Chapter 5

Ecology of forest elephants.

A seventeenth-century artist's impression of elephants laying waste a forest.
From Ludolphus (1681)

introduction.

The elephant *(Loxodonta africana* Blumenbach 1797) is Africa's largest mammal, but current knowledge of it's natural history is biased. Excellent long-term studies have been undertaken, but all in savanna dominated habitats of eastern and southern Africa, where good visibility facilitates uninterrupted observation. Elephants living in forests are difficult to study because both access and visibility are limited, and the work undertaken to date is confined to population surveys and basic dietary information (Alexandre, 1977; Barnes *et al,* 1991; Chapman et al., in press[b]; Dudley et al., 1992; Fay, 1991; Laws et al, 1975; Lieberman et al., 1987; Martin, 1991; Merz, 1981, 1986a, 1986b, 1986c; Roth, Merz & Steinhauer, 1984; Short, 1981, 1983; Wing & Euss, 1970).

The social organisation of African elephants has been studied in detail in savanna areas (e.g., Euss, 1961; Douglas-Hamilton, 1972; Laws & Parker, 1968; Laws ai al., 1975; Moss, 1988; Moss & Poole, 1983). The social organisation of savanna elephants studied in East Africa is based around the 'family unit', consisting of one or more related adult females and their offspring (Buss 1961; Douglas-Hamilton, 1972; Laws and Parker, 1968; Moss 1988; Moss & Poole, 1983). Family units are stable, but aggregate to form 'kin' or bond groups, clans, subpopulations and populations (Douglas-Hamilton, 1972; Moss 1988; Moss & Poole, 1983). Laws et a?(1975) demonstrated that although the mother-offspring unit (average size = 2.75 individuals) is the fundamental unit within elephant populations, elephant group size frequency distribut-ions are polymodal in nature and suggest the basic social unit is a group of 5-6, consisting of 2-3 adult females and their offspring. In Amboseli National Park, Kenya, family units averaged 9.4 individuals (range 2-29) typically with 2-3 adult fernales (range 1-9) (Moss, 1988; Moss and Poole, 1983). Olivier (1978) gave a figure of 5-6 for the family unit of the Asian elephant, Elephasmaximus, in rain forest in Malaya. There is one published account of group structure in forest elephants (Merz, 1986c), based on 37 group counts, which suggested that average group size was smaller than for savanna elephants.

The diet of elephants in eastern and southern Africa is well documented (e.g., Barnes,1982; Buss, 1961; Field, 1971; Field & Ross, 1976; Guy, 1976; Laws & Parker, 1963; Napier Bax & Sheldrick, 1963; Williamson,1975; Wing & Euss, 1970: see Owen-Smith, 1988, for a review). It is dominated by grasses, especially in open grassland areas, where they often form 60% or more of the bulk throughout the year. In wooded savannas grass is generally equally important in the wet season, but browse from woody plants tends to provide the bulk of the diet in the dry season. Fruits are eaten when available.

Olivier (1978) listed 290 species of food plant for Asian elephants, with a further 100 that could not be identified. The majority were trees, but the bulk of the diet was made up of palms and grasses which are low quality foods with low levels of secondary compounds. He suggested that small quantities of leaves from trees, which are of better quality but which contain high levels of toxic secondary compounds, were eaten in order to obtain certain essential nutrients and amino acids. Data on the diet of forest elephants, Loxodonta africana cyclotis Matschie 1900, are available for two sites in West Africa (Lieberman et al, 1987; Short, 1981: Bia National Park, Ghana and Alexandre, 1977; Merz, 1981: Tai National Park, Ivory Coast), and suggest that fruit is an important component of the diet, along with bark and foliage. No data have been published for elephants in the forests of Central Africa.

Elephants play an important role in African rain forests, influencing their structure and composition (Jones, 1955; Kortlandt, 1984; Laws, 1970; Martin, 1991; Western, 1989; Wing & Buss, 1970), and are important, and sometimes the only, seed dispersers for some species of plant, (Alexandre 1978; Chapman et al., in press[b]). In Sierra Leone, elephants are held in high esteem by the Mendeh tribe (Richards, unpublished manuscript): These rice farmers used to be restricted in their abilities to clear large forest trees, so when they first entered the forest they exploited natural gaps and clearings, especially grassy swamp basins. According to local tradition, such areas were opened up for farming by elephants, which thinned the forest, letting in light, puddled the swampy soils and encouraged the growth of grassy plants. They then sowed undigested rice seeds, carried in their digestive systems from far away villages. By dispersing rice seeds over long distances, the elephants would sometimes introduce new types (strains) of rice, and in times of famine "elephant dung" rice was collected for food. Hence, by their ecological role, they undertook the hard work of establishing farms, and in times of hunger they fed the Mendeh. In some forests in Central Africa elephants account for 50-80% or more of the mammalian biomass (Prins & Reitsma, 1989; Chapter 6). Therefore, elephants are an integral component of African forests as we find them today.

Seasonal migration in response to food availability is a widely accepted feature of the biology of elephants living in savanna areas (e.g., Bosman & Hall-Martin, 1986; Caughly & Goddard, 1975; Laws et al, 1975; Leuthold, 1976; Moss, 1988; Sikes, 1971; Western & Lindsay, 1984), and once enabled them to utilise almost all available habitat types in the region to some degree (Bosman & Hall-Martin, 1986; Sikes, 1971). These migrations are not well documented in the scientific literature, since humans have disrupted the movements of elephants in recent times and many populations are now confined to limited protected areas and are no longer able to migrate (Douglas-Hamilton, 1987; Sikes, 1966,1971;

Western & Lindsay, 1934). Early reports told of large gatherings of elephants at certain times of year in preparation for large scale movements (Barker, 1866; Bell, 1923; Rushby 1953, 1965) and these migrations are sometimes a part of local folklore, since pasturalists such as the Maasai in Amboseli, Kenya, used to follow the same routes (Moss, 1938; Western & Lindsay, 1984). Some populations are believed once to have migrated annually over up to about 650 km (Sikes, 1971, p. 245), although distance travelled was generally less than this (e.g., Western & Lindsay, 1984). Such migrations allowed elephants to make temporary use of habitats which would not have supported a resident population, but exhibit ephemeral peaks in productivity, such as the Kaokoveld in Namibia, where rains stimulate the growth of short-lived grasses, briefly changing desert to a habitat for herbivores (Bosman & Hall-Martin, 1986). Migrations of other East African savanna species, particularly ungulates, have been well documented (e.g., Pennycuik, 1975). Short (1983) reported seasonal movements of forest elephants in response to fruiting patterns in Bia National Park, Ghana, and other authors have noted movements within forest or between forest and savanna (e.g., Buechner **et al.,** 1963; Wing & Euss, 1970).

The numbers of elephants living in African forests now exceeds those found in savannas (IUCN, 1989). Over the last decade populations in many savanna regions have been fragmented by loss of habitat, and in some cases decimated by poaching (see Poole and Thomsen, 1989). When elephants have been concentrated into protected areas of limited size, such as National Parks, unnaturally high population densities have resulted in severe damage to the environment (e.g., Buechner & Dawkins, 1961; Laws, 1970; Laws et al, 1975).

