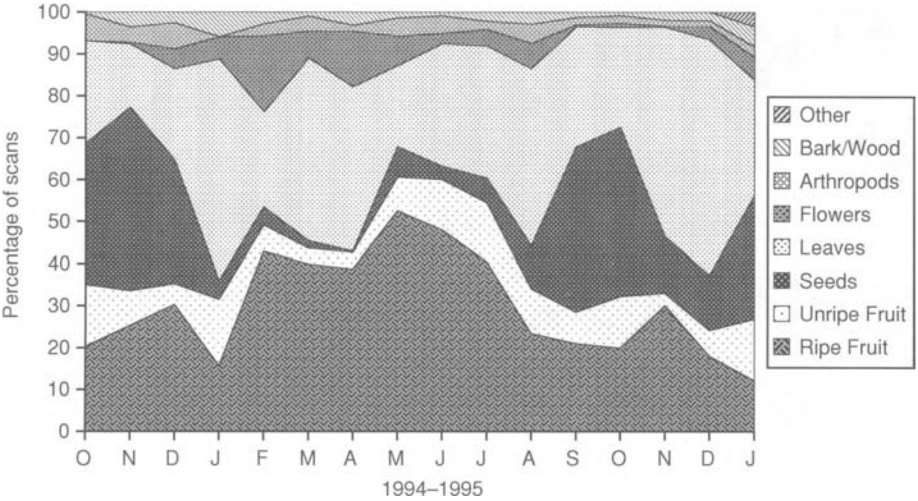

Figure 5. The diets of the *Cercopithecus mitis* groups in compartment N3, logged. These diets are calculated from dawn-to-dusk follows of groups and averaged for the species.

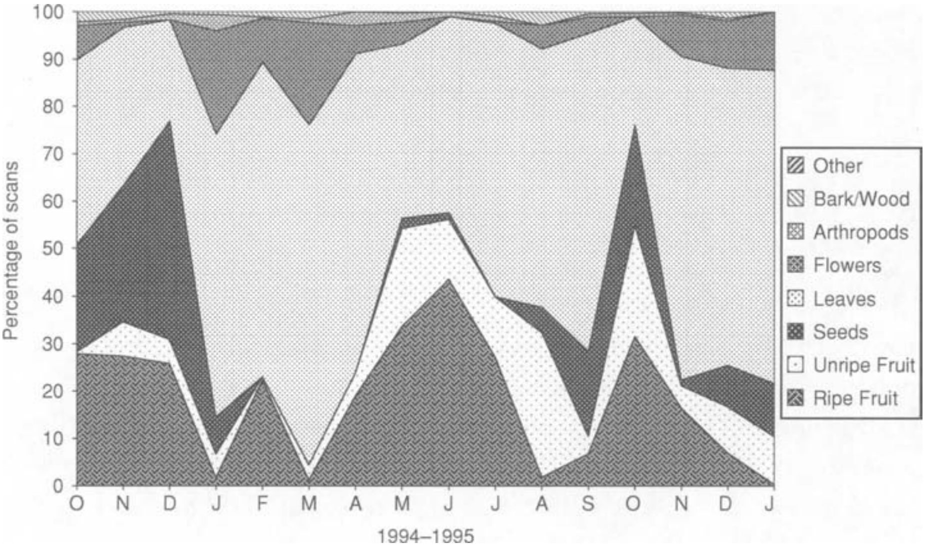

Figure 6. The diets of the *Colobus guereza* groups in compartment N3, logged. These diets are calculated from dawn-to-dusk follows of groups and averaged for the species.