In West Africa deforestation has greatly reduced the forested area (e.g., Barnes 1990; FAO, 1981). Most of the remaining forest is located in relatively small Forest Reserves, surrounded by densely populated rural areas where elephants have been hunted out (e.g.,: Douglas-Hamilton, 1987; Merz, 1986; Roth et ***al.,*** 1981). Where elephants survive they are usually isolated in small populations. Even in the extensive forests of Central Africa there is evidence that hunting is exterminating elephants in some areas, again fragmenting and isolating populations (Alers *et* **al.,** 1990).

The fragmentation of a once continuous population into many genetic isolates has serious implications for the conservation of elephants (Poole and Thomson, 1989) and the elimination of elephants from tropical forest would affect both the structure and species composition of the forest. Data un the biology of elephants and the roles they play in forest ecosystems are required to formulate effective conservation strategies. These are essential to ensure the long-term survival of elephants, and to assess the consequences of their disappearance for the structure and composition of forests. It has been suggested that if Africa's rain forest ecosystems are to be protected then Africa's forest elephants must receive active protection (Prins & Reitsma, 1989).

This Chapter describes the diet, group structure, seasonal movements and ecological role played by elephants in Lopé. Elephants were observed at SEGC on an opportunistic basis, between 1984-1991 by researchers working on apes. Elephants were almost all (99%) of the forest form (Plate 5.1), ***Loxodonta africana* cyclotis** Matschie and densities averaged over 2 km^{-2} (Chapter 6). In addition, I undertook a more intensive study of elephant feeding ecology from June 1990-May 1991.

Methods.

During an on-going study of gorillas and chimpanzees at SEGC from February 1984, all observations of elephants in the study area, which covers **40** km^2 of Marantaceae Forest (see Chapter 2), were recorded. Whenever possible, the number of individuals seen and their age classes (assessed subjectively according to size as adult, sub-adult, juvenile, infant) were noted. If observation conditions precluded this, the minimum group size (i.e., the number of individuals detected by sight or sound) was estimated. In addition, distinctive characteristics to enable individual recognition (e.g., torn ears), activity, foods consumed, and any notable behaviour were recorded. Feeding sign that could be attributed with certainty to elephants (either directly by sight, sound, or smell, or indirectly by association with footprints or dung) was inspected as and when it was encountered and the species and part(s) consumed noted. M. Fernandez (unpublished data) recorded the size of all elephant groups encountered during 732 return trips made by car on a dirt track between SEGC and Lope Village, a distance of 12 km through savanna and savanna-forest mosaic, between October 1985 and June 1987. These data are presented for comparison with forest observations.

A more intensive investigation of fresh sign along feeding trails was undertaken between June 1990-May 1991. Unknown plant species were collected

Plate 5.1.

A forest elephant, *Loxodonta africana cyclotis*, characterised by general smaller size (here about 2.25m) rounded ears, thin, down-pointing tusks, and the highest part of the body above the hind legs.

A famliy unit feeding in a saline.

and pressed, and where possible were identified later at herbaria in Libreville, Gabon and Missouri Botanical Garden. Voucher specimens are lodged with both these institutions. Additional data on foods were collected by searching through all undisturbed dung piles that were encountered in the forest and judged to be less than three days old, for identifiable remains. Seeds above about 1 cm diameter were counted. The abundances of fibre, green leaf fragments, small seeds and other remains were quantified on a four-point scale of relative abundance: rare, few, common abundant (after Tutin and Fernandez, 1985).

Fruit availability was monitored between June 1990-May 1991 by counting the number of fresh ripe and unripe fallen fruits on a strip one metre wide along transects once a month (see Chapter 3). All trees and lianes in botanical transects (Chapter 2) were checked for signs of bark feeding by elephants, to obtain an idea of which species were most important in the diet. Trees below 10cm dbh were rarely barked.

Wonparametric statistics (Siegel & Castellan, 1988) were used to investigate correlations between fruit availability and its occurrence in the diet, and to test for deviations from the expected frequency of bark feeding on trees of different girth classes.

Results

6roup Composition

Between February 1984 and December 1990, elephants were encountered 645 times in the forest. On 383 occasions complete group counts were obtained. Table 5.1 shows that the average group size for the 383 complete counts was 1.8 individuals and the minimum estimated group size, when observation conditions did not permit complete counts, was 2.5 individuals. Complete group counts were possible whenever elephants were encountered feeding at salines in the forest (Plate 5.1) or were observed in savannas. The 37 groups observed at salines had an average group size of 2.6 and the average size of the 86 groups sighted in the savanna was 2.8.

Of 572 elephants seen in the 645 forest encounters, 395 were adults or sub-adults, 121 were juveniles and 56 were infants. The age-classes of 94 individuals seen in 37 groups at salines were: 59 adults and sub-adults, 23 juveniles, 11 infants, and one undetermined. **Age** classes were not noted systematically on groups seen in the savanna. Table 5.2 shows the group compositions observed at salines: lone males, and adult females accompanied **by** one or two offspring, accounted for almost 60% of observations.

The presence of a few individually recognisable elephants enabled us to monitor movements to a limited extent, but such individuals were rarely sighted more than once. One group of three, a female with a juvenile and infant, were seen repeatedly over a period of 19 months from March 1989, but have not been seen since October 1990. Other such family groups, as well as solitary animals, have appeared to be resident in the SEGC study area for shorter periods.

Table 5.1: Group size in forest, savanna and at salines.

No. in Group	**Forest** Complete Counts	**Forest** Minimum Counts	**Salines**	**Savanna**
1	207	207	12	26
2	90	90	8	20
2 - 3		97		
3	51	51	7	17
3 - 4		108		
4	20	20	8	13
4 - 5		38		
5	6	6	1	3
5 - 6		15		
6	6	6	1	2
6 - 7		0		
7	3	3	1	2
7 - 8		3		
8				1
8 - 9				
9				0
9 - 10				
10				2
Total Encounters	383	645	38	86
Av. group size	1.8	2.5	2.6	2.8

Table 5.2: Group composition at Salines.

Number in Group	Composition	Frequency
1	Lone Adult	12
2	Two Adults	2
	1 Adult/1 juv or inf	6
3	2 Adults/1 u/k	1
	2 Adults/1 Juv or inf	2
	1 Adult/2 Juv or inf	4
4	3 Adults/1 juv or inf	2
	2 Adults/ 2 juv or inf	4
	1 Adult/2 sub-adults/1 juv	1
	1 Adult/3 juv or inf	1
5	3 Adults/2 juvs	1
6	5 Adults/1 juv	1
7	5 Adults/1 Juv/1 Inf	1

Diet and ecological role in the forest.

Elephants at Lopé ate 304 parts of 230 plant species from at least 52 taxonomic families, as well as one species of fungus, and soil. Table 5.3 lists all species and parts eaten. Leaves and twigs, bark, and fruit represented 92.8% of all items eaten (39.2%, 30.4% and 23.2% respectively). At least 73.5% (N=169) of food species were trees. Table 5.4 summarises the life-forms of the plants utilised, and the parts eaten.

Table 5.3: Elephant foods.

Species	Family	Life-Form[1]	Sign[2]	F	L	B	Ot
Monocotyledons							
Aframomum longipetiolatum	ZINGIBERACEAE	H	O/T/D	*	*		root
Aframomum sp. ?nov.	ZINGIBERACEAE	H	O/T/D	*	*		root
Aframomum ?leptolepis	ZINGIBERACEAE	H	O/T		*		root
Anchomanes difformis	ARACEAE	H	T		*		
Ataenidia conferta	MARANTACEAE	H	O/T		*		root
Costus afer	ZINGIBERACEAE	H	T		*		
Costus gabonensis	ZINGIBERACEAE	H	T		*		
* **Eulophia* sp.	ORCHIDACEAE	H	O				flower
Halopegia azurea	MARANTACEAE	H	O/T		*		root
Haumania liebrechtsiana	MARANTACEAE	H	O/T		*		root
Hypselodelphys poggeana	MARANTACEAE	H	T		*		root
Hypselodelphys violacea	MARANTACEAE	H	O/T		*		root
Marantochloa cordifolia	MARANTACEAE	H	O/T		*		root
Marantochloa filipes	MARANTACEAE	H	O/T		*		root
Marantochloa purpurea	MARANTACEAE	H	O/T		*		root
Megaphrynium gabonense	MARANTACEAE	H	O/T/D	*	*		root
Megaphrynium macrostachyum	MARANTACEAE	H	O/T/D	*	*		root
Palisota ambigua	COMMELINACEAE	H	T		*		
Renealmia cincinnata	ZINGIBERACEAE	H	O/T		*		root
Renealmia macrocolea	ZINGIBERACEAE	H	O/T		*		root
**SEGC 420	GRAMINAE	H	O		*		
**LJTW 0384	GRAMINAE	H	T		*		
**LJTW 0387	GRAMINAE	H	T		*		
**LJTW 0388	GRAMINAE	H	T		*		
LJTW 0463	GRAMINAE	H	T		*		

Table 5.3: Elephant foods / continued.

Species	Family	Life-Form[1]	Sign[2]	F	L	B	Ot
DICOTYLEDONS							
Afzelia sp.	CAESALPINIACEAE	Tr	S			*	
Allanblackia sp.	GUTTIFERAE	Tr	S			*	
Allophylus ?oyemensis	SAPINDACEAE	Tr	T		*		
Angylocalyx sp. LJTW 0191	PAPILIONACEAE	Tr	T		*		
Anthocleista sp. 1	LOGANIACEAE	Tr	T		*		
Anthocleista sp 2.	LOGANIACEAE	Tr	T		*		wood
Amphimas ferrugineus	CAESALPINIACEAE	Tr	S			*	
Anisotes macrophyllus	ACANTHACEAE	H	T		*		
Antidesma laciniatum	EUPHORBIACEAE	Tr	T		*		
Antidesma vogelianum	EUPHORBIACEAE	Tr	O/T/D	*	*		
Antrocaryon klaineanum	ANACARDIACEAE	Tr	S/D	*		*	
Aucoumea klaineana	BURSERACEAE	Tr	T		*		
Augouardia letestui	CAESALPINIACEAE	Tr	T		*		
Baillonella toxisperma	SAPOTACEAE	Tr	S/D	*		*	
Barteria fistulosa	PASSIFLORACEAE	Tr	T		*		
Campostyles mannii	FLACOURTIACEAE	Tr	T		*		
Canarium schweinfurthii	BURSERACEAE	Tr	D	*			
Ceiba pentandra	BOMBACACEAE	Tr	O/S			*	
Celtis tessmannii	ULMACEAE	Tr	S			*	
Centroplacus glaucinus	PANDACEAE	Tr	T		*		
Chlorophora excelsa	MORACEAE	Tr	S			*	
Cissus dinklagei	VITACEAE	L	T/S		*	*	
Cissus ruginosicarpa	VITACEAE	L	T		*		
Citrus sp.	RUTACEAE	Tr	D	*			
Cola lizae	STERCULIACEAE	Tr	O/T		*		root
Cola sp.	STERCULIACEAE	Tr	T		*		
Conceveiba africana	EUPHORBIACEAE	Tr	T		*		
Corynanthe mayumbensis	RUBIACEAE	Tr	T		*		

Table 5.3: Elephant foods / continued.

Species	Family	Life-Form[1]	Sign[2]	F	L	B	Ot
Coula edulis	OLACACEAE	Tr	O/D/S	*	*	*	
Croton sp.	EUPHORBIACEAE	Tr	T		*		
Crotonogyne argentea	EUPHORBIACEAE	Tr	T			*	
Crudia gabonensis	CAESALPINIACEAE	Tr	T		*		
Cryptosepalum staudtii	CAESALPINIACEAE	Tr	O/T		*	*	
Cylicodiscus gabunensis	MIMOSACEAE	Tr	S			*	
Dacryodes buettneri	BURSERACEAE	Tr	S		*	*	
Dacryodes normandii	BURSERACEAE	Tr	T/D	*	*		
Desbordesia glaucescens	IRVINGIACEAE	Tr	S			*	
Detarium macrocarpum	CAESALPINIACEAE	Tr	S/D	*		*	
Dialium sp. ?nov	CAESALPINIACEAE	Tr	T	*	*		
Dichapetalum sp. 1	DICHAPETALACEAE	L	T		*		
Dichapetalum sp. 2	DICHAPETALACEAE	Tr	T		*		
Diospyros abyssinica	EBENACEAE	Tr	D	*			
Diospyros dendo	EBENACEAE	Tr	O/D/T	*	*		
Diospyros polystemon	EBENACEAE	Tr	O/D/T	*			
Diospyros mannii	EBENACEAE	Tr	D/T	*			
Diospyros viridicans	EBENACEAE	Tr	T		*		
Diospyros zenkeri	EBENACEAE	Tr	D/T		*		
Distemonanthus bethamianus	CAESALPINIACEAE	Tr	O/S			*	
Duboscia macrocarpa	TILIACEAE	Tr	O/D/S/T	*	*	*	
Enantia chlorantha	ANNONACEAE	Tr	T			*	
Erismadelphus exsul	VOCHYSIACEAE	Tr	S			*	
Ficus cf. dicranostyla	MORACEAE	Tr	S			*	
Ficus mucuso	MORACEAE	E/Tr	O/T	*			
Ficus recurvata	MORACEAE	E/Tr	O/T	*		*	
Ficus thonningii	MORACEAE	E	T		*	*	
Fillaeopsis discophora	MIMOSACEAE	Tr	S			*	
Gambeya africana	SAPOTACEAE	Tr	D	*			
Gambeya subnuda	SAPOTACEAE	Tr	T/D	*		*	

Table 5.3: Elephant foods / continued.