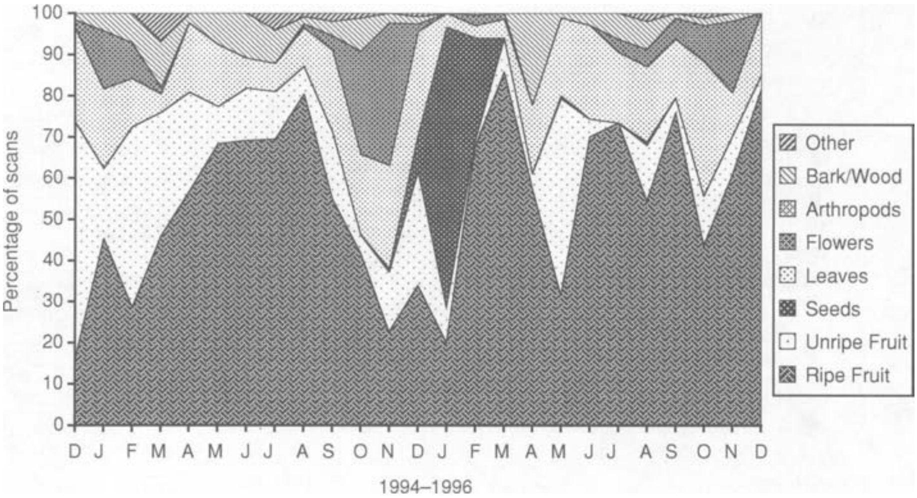

Figure 7. The diets of *Pan troglodytes* compartment N3, logged. A mean diet was calculated across the individuals followed.

30–50% of this fruit consumption (9.3% of the diet in N3 and 12.0% in N15). *Celtis durandii* is preferred by this primate for both fruit and leaves throughout Budongo (Tables 3 and 4) and forms a large percentage of its diet (31.4% in N3 and 14.6% in N15). This tree is abundant across Budongo and is in the top 10 trees by basal area for half of the compartments measured.

Dietary Overlap

Overlap Between the Same Species in Different Compartments

The overlap between diets of the same species in different compartments would have been low if based on species eaten because the tree species vary greatly between compartments. Consequently, overlap was calculated using the percentage intake of plant parts (buds, young leaves, mature leaves, ripe and unripe fruit, flowers, arthropods, and "other" [a category for minor dietary items such as fungi, resin, etc.]). The results showed that overlap was significantly higher than would be expected if these primates ate these plant parts at random for 78% of the 63 comparisons. All overlap values exceeded 89%, and 56 of the 63 comparisons were 95% or higher. Consequently the selection of plant parts was important for the diets of these monkeys. The compartments where overlap was lowest and not significantly different from random for *C. mitis* and *C. ascanius* (K4 and N15) are where these species were at lowest density. However, this

Table 4. The top 10 dietary items for each of the monkey species in N15 and N3 and for chimpanzees in N3

		N3				N15		
Species		*C. mitis*	*C. ascanius*	*C. guereza*	*P. troglodytes*	*C. mitis*	*C. ascanius*	*C. guereza*
Scans	Part[a]	6,807	6,004	4,910	4,318	4,394	2,063	3,872
Maesopsis eminii	Rf	8.9	9.0	7.4	7.6	6.3	4.3	3.5
Celtis durandii	Rf	7.2	8.4	10.7	5.4	3.0	3.6	
Croton macrostachys	Rf	5.8	4.9					
Ficus sur	Rf	3.5	3.2		14.8			
Broussonetia sp.	Rf	3.7			9.1			
Ficus exasperata	Rf	2.6						
Celtis zenkeri	Rf					4.8		
Cynometra alexandri	Sd				4.2		6.0	
Celtis durandii	Ur	3.1	2.8	7.7			3.4	3.2
Celtis mildbraedii	Ur		2.7					
Bosqueia phoberos	Ur			7.4				
Ficus sur	Ur				7.6			
Alstonia boonei	Fl			2.6			3.5	3.7
Broussonetia sp.	Fl				4.8			
Celtis zenkeri	Yl		3.1			3.3	4.2	
Ficus sur	Yl		2.9					
Cynometra alexandri	Yl	2.7				11.1	7.7	6.4
Broussonetia sp.	Yl				8.9			
Celtis durandii	Yl			7.0				6.4
Alstonia boonei	Yl			3.7		3.4		7.8
Celtis mildbraedii	Yl				4.2	3.7	3.7	4.0
Celtis mildbraedii	Ml	3.0	2.6	4.0		4.6	6.2	7.3
Celtis durandii	Ml			6.0				5.0

(*Cont.*)

Table 4. *(Continued)*

		N3				N15		
Species		*C. mitis*	*C. ascanius*	*C. guereza*	*P. troglodytes*	*C. mitis*	*C. ascanius*	*C. guereza*
Scans	Part[a]	6,807	6,004	4,910	4,318	4,394	2,063	3,872
Alstonia boonei	Ml			3.0				4.5
Cynometra alexandri	Ml					4.0		
Arthropods		2.9	3.8			5.8	6.5	
Khaya anthotheca	Bk				4.2			
1st 10 items (%)		43.4	43.4	59.5	70.8	50.0	49.1	51.8
No. items >1% of diet		33	33	27	19	22	23	30
Total number of items		152	128	112	98	152	116	111
Species of tree		58	49	47	62	63	48	48

The percentage of scans in which the species and part were observed being eaten are given for these 10 dietary items. Data were collected in dawn-to-dusk follows.