Species	Family	Life-Form[1]	Sign[2]	F	L	B	Ot
Ganophyllum giganteum	SAPINDACEAE	Tr	S			*	
Garcinia afzelii	GUTTIFERAE	Tr	T		*		
Grewia coriacea	TILIACEAE	Tr	T		*		
Heinsia crinata	RUBIACEAE	Tr	T		*		
Heisteria parvifolia	OLACACEAE	Tr	O		*	*	
Hexalobus crispiflorus	ANNONACEAE	Tr	D	*			
Homalium letestui	FLACOURTIACEAE	Tr	S			*	
Hylodendron gabunense	CAESALPINIACEAE	Tr	O/S			*	
Hypodaphnis zenkeri	LAURACEAE	Tr	T		*		
Irvingia gabonensis	IRVINGIACEAE	Tr	O/D/S	*	*	*	
Irvingia grandiflora	IRVINGIACEAE	Tr	O/D/S	*		*	
Irvingia robur	IRVINGIACEAE	Tr	D/S	*		*	
Klainedoxa gabonensis	IRVINGIACEAE	Tr	D	*			
Klainedoxa trilesii	IRVINGIACEAE	Tr	D	*			
Landolphia cf. parvifolia	APOCYNACEAE	L	D	*			
Lecaniodiscus cupanioides	SAPINDACEAE	Tr	S			*	
Leptactina cf. arnoldiana	RUBIACEAE	Sh/Tr	T		*		
Leptoderris sp.	PAPILIONACEAE	Tr	T		*		
Letestua durissima	SAPOTACEAE	Tr	S			*	
Lingelsheimia sp.	EUPHORBIACEAE	Tr	T		*		root
Lophira alata	OCHNACEAE	Tr	T		*		
Lovoa trichilioides	MELIACEAE	Tr	S			*	
Macaranga monandra	EUPHORBIACEAE	Tr	T		*		
Macaranga barteri	EUPHORBIACEAE	Tr	T		*		
Mammea africana	GUTTIFERAE	Tr	O/S	*		*	
Mangifera indica	ANNONACEAE	Tr	S/D	*		*	
Mapraunea membranacea	EUPHORBIACEAE	Tr	T		*		
Marquesia excelsa	DIPTEROCARPACEAE	Tr	S			*	
Massularia acuminata	RUBIACEAE	Tr	T/D	*	*		
Memecylon diluviorum	MELASTOMATACEAE	Tr	T		*		

Table 5.3: Elephant foods / continued.

Species	Family	Life-Form[1]	Sign[2]	F	L	B	Ot
Milletia sarengana	PAPILIONACEAE	Tr	T		*		
Milletia sp.	PAPILIONACEAE	Tr	T		*		
Mitragyna ciliata	RUBIACEAE	Tr	T/S		*	*	
Monanthotaxis congensis	ANNONACEAE	Sh	D	*			
Monopetalanthus letestui	CAESALPINIACEAE	Tr	S			*	
Myrianthus arboreus	MORACEAE	Tr	O/D	*			
Napoleona imperialis	LECYTHIDACEAE	Tr	T		*		
Nauclea diderrichii	RUBIACEAE	Tr	D/S/T	*	*	*	
* **Nauclea latifolia*	RUBIACEAE	Tr	O	*	*		
Nauclea vanderguchtii	RUBIACEAE	Tr	D/S	*		*	
Newtonia leucocarpa	MIMOSACEAE	Tr	S			*	
Ochna sp.	OCHNACEAE	Sh/Tr	T		*		
Ochthocosmus congolensis	IXONANTHACEAE	Tr	T		*		
Omphalocarpum procerum	SAPOTACEAE	Tr	O/D/S	*		*	
Ongokea gore	OLACACEAE	Tr	O/D	*		*	
Panda oleosa	PANDACEAE	Tr	D/S/T	*	*	*	
Parinari excelsa	CHRYSOBALAN.	Tr	D	*			
Parkia bicolor	MIMOSACEAE	Tr	S/D	*		*	
Parkia filicoidea	MIMOSACEAE	Tr	S/D	*		*	
Pauridiantha callicarpoides	RUBIACEAE	Tr	T		*		
Pauridiantha efferata	RUBIACEAE	Tr	T		*		
Pauridiantha floribunda	RUBIACEAE	Tr	T		*		
Pausinystalia johimbe	RUBIACEAE	Tr	T		*		
Pavetta puberula	RUBIACEAE	Tr	O/T		*		
Pentaclethra eetveldeana	MIMOSACEAE	Tr	S/T		*	*	
Pentaclethra macrophylla	MIMOSACEAE	Tr	S			*	
Pentadesma butyracea	GUTTIFERAE	Tr	O/T/D/S1	*		*	
Pentadesma sp. ?nov	GUTTIFERAE	Tr	D	*		*	
Petersianthus macrocarpus	LECYTHIDACEAE	Tr	S			*	
* **Phyllanthus* sp.	EUPHORBIACEAE	H	T		*		

Table 5.3: Elephant foods / continued.

Species	**Family**	**Life-Form**[1]	**Sign**[2]	**F**	**L**	**B**	**Ot**
Picralima nitida	APOCYNACEAE	L	D	*			
Piptadeniastrum africanum	MIMOSACEAE	Tr	S			*	
Plagiostyles africana	EUPHORBIACEAE	Tr	S			*	
Poga oleosa	RHIZOPHORACEAE	Tr	D/S/T	*		*	
Polyalthia suaveolens gabonica	ANNONACEAE	Tr	T		*		
Pawia sp.	ANNONACEAE	L	D	*			
Pterocarpus soyauxii	PAPILIONACEAE	Tr	T				
Pseudospondias longifolia	ANACARDIACEAE	Tr	O	*			
Pseudospondias microcarpa	ANACARDIACEAE	Tr	O/D/S	*		*	
* **Psidium guineensis*	MYRTACEAE	Sh	O/D	*			root
Psorospermum tenuifolium	HYPERICACEAE	Tr	T		*		
Psychotria vogeliana	RUBIACEAE	Sh	T	*	*		
Ptychopetalum sp.	OLACACEAE	Tr	T		*		
Pycnanthus angolensis	MYRISTICACEAE	Tr	O			*	wood
Quassia africana	SIMOUBIACEAE	Sh	T		*		
Sacoglottis gabonensis	HUMIRIACEAE	Tr	O/T/D/S	*	*	*	
Santiria trimera	BURSERACEAE	Tr	T		*		
Scaphopetalum blackii	STERCULIACEAE	Tr	T		*		
Schefflera sp.	ARALACEAE	Tr	S			*	
Scorodophloeus zenkeri	CAESALPINIACEAE	Tr	S/T		*	*	
Scyphocephalium ochocoa	MYRISTICACEAE	Tr	S			*	
Scytopetalum klaineanum	SCYTOPETALACEAE	Tr	S			*	
Scytopetalum sp.	SCYTOPETALACEAE	Tr	S			*	
Sindoropsis le-testui	CAESALPINIACEAE	Tr	S			*	
Staudtia gabunensis	MYRISTICACEAE	Tr	O	*			
Sterculia tragacantha	STERCULIACEAE	Tr	S			*	
Strombosia pustulata	OLACACEAE	Tr	T		*		
Strombosiopsis sp. ?nov	OLACACEAE	Tr	T/S		*	*	
Strombosiopsis tetrandra	OLACACEAE	Tr	T/S		*	*	
Swartzia fistuloides	CAESALPINIACEAE	Tr	D	*			

Table 5.3: Elephant foods / continued.

Species	Family	Life-Form[1]	Sign[2]	F	L	B	Ot
Symphonia globulifera	GUTTIFERAE	Tr	S			*	
Syzygium sp.	MYRTACEAE	Tr	S			*	
Testulea gabonensis	LUXEMBURGIACEAE	Tr	T		*		
Tetrapleura tetraptera	MIMOSACEAE	Tr	S/D	*		*	
Thomandersia hensii	ACANTHACEAE	Tr	T		*	*	
Tieghemella africana	SAPOTACEAE	Tr	S/D	*		*	
Treculia obovoidea	MORACEAE	Tr	S			*	
Tricalysia anomala	RUBIACEAE	Tr	T		*		
? *Tricalysia* sp.	RUBIACEAE	Tr	T		*		
Trichilia cf. prieureana	MELIACEAE	Tr	T		*		
Trichoscypha acuminata	ANACARDIACEAE	Tr	T/D	*	*		
* * *Triumfetta cordifolia*	TILIACEAE	Sh	T/D	*	*		
Uapaca guineensis	EUPHORBIACEAE	Tr	O/D	*			
Uapaca heudelotii	EUPHORBIACEAE	Tr	O/D/S	*		*	
Uapaca aff. togoensis	EUPHORBIACEAE	Tr	O/D	*			
Uapaca vanhouttei	EUPHORBIACEAE	Tr	T	*			
Uvariastrum pierreanum	ANNONACEAE	Tr	D	*			
Xylopia aethiopica	ANNONACEAE	Tr	O/T		*	*	
Xylopia hypolampra	ANNONACEAE	Tr	T			*	
Xylopia quintasii	ANNONACEAE	Tr	T		*		
Xylopia staudtii	ANNONACEAE	Tr	T			*	
LJTW 0050	RUBIACEAE	Sh	T		*		
LJTW 0254	HYPERICACEAE	Tr	T		*		
**LJTW 0389	COMPOSITAE	H	T		*		
**LJTW 0390		V	T		*		
**LJTW 0391	MELASTOMATAC.	H	T		*		
LJTW 0481	MELASTOMATAC.	H	T		*		
LJTW 0484	RUBIACEAE	Tr	T		*		
LJTW 0486	RUBIACEAE	Tr	T		*		
LJTW 0585	EUPHORBIACEAE	Tr	T		*		

Table 5.3: Elephant foods / continued.

Species	Family	Life-Form[1]	Sign[2]	F	L	B	Ot
LJTW 0605		L	S				
LJTW 237	SAPOTACEAE	Tr	S			*	
LJTW 243	EUPHORBIACEAE	Tr	T		*		
LJTW 336	CAESALPINIACEAE	Tr	S			*	
LJTW 340		Tr	S/T			*	
LJTW 363	SAPOTACEAE	Tr	S			*	
LJTW 365	MIMOSACEAE	Tr	S			*	
LJTW 425	SAPOTACEAE	Tr	S			*	
LJTW 441	EUPHORBIACEAE	Tr	T		*		
LJTW 471	SAPOTACEAE	Tr	S			*	
LJTW 478		L	S			*	
LJTW 504		Tr	S			*	
LJTW 506		Tr	S			*	
LJTW 507		Tr	S			*	
LJTW 513		L	S			*	
LJTW 564	SAPOTACEAE	Tr	S			*	
LJTW 593	PAPILIONACEAE	L	S			*	
SEGC 412		L	T		*		
U/K Fungus		F	O				
U/K Seed 1		U/K	D	*			
U/K Seed 11		U/K	D	*			
U/K Seed 3	SAPOTACEAE	U/K	D	*			
U/K Seed 4		U/K	D	*			
U/K Seed 5		U/K	D	*			
U/K Seed 8		U/K	D	*			
U/K Seed 9		U/K	D	*			
Water liane	VITACEAE	L	S			*	

1- H = herb, Sh = shrub; Tr = tree; L = liane; E = epiphyte; U/K = unknown.
2 - O = observed; D = in dung; T = on feeding trail; S = scar tissue on tree trunk.
F = fruit; L = leaves and twigs; B = bark; Ot = other.
** = savanna species.

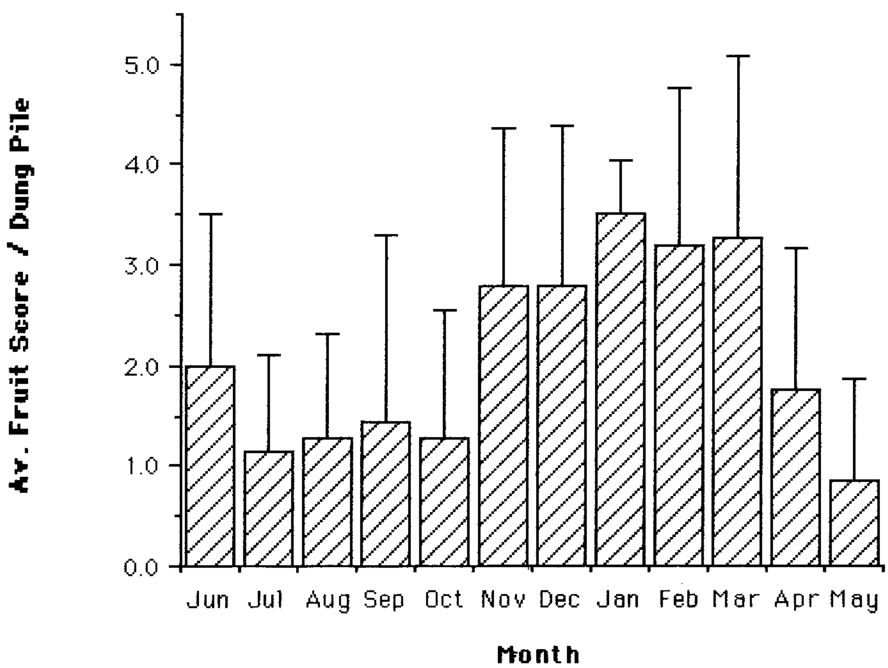
Table 5.4: Life forms of elephant foods at Lopé.

Food Class	Life Form	No. Species	%
Monocotyledons			
Fruit	Herb	4	1.3
Leaves/Stems	Herb	24	7.8
Root	Herb	15	4.9
Flower	Herb	1	0.3
TOTAL		**44**	**14.4**
Dicotyledons			
Fruit	Tree	49	16.0
	Shrub	5	1.6
	Liane	4	1.3
	Epiphyte/Tree	2	0.7
	U/K	7	2.3
TOTAL		**67**	**21.9**
Leaves/Twigs	Tree	79	25.8
	Shrub	7	2.3
	Herb	5	1.6
	Liane	4	1.3
	Epiphyte	1	0.3
TOTAL		**96**	**31.4**
Bark	Tree	85	27.8
	Epiphyte/Tree	1	0.3
	Epiphyte	1	0.3
TOTAL		**87**	**28.4**
Bark/Stem	Lianes	6	2.0
Wood	Tree	2	0.6
Roots	Tree	2	0.6
	Shrub	1	0.3
Total number of plant items		**304**	**99.3**
Other			
Fungus		1	
Soil		1	
Total number of items		**306**	

Between June 1990-May 1991, 311 fresh dung piles were inspected. Dung was dominated by fibre and leaf fragments, which were generally given the maximum "abundant" rating. In Marantaceae Forest herbaceous vegetation is abundant, and Marantaceae and Zingiberaceae were major components of the diet. In the other parts of the forest, characterised by a sparse understorey, most feeding was on leaves and twigs of small trees, which sometimes lost branches or were pushed over or snapped during feeding.