[a] Plant parts: rf = ripe fruit; ur = unripe fruit; fl = flower; yl = young leaf; ml = mature leaf, sd = seed, bk = bark.

Table 5. Manly's alpha preference values calculated for the same tree species as in Table 3 with a few others preferred by chimpanzees for the dawn-to-dusk follows data

		N3				N15		
Species	Part	*C. mitis*	*C. ascanius*	*C. guereza*	*P. trogodytes*	*C. mitis*	*C. ascanius*	*C. guereza*
Aningeria altissima	F							
Albizia spp.	L	+	+	+		+	+	+
Bosqueia phoberos	F	+	+	+				+
Broussonetia papyrifera	F	+	+	+	+			
	L	+	+	+	+			
Chrysophylum albidum	F							
	L	+					+	
Celtis durandii	F	+	+	+	+	+	+	+
	L		+	+		+	+	+
Celtis zenkeri	F	+	+			+	+	+
	L	+	+			+	+	+
Cleistopholis	F					+	+	
Cynometra alexandri	F				+		+	
	L	+	+	+		+	+	+
Erythrophleum suaveolens	F	+		+		+		+
	L	+	+	+		+	+	+
Ficus exasperata	F	+	+	+	+			
Ficus sur	F	+	+	+	+			
Ficus mucuso	F				+			
Funtumia elastica	F						+	
Holoptelea grandis	L	+	+	+		+	+	+
Maesopsis eminii	F	+	+	+	+	+	+	+
	L	+	+	+		+	+	+
Myrianthus holstii	F				+			

Part eaten is either fruit (F) or leaf (L); + = preference.

pattern did not hold for *C. guereza*, which had low overlap values in these compartments too but was at a relatively high density in K4.

Overlap Between Different Species in the Same Compartments

To compare diets between species in the same compartment, more detailed measures of the diets based on tree species and plant part were used (e.g., *Celtis durandii*, ripe fruit would differ from *C. durandii* flower) using transect scan data. Results showed that overlap between *C. mitis* and the other two species was always significantly higher than would be expected from neutral models (*C. mitis* vs. *C. ascanius*: 65–84% overlap; *C. mitis* vs. *C. guereza*: 43–66% overlap) but that overlap between *C. ascanius* and *C. guereza* (34–68% overlap) was only significantly higher about 50% of the time (in compartments K4, N3, and W21).

Overlap Between Adjacent Groups of the Same Species

The overlap in diet (plant parts of different tree species) between adjacent groups of the same species within a compartment were all higher than would be expected from random neutral models (*C. mitis*: 73–81% overlap; *C. ascanius*: 74–80%; *C. guereza*: 76–82%). This means that not only were similar tree species eaten but also similar parts of the species in similar proportions.

Overlap Between Species Whose Home Ranges Overlap Extensively

The dawn-to-dusk follows of the monkey groups allowed the calculation of home ranges of the various groups followed. Interestingly, in both N15 and N3, home range overlapped between species extensively, such that there was approximately one group of each of the three species for each region of the forest. For groups that occupied approximately the same home range, overlap was calculated on the basis of plant parts of each tree species (Plumptre *et al.*, 1997). Results show that all overlap values were significantly higher than expected (*C. mitis* vs. *C. ascanius*: 75–90%; *C. mitis* vs. *C. guereza*: 70–73%; *C. ascanius* vs. *C. guereza*: 69–76%). It is interesting to note that overlap between *C. mitis* and *C. ascanius* in compartment N3 was higher than values between the same species in adjacent groups.