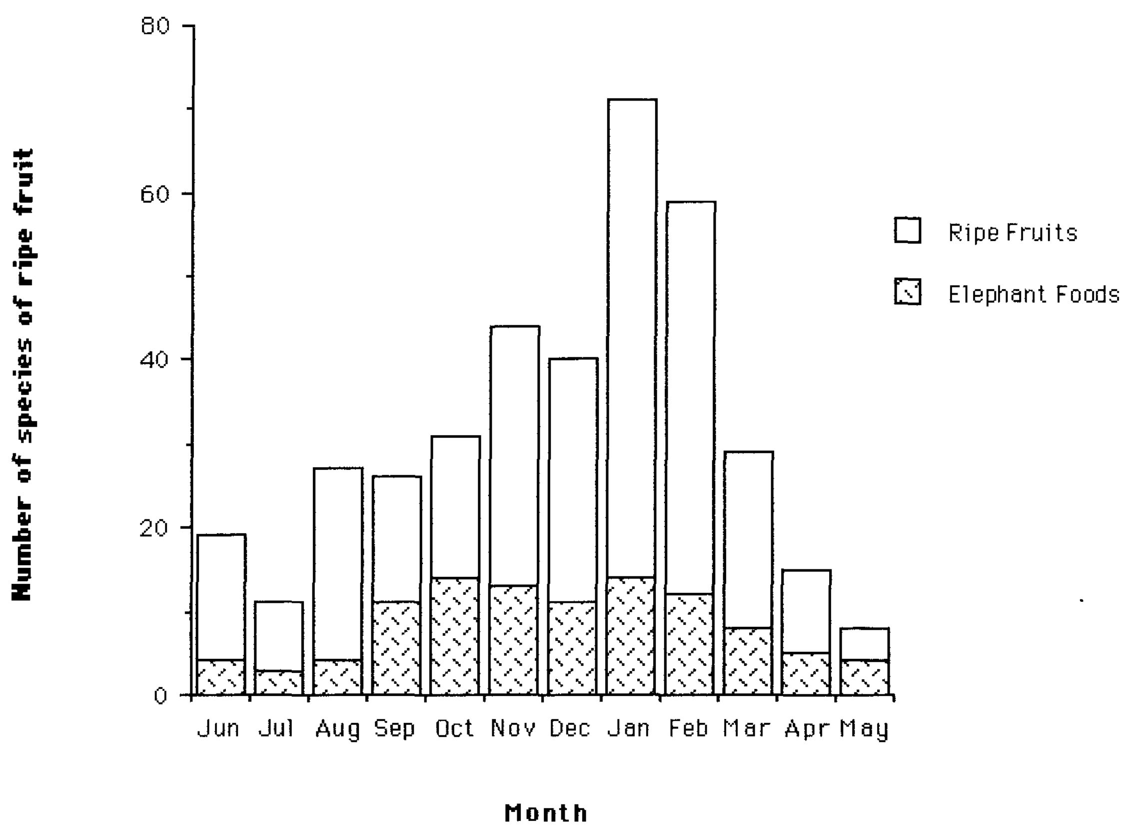
Overall, 82% of dung piles contained fruit remains, but there was a distinct seasonal difference in the quantity and diversity of fruit eaten. In the period November-March dung piles contained an average of 3.1 fruit species (range 0-7), with 99% of dung piles inspected containing fruit remains (N=124). During the remaining 7 months the average was 1.4 (range 0-7) with 71% of dung piles containing fruit remains (N=187). Figure 5.1 shows the average number of fruit species found in dung piles each month.

Figure 5.1: Average fruit score for dung piles (1990-1991) with standard error.



On fruit fall transects 140 species of ripe fruit were recorded, of which 33 were known elephant foods. Figure 5.2 shows that there was a peak in overall availability of ripe fruit in January and February (see also Figures 3.2 and 3.4), whilst availability *was* lowest in the May-July period. Production *of* fruits eaten by elephants was less seasonal (Figure 5.2). The average number of fruit species recorded in dung each month was significantly correlated with both the overall number of ripe fruits on fruit-fall transects (Spearman rank correlation: $r_s=0.751$, $P<0.01$) and the number of species of ripe fruit known to be elephant foods ($r_s=0.536$, $P<0.05$).

Figure 5.2: Number of species of ripe fruit on transects (1990-1991).



Elephants ate a large range of fruit 171 species), which varied widely in shape, size, colour and smell. One species, *Triumfetta cordifolia* was probably consumed accidentally with foliage. Three quarters of the fruit species eaten were from trees. Whilst the majority of fruits were collected once they had fallen to the ground, those from smaller trees and shrubs were often delicately picked with the trunk. These included very small fruits, such as those of Antidesma vogelianum, which are small, short-stalked, fleshy drupes which hang below the leaves in conspicuous racemes. Each fruit is about 5mm long, and they ripen individually, no doubt to encourage dispersal by birds, but the racemes are stripped by elephants, causing little or no damage to the trees. Preferred tree species are often surrounded by an open area of trampled ground and connected by paths.

Elephants disperse seeds of fruits ingested by depositing them in faeces, a 'gut passage time' later. The majority of seeds were passed intact, the only exception being those of ***Coula edulis,*** of which elephants are seed predators. Elephants were the only known dispersers of 23 species, although it is likely that duikers disperse many of these (J. and T. Hart, personal communication). Table 5.5 lists and describes all fruit species consumed and gives details of other known animal seed dispersers (see also Plate 5.2).

Many of the fruit species recorded were present in fewer than 1% of dung piles inspected, and only observed during one month. These species were not considered to play an important role in the diet of elephants during the course of the study (but see below). However, 13 species were present in 5% or more of dung piles, or during at least six months, and were probably important components in elephant nutrition (e.g., *Duboscia macrocarpa* was present in 30% of dung piles and in all 12 months of the study, whilst both ***Swartzia fistuloides*** and **Klainedoxa** gabonensis were each present during 10 months, in 18% and 20% of dung piles respectively - see Table *5.5).* These important species generally have large, dull, fleshy fruits or pods, absciss as they become ripe, and have a strong, often yeasty, smell (see Table *5.5).* Other species possessing these general characteristics were also eaten, but occurred at low densities in the study area, so were rarely recorded as foods.

Plate 5.2.

Omphalocarpum procerum, has fruits with a hard shell which only elephants can break into. Fruits fall when ripe, and have a strong smell of garlic. Only elephants disperse its seeds.

The characteristically bulbous, trunk of *Deterium macrocarpum* scarred by elephants feeding on its bark.

Bark from 85 free standing tree species was removed, using the tusks as levers, and eaten. In addition, bark was removed from two *Ficus* species, one of which is epiphytic, whilst the second can survive as a free standing tree once its original host dies, and from 6 species of liane (see Table 5.3). Of 4138 trees of > 10 cm dbh inspected on transects (Sites 2-5), 70 (1.7%) had scars due to bark removal by elephants (see Plate 5.2). A further 1335 trees of diameter greater than 70cm were checked and 69 *(5.2%)* showed signs of elephant damage. Table 5.6 lists those species encountered on transects whose bark was removed by elephants and gives the ratio of barked and un-barked individuals. At least one individual from each of **48** out of a total of 338 species of trees and lianes on the transects showed signs of barking. Many or all individuals of certain species recorded (e.g., *Piptadeniastrum africanum, Petersianthus* macrocarpus *Pentaclethra eetveldeana),* showed signs of barking. Some species were rare, so were not abundant on transects, but observations elsewhere showed that most individuals were barked (e.g., *Detarium macrocarpum*, *Pentadesma butyracea*, ***Panda** oleosa*). Other species were barked less regularly (e.g., *Pentaclethra macrophylla,* Sacoglottis gabonensis), or only exceptionally fed upon (e.g., Desbordesia *glaucescens,* Strombosiopsis *tetrandra*).

The 4138 trees > 10 cm dbh inspected on transects were classified into diameter categories. Table 5.6 gives the number of individuals in each category, and shows numbers that had been barked in each size class. The expected distribution of barked individuals was calculated, assuming the number of trees barked in any size class would be proportional to the number in that class. The observed distribution of barking was significantly different to that expected (Kolmogorov-Smirnov one-sample test, D=0.505, P<0.01, N=14), suggesting that elephants tended not to bark trees in lower diameter classes. Of the 15 individuals below 30 cm dbh that had been barked, seven were lianes, six were trees that grow to large diameter, and the only two individuals of trees that rarely exceed 20cm diameter were both **Diospyros** ***dendo,*** a common small tree whose fruits were also eaten.

Table 5.5: Characteristics of fruits consumed by elephants.

Family / Species	Fruit Characteristics					Seed fate	Dispersers	Months present	% in dung
	Fruit size	Seed size	Colour (ripe)	Fall	Smell				
ANACARDIACEAE									
Antrocaryon klaineanum	M	M	Yellow	1	2	1	2	1	<1
Pseudospondias longifolia	M	M	Red	1	2	1	2		
Pseudospondias microcarpa	M	M	Purple	1	2	1	2	3	2
Trichoscypha acuminata	M	M	Red	1	2		2		
ANNONACEAE									
* *Hexalobus crispiflorus*	VL	S	Brown	1	2	1	2	5	9
Mangifera indica	L	L	Green	2	2	1	3		
Monanthotaxis congensis	S	S	Red	1	1	1	1	1	2
* *Uvariastrum pierreanum*	VL	S	Yellow	1	2	1	2	2	5
Pawia sp.	S	S	Brown	1	1	1	1	2	3
APOCYNACEAE									
Landolphia sp.	VL	M	Yellow	1	2	1	2	1	1
Picralima nitida	L	M	Yellow	2	2	1	3		
BURSERACEAE									
Canarium schweinfurthii	M	M	Purple	1	1	1	2a		
Dacryodes normandii	M	M	Purple	1	1	1	2	1	<1

Table 5.5: Characteristics of fruits consumed by elephants / continued.

Family / Species	**Fruit Characteristics**					**Seed fate**	**Dispersers**	**Months present**	**% in dung**
	Fruit size	Seed size	Colour (ripe)	Fall	Smell				
CAESALPINIACEAE									
Detarium macrocarpum	L	VL	Green	2	3	1	3	3	<1
Dialium sp. nov	S	S	Black	1	1	1	1	1	<1
* *Swartzia fistuloides*	VL	S	Black	2	3	1	3	10	18
CHRYSOBALANACEAE									
Parinari excelsa	L	L	Brown	2	2	1	3		
EBENACEAE									
Diospyros abyssinica	S	S	Black	1	1	1	1		
Diospyros dendo	M	S	Red	1	1	1	2		
Diospyros polystemon	M	M	Red	1	1	1	2	1	<1
Diospyros suaveolens	L	L	Brown	2	2 / 3	1	2		
EUPHORBIACEAE									
* *Antidesma vogelianum*	S	S	Purple	1	1	1	1	3	6
* *Uapaca* spp.	M	M	Green	1	2	1	2	5	5
GUTTIFERAE									
Mammea africana	L	L	Brown	2	2	1	3		
* *Pentadesma butyracea*	VL	L	Brown	2	3	2 / 3	3	9	12

Table 5.5: Characteristics of fruits consumed by elephants / continued.

Family / Species	**Fruit Characteristics**					**Seed fate**	**Dispersers**	**Months present**	**% in dung**
	Fruit size	Seed size	Colour (ripe)	Fall	Smell				
GUTTIFERAE / continued									
Pentadesma sp.?nov	L	L	Brown	1	1	2 / 3	3		
HUMIRIACEAE									
* *Sacoglottis gabonensis*	M	M	Green	2	3	1	3	6	8
IRVINGIACEAE									
* *Irvingia gabonensis*	L	L	Yellow	2	3	1	3	4	5
Irvingia grandifolia	M	M	Yellow	2	3	1	3		
Irvingia robur	L	L	Yellow	2	3	1	3	1	<1
* *Klainedoxa gabonensis*	L	L	Green	2	1	1	3	10	20
Klainedoxa microphylla	M	M	Green	2	1	1	3		
MARANTACEAE									
Megaphrynium gabonense	S	S	Red	1	1	1	1		
Megaphrynium macrostachyum	S	S	Orange	1	1	1	1	1	<1
MIMOSACEAE									
Parkia bicolor	VL	M	Purple	1	1	1	2		
Parkia filicoidea	VL	M	Green	1	1	1	2		
* *Tetrapleura tetraptera*	VL	S	Black	2	3	1	3	8	16

Table 5.5: Characteristics of fruits consumed by elephants / continued.

Family / Species	**Fruit**	**Characteristics**				**Seed fate**	**Dispersers**	**Months present**	**% in dung**
	Fruit size	Seed size	Colour (ripe)	Fall	Smell				
MORACEAE									
Ficus mucosa	M	S	Red	1	3	1	1		
Ficus recurvata	M	S	Yellow	1	3	1	1		
Myrianthus arboreus	VL	M	Yellow	2	2 / 3	1	2	4	2
MYRISTICACEAE									
Staudtia gabunensis	M	M	Green	1	1	1	2a		
MYRTACEAE									
* *Psidium guinensis*	M	S	Yellow	1	2	1	1	9	21
OLACACEAE									
Coula edulis	M	M	Pink	2	1	3	4	2	2
Ongokea gore	M	M	Yellow	2	1	?	3		
PANDACEAE									
* *Panda oleosa*	L	L	Green	2	1	1	3	5	5
RHIZOPHORACEAE									
Poga oleosa	L	L	Green	2	3	1	3	1	<1
RUBIACEAE									
* *Massularia acuminata*	VL	S	Yellow	2	1	1	3	4	5

Table 5.5: Characteristics of fruits consumed by elephants / continued.