Table 6. Dietary overlap (Horn's Index) based on detailed follows of primate groups but averaged for compartments N3 and N15

Species pairs	N3	N15
C. mitis vs. *C. ascanius*	**0.94**	**0.87**
C. mitis vs. *C. guereza*	**0.78**	**0.80**
C. ascanius vs. *C. guereza*	**0.79**	**0.78**
C. mitis vs. *P. troglodytes*	**0.50**	
C. ascanius vs. *P. troglodytes*	**0.45**	
C. guereza vs. *P. troglodytes*	**0.35**	

Overlap is calculated on the percentage intake of plant parts of different tree species, as well as arthropods, and other items. Where a value is higher than expected from random Monte Carlo analyses, it is marked in bold.

Overlap Between Species for Average Diets in a Compartment

This measure of overlap is similar to the measure calculated above but is based on the dawn-to-dusk follows of the monkeys rather than opportunistic scans from walking transects. It also allows a calculation of dietary overlap between the monkey species and chimpanzees (Table 6). All species pairings were significantly higher than expected, indicating that, despite very different diets in the case of chimpanzees (low overlap values), there was still selection for similar plant species and parts where they both did consume the same items.

DISCUSSION

Diets of the Budongo Primates

This study investigated the primate diets in Budongo at two different scales; one a coarser scale overview of the diets of three monkeys in eight compartments of the forest and the other, a more detailed study of the diets in two of these compartments including the diet of *Pan troglodytes.* Diets measured at both scales were within the same ball-park values, but the scans of unhabituated monkeys were very variable, depending on which site was considered. The preferences for dietary items were similar at both scales for the three monkeys (Tables 3 and 5). It appears therefore that diets observed from transects of many different groups can provide a reasonable measure of the dietary preference over a larger area than can be obtained by observing habituated groups. However, the diets were not as accurate and tended to miss certain food items such as arthropods.

Table 7 shows the relative proportions of the diets of these monkeys in comparison with the same species at other sites. This table shows that *C. mitis* and *C. ascanius* during this study ate more seeds than in other sites although Fairgrieve (1995) did not find this in his study in 1992–1993. The seeds that were primarily eaten in Budongo are those of *Funtumia elastica* (unripe), *Croton macrostachys* (ripe), *Celtis durandii* (ripe), *Bosqueia phoberos* (ripe and unripe), *Maesopsis eminii* (unripe), and *C. alexandri* (ripe). *C. alexandri* was very seasonal and develops unripe fruits between November and December, which ripen in January, which is when the large seed intake for *P. troglodytes* occurs (Figure 7). *F. elastica*, however, fruited throughout most of the year, and the unripe pods were eaten for the immature seeds and their plumes. This species was not usually a preferred food item though and may act as a fall-back food when nothing else can be found. Ripe and unripe whole fruit of the other tree species were consumed as well as the seeds alone and when the seeds are eaten they are squeezed out of the fleshy pulp into the mouth and the pulp is dropped to the forest floor. For some species, such as *C. durandii*, it is possible that these monkeys were storing seeds in cheek pouches to spit out later, as has been closely observed in *C. ascanius* in Kibale forest (Lambert, 1999), and that some of the pulp was dropped as part of this process. This would have made it appear that the pulp was being rejected in favor of the seed when it was not in fact the case. This is why Table 7 lists seeds as a subset of the fruit diet. Arthropod intake seems to be lower in Budongo in comparison with Kibale and Kakamega for these two monkeys, but for *C. guereza* it is slightly higher. Fruit intake is lower in Budongo if seed intake is partitioned out for the two cercopithecines, but if seed intake is included then the fruit intake is more similar to other studies. Fruit intake for *C. guereza* in logged forest was higher but the two unlogged forest compartments in Kibale and Budongo were about the same.

Fruit Availability

Measures of fruit availability in tropical rainforests are fraught with problems. Most use observations of certain tree species and usually pick 5–20 individuals to monitor. Then the density of these trees is calculated and multiplied by the mean abundance of fruits on the monitored trees to obtain a measure of availability. Usually mature individuals are selected for monitoring so that there is no allowance for variation in fruiting with tree size. Plumptre (1995a)

Table 7. Percentage contribution of plant parts to the diets of these primates in several study sites in East Africa

	YL	ML^a	FL	FR^b	SD	Arth.	Other	Reference
C. mitis								
Budongo Forest								
N3 logged	22.4	10.8	4.9	56.0	16.5	2.9	3.0	This study
N3 logged	26.2	0.6	4.6	57.3	1.5	8.6	2.7	Fairgrieve, 1995
N15 unlogged	33.8	13.1	7.4	38.0	14.8	5.9	1.8	This study
N15 unlogged	32.4	0.4	6.2	50.8	5.9	9.7	0.5	Fairgrieve, 1995
Range of 8 comp.	13–29	2–13	3–6	33–40	1–5	0–1	1–5	This study
Kibale Forest	13.7	6.8	12.5	45.1	2.4	19.8	2.1	Struhsaker, 1978
Kibale logged	42.3^c		3.6	54.0	3.1	—	0.1	Wrangham *et al.*, 1998
Kibale unlogged	40.6^c		4.2	55.3	7.1	—	0.0	Wrangham *et al.*, 1998
Kakamega Forest	16.6	2.3	3.7	57.1	2.5	16.8	3.5	Cords, 1986
Zomba Plateau	32.6^c		10.2	51.9	—^{b}	0.8	2.9	Beeson *et al.*, 1996
C. ascanius								
Budongo Forest								
N3 logged	24.8	9.4	6.1	53.3	18.3	3.8	2.6	This study
N15 unlogged	28.3	12.4	10.4	38.7	17.6	7.5	2.7	This study
Range of 8 comp.	12–20	2–10	0–16	61–73	1–5	0–1	0–4	This study
Kibale Forest	11.4	4.5	15.3	43.7	0.1	24.7	0.4	Struhsaker, 1978
Kibale logged		38.52	0.6	60.9	3.7	—	0.0	Wrangham *et al.*, 1998
Kibale unlogged		37.52	2.3	60.1	6.2	—	0.1	Wrangham *et al.*, 1998
Kakamega Forest	6.8	0.4	2.0	61.7	0.4	25.1	4.0	Cords, 1986
Kakamega Forest	8.9	0.3	1.4	55.0	—	29.5	4.9	Gathua, 1999
C. guereza								
Budongo Forest								
N3 logged	33.1	19.8	7.7	36.3	9.3	1.0	2.1	This study
N15 unlogged	36.9	24.8	8.9	25.6	12.0	1.2	2.6	This study
Range of 8 comp.	19–36	9–22	1–8	36–70	1–10	0	0–9	This study

(*Cont.*)

Table 7. *Continue.*

	YL	ML[a]	FL	FR[b]	SD	Arth.	Other	Reference
Kibale Forest	60.0	12.3	2.1	13.2	0	0	12.4	Struhsaker, 1978
Kakamega Forest	23.7	29.1	0.5	38.6	1.2	0	8.1	Fashing, 1999
Ituri Forest	29.7	28.0	2.9	24.6	22.0	0	14.5	Bocian, 1997
P. troglodytes								
Budongo Forest								
Sonso (incl. N3)	19.7[c]		8.8	64.5	—	0.0	7.0	Newton-Fisher, 1999a,b,c
N3	15.0	0.1	6.4	73.4	4.2	0.0	5.1	This study
Kibale Forest	9.3[c]		0.6	78.6	0.1	—	11.5	Wrangham *et al.*, 1998

Kibale Forest is in Uganda and Kakamega Forest is in Kenya. Where seed intake is known it has been added as an additional column but it is also combined with the fruit intake percentage data to allow comparison. Therefore total percentages sum to 100% + seed contribution. YL = young leaves; ML = mature leaves; FL = flowers; FR = Fruit; SD = seeds; Arth. = arthropods.

[a] In some studies there were unclassified as well as classified leaves. In this Table the unclassified leaves are included with mature leaves.

[b] Fruit includes consumption of seeds. Beeson *et al.* (1996) did not separate seeds and fruit.

[c] Wrangham *et al.* (1998), Beeson *et al.* (1996), and Newton-Fisher (1999a,b,c) did not separate young and mature leaves.

showed that some trees fail to fruit until they reach quite large sizes, sometimes up to 60–70 cm DBH. This study of phenology was more representative in that all trees were monitored in 100 or more plots sited in each study area in a stratified random manner. However, there were still problems in that there was no real method of combining tree species to form one measure of availability unless the biomass of fruit had been measured during the phenology (and even this would assume that the quality of the fruits was equal). Phenology measures are also affected by the fact that you see a tree at a certain point in time. Monkeys can strip a tree of its fruit within a few days and if you measure the tree just before they do and just after, you will get very different results. Where primate density is high, consumption of fruits will be heavy, so that fruits will be removed from trees more quickly than where primate density is low. Consequently it is theoretically possible that in areas of high primate density, less food will be found on the trees when being measured for phenology. Measures of potential availability such as sum DBH values can be used as an alternative method, but this method does not allow you to investigate seasonal and annual changes. Consequently, for seasonal availability I preferred to use a simple measure of whether the tree fruited or not and the sum of the DBH values for the monthly analyses in N15 and N3 and a simple measure of sum DBH for potential availability in all the compartments.

Apart from *P. troglodytes*, none of the primate densities showed any correlation with overall measures of potential fruit availability (Table 2(a)), and yet the two cercopithecines did show strong correlations with fruit intake in the diet (Table 2(b)). This result may be due to the problems with measuring availability, as outlined above, or it may be a function of variation in fruit quality between sites and that it is probably not valid to combine different species into fruit types. When comparing the data from the dawn-to-dusk follows in N15 and N3, it is clear that in the logged compartment there was a higher production of fruit throughout the year using this measure of availability. The variation between fruiting in plots is also less, indicating that the fruit is more evenly distributed. These two compartments are close and have similar tree species compositions so that the variation due to different tree species is lessened. Consequently the differences in the densities of monkeys between these two compartments was probably related to this more abundant and more even food production.

The dietary overlap analyses showed significantly higher overlap values than would be expected from random neutral models for most of the comparisons made. It would be expected that competition would lead to niche differentiation and low dietary overlap values. The fact that the overlap is higher than would be expected indicates how important the relative intake of plant species and their parts (and hence nutrient values) is for these primates. There is little indication therefore that competition is important in determining primate densities in these compartments at this scale of analysis, although for the two cercopithecines there may be increased competition for food where they occur at low density where overlap values become lower. It is possible that what is more important to these primates is whether competition is fierce during certain seasons when good food is scarce, and it is possible that dietary overlap during these "lean" times may drop. The data I have for each month though is probably not sufficient to validly calculate overlap because the sample sizes are low (only 2 days of observations per group).

Effects of Logging on Diets

Colobus monkey density was significantly correlated with the density and basal area of *C. durandii*, a species of tree whose leaves and fruits are preferred food items in every compartment studied for this primate (Table 3). This tree species also forms the greatest percentage contribution to the diet of this monkey (32.7% of colobus diets in N3, 17.3% in N15). *C. durandii* is not as good for timber as the other *Celtis* species (R. Plumptre, personal communication) and is unlikely to be harvested heavily even if the Uganda Forest Department promotes the use of more tree species for timber production. Consequently colobus are not likely to be at great risk from timber harvesting unless this tree species is targeted for removal in order to increase the stocking density of more desirable species. *C. durandii* was treated with arboricide during the 1950s and 1960s but has recolonised or regenerated in treated areas. In 1953 an experimental plot (RP100) was established in compartment N2 of Budongo to investigate the effects of different treatment programs on regeneration. Five replicates of four treatments and a control were established in a latin square design, each square of 100 × 100 m (only the central 60 × 60 m were measured to avoid edge effects). Rukundo (1996) remeasured the plot in 1994 and showed that where the treatments had occurred, *C. durandii* was more abundant (5–14% of trees) than in the untreated control plots (3% of trees). Consequently this tree seems to be a good colonizing species that can establish itself even where it has been selectively poisoned. This may explain why *C. guereza* often seems to survive in scrubby or isolated patches of forest throughout western Uganda where *C. durandii* also often occurs.

The two cercopithecines showed a strong correlation between fleshy fruit intake and density and are consequently likely to be affected by some aspect of food availability. To fully confirm this, populations need to be monitored over time to see how they fluctuate and to confirm that density has not been affected by some other factor such as a disease in some compartments. However, the preference analyses for these two species showed that fleshy fruits were often preferred dietary items, and the diet measures showed that they spent about 50% of their time feeding on these. Consequently, it is likely that food availability will be of some importance for determining densities of primate populations and that if logging affects this in one way or another then the primate populations will change. However, given the high dietary overlap values it is unlikely that food supply is limiting the primate populations except possibly where they are occurring at low densities. In Budongo, the removal of the monodominant *Cynometra* forest led to an increased diversity of tree species (Plumptre, 1996), and a consequent increase in the number of trees bearing fleshy fruits, particularly *C. durandii.* Consequently cercopithecine populations are higher in the logged and treated areas (Plumptre & Reynolds, 1994). The dawn-to-dusk follows in N3 and N15 showed that in the unlogged compartment N15, fruit intake was low for *C. mitis*, *C. ascanius*, and *C. guereza*. The values were lower than studies at most other sites, indicating that N15 is probably a suboptimal habitat for these species, which would explain why they occur here at low densities.

P. troglodytes nest density correlated with the density of trees bearing large fleshy fruits. Large fleshy fruits formed 22.85% of the diet of the Sonso community, a much larger contribution than for the monkey species, and consequently this correlation makes sense. Of particular importance were *Chrysophyllum* species, *Uvariopsis congensis*, *Ficus mucuso*, *Ficus sansibarica* and *Ficus saussureana.* The latter three fig species and the *Uvariopsis* are not considered to be valuable timber species, but the *Chrysophyllum* trees are. In a separate study of chimpanzee diet in the Sonso community Newton-Fisher (1999a,b,c) found that four timber species were among the top seven species in the chimpanzees' diet, although two (*Celtis* species) are not valuable woods and not in high demand: *Khaya anthotheca*, *Maesopsis eminii*, *Celtis mildbraedii*, and *C. durandii.* Chimpanzees also were observed to consume significant amounts of dietary parts of three of these timber species in this study (Table 4).

Following this research the Budongo Forest Project has recommended to the Uganda Forest Department that some large *Chrysophyllum* trees are left in each logging concession to support the chimpanzee populations and also to provide seed for a future crop. Arboricide treatment of the forest in the past did target fig trees, because many species strangle other trees, and this will have had an effect on fig supply; however, fig trees seem to be able to recover quickly and are now more abundant in logged forest than unlogged forest (Earl, 1992). At present, a greater threat to chimpanzees in Budongo is probably the presence of large numbers of people in pit-sawing concessions. During 1996, numbers exceeding 100 men or more were common in and around two pit-sawing concessions. Most of these people were carrying out planks of timber to the loading bays. Human disturbance may cause chimpanzees to leave an area because of disturbance and noise rather than problems with food availability. If the disturbance is over a large area, it may lead to conflicts between neighboring chimpanzee communities, which can lead to the elimination of a chimpanzee community (Goodall, 1986). Pit-sawyers also set snares to catch duikers and bushpigs for meat and chimpanzees are accidentally trapped in these. At present, 25% of identified chimpanzees in Budongo forest have injuries to their limbs from snares, indicating that this may be a more significant determinant for this species rather than food availability (Plumptre *et al.*, 2003; see Reynolds, Chapter 22, this volume).

CONCLUSIONS

The forest management in Budongo over the past 60 years has reduced the dominance of *C. alexandri* and encouraged a more diverse and mixed forest. This has led to a greater density of trees bearing fleshy fruits, particularly *C. durandii*, which forms an important component of the diet for all the primates. Food availability is probably not the only factor determining primate densities in this forest though, as there is little indication that there is competition for food. It is possible that at the low density sites, food is a determining factor but that at high density sites social factors between primate groups may determine densities rather than food supply. Much of the change in the forest can be attributed to the arboricide treatment rather than the logging because it was not the logging that reduced the monodominance in the forest. In Uganda there has been little hunting of primates for meat because most Ugandans will not eat primate meat. More recently, with movements of people between the

Democratic Republic of Congo and Uganda, there are now some people who will hunt primates for meat; however, the level of hunting is still very low in comparison with Central Africa. Care must therefore be taken when extrapolating from these results to other logging sites in Africa. In Central and West Africa, the building of roads by logging companies opens up the forest and encourages hunters to penetrate deeper into the forest. Hunting, rather than the logging practices themselves, exacts a major toll on the wildlife, including primates, in these regions.

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