Family / Species	Fruit Characteristics					Seed fate	Dispersers	Months present	% in dung
	Fruit size	Seed size	Colour (ripe)	Fall	Smell				
RUBIACEAE / continued									
Nauclea didderichi	L	S	Brown	2	3	1	1		
Nauclea vanderguchtii	L	S	Green	2	3	1	1		
Psychotria vageliana	S	S	White	1	1	1	1	1	3
RUTACEAE									
Citrus sp.	L	S	Yellow	1	1	1	3	1	<1
SAPOTACEAE									
Baillonella toxisperma	L	L	Green	2	3	1	3		
Gambeya africana	L	L	Yellow	1	2 / 3	1	2b	1	<1
Gambeya subnuda	M	M	Green	1	3	1	2	2	2
* *Omphalocarpum* sp.	VL	L	Brown	2	3	1	3	9	9
Tieghemella africana	L	L	Yellow	2	2 / 3	1	3		
U/K Seed 3		M						1	<1
TILIACEAE									
* *Duboscia macrocarpa*	L	S	Brown	2	3	1	1	12	30
Triumfetta cordifolia	S	S	Brown	1	1	1	1		

Table 5.5: Characteristics of fruits consumed by elephants / continued.

Family / Species	Fruit Characteristics					Seed fate	Dispersers	Months present	% in dung
	Fruit size	Seed size	Colour (ripe)	Fall	Smell				
VITACEAE									
Cissus ruginosicarpa	S	S	Pink	1	1	1	1		
ZINGIBERACEAE									
Aframomum longipetiolatum	L	S	Red	1	1	1	1	1	<1
Aframomum sp. ?nov.	L	S	Red	1	1	1	1	1	<1
INDETERMINED									
U/K Seed 1		S				1		1	<1
U/K Seed 4		S				1		1	<1
U/K Seed 5	L	S				1		2	<1
U/K Seed 8		M				1		1	<1
U/K Seed 9		M				1		1	<1
U/K Seed 11		M				1		1	<1

Key:

* = fruit species present in >5% of dung piles or during at least 6 months of the study.

Fruit size - largest diameter of whole fruit: S=Small, <10mm; M=Medium, 10-40mm; L=Large, 40-100mm; VL=Very Large, >100mm.

Seed Size - largest diameter: S=Small,<10mm; M=Medium, 10-30mm; L=Large, >30mm.

Table 5.5: Characteristics of fruits consumed by elephants / continued.

Key: / continued

Fall - Stage of development at which fruit abscisses: 1 = When fruit over-ripe, or dropped by arboreal species; 2 = As soon as fruit ripens.

Smell - 1: No detectable smell; 2: Strong smell of fermenting when ripe fruit is falling; 3: Ripe fruit with a strong, often 'yeasty' smell.

Fate of Seeds - 1: Passed intact in faeces; 2: Majority passed intact, minority destroyed; 3: Minority passed intact, majority destroyed.

Dispersers (Other species known to swallow and pass seeds in faeces) - 1: Many dispersers including birds, primates and elephants;
2: Only other dispersers are Chimpanzees and Gorillas; 2a: Only Chimpanzees; 2b: Only Gorillas; 3: Elephants are the only dispersers;
4: Elephants only, but most seeds are destroyed by chewing.

Table 5.6: Frequency of barked trees on transects.

Species	Family	No. Barked	No. Present	% Barked
Pentaclethra eetveldeana	MIMOSACEAE	23	38	61
Piptadeniastrum africanum	MIMOSACEAE	14	16	88
Pentaclethra macrophylla	MIMOSACEAE	10	104	10
Sacoglottis gabonensis	HUMIRIACEAE	7	38	18
Petersianthus macrocarpus	LECYTHIDACEAE	6	6	100
Scyphocephalium ochocoa	MYRISTICACEAE	5	135	4
Baillonella toxisperma	SAPOTACEAE	4	4	100
Irvingia gabonensis	IRVINGIACEAE	4	353	1
*LJTW 478	CONNARACEAE	4	6	67
Newtonia leucocarpa	MIMOSACEAE	4	2	50
Parkia bicolor	MIMOSACEAE	4	6	67
Ceiba pentandra	BOMBACACEAE	3	3	100
Fillaeopsis discophora	MIMOSACEAE	3	8	38
*LJTW 593	PAPILIONACEAE	3	8	38
LJTW 425	SAPOTACEAE	3	4	75
Amphimas ferrugineus	CAESALPINIACEAE	2	2	100
Cylicodiscus gabonensis	MIMOSACEAE	2	2	100
Detarium macrocarpum	CAESALPINIACEAE	2	2	100
Diospyros dendo	EBENACEAE	2	49	4
Irvingia grandifolia	IRVINGIACEAE	2	9	22
LJTW 526	EUPHORBIACEAE	2	2	100
Plagiostyles africana	EUPHORBIACEAE	2	45	4
Poga oleosa	RHIZOPHORACEAE	2	3	67
Sindoropsis le-testui	CAESALPINIACEAE	2	58	3
Afzelia sp.	CAESALPINIACEAE	1	1	100
Antrocaryon klaineanum	ANACARDIACEAE	1	1	100
Celtis tessmannii	ULMACEAE	1	14	7
Desbordesia glaucescens	IRVINGIACEAE	1	82	1
Hylodendron gabunense	CAESALPINIACEAE	1	1	100

Table 5.6: Frequency of barked trees on transects / continued.

Species	Family	No. Barked	No. Present	% Barked
Lecaniodiscus cupanioides	SAPINDACEAE	1	1	100
Macaranga monandra	EUPHORBIACEAE	1	21	5
Panda oleosa	PANDACEAE	1	1	100
Pentadesma butyracea	GUTTIFERAE	1	2	50
Pseudospondias microcarpa	ANACARDIACEAE	1	3	33
Scorodophloeus zenkeri	CAESALPINIACEAE	1	4	25
Scytopetalum sp.	SCYTOPETALACEAE	1	30	3
Strombosiopsis sp.	OLACACEAE	1	17	6
Strombosiopsis tetrandra	OLACACEAE	1	114	1
Symphonia globulifera	GUTTIFERAE	1	14	7
Tetrapleura tetraptera	MIMOSACEAE	1	1	100
LJTW 363	SAPOTACEAE	1	1	100
LJTW 365	MIMOSACEAE	1	1	100
LJTW 471	SAPOTACEAE	1	1	100
LJTW 504		1	1	100
LJTW 506		1	1	100
LJTW 507	?FLACOURTIACEAE	1	1	100
*LJTW 513	?Legume	1	1	100
LJTW 564	SAPOTACEAE	1	1	100

* = liane.

Elephants pushed over trees up to 45 cm dbh, and this was most apparent along old logging roads with a high proportion of secondary species. However, in an area of 0.25 km^2 (5m either side of the five transects), a total of only 20 trees up to 42 cm dbh (9 individuals > 10 cm dbh) were pushed over by elephants during the course of the study, of which 10 were secondary species. This was equivalent to *7.6* trees km^{-2} year-' (3.4 km-2 year-' for trees > 10 cm dbh). Assuming a stocking density of 390 trees ha-1 > 10 cm dbh (equal to the average for the five sites - Chapter *2)* this was equivalent to an annual mortality of less than *0.0*1%.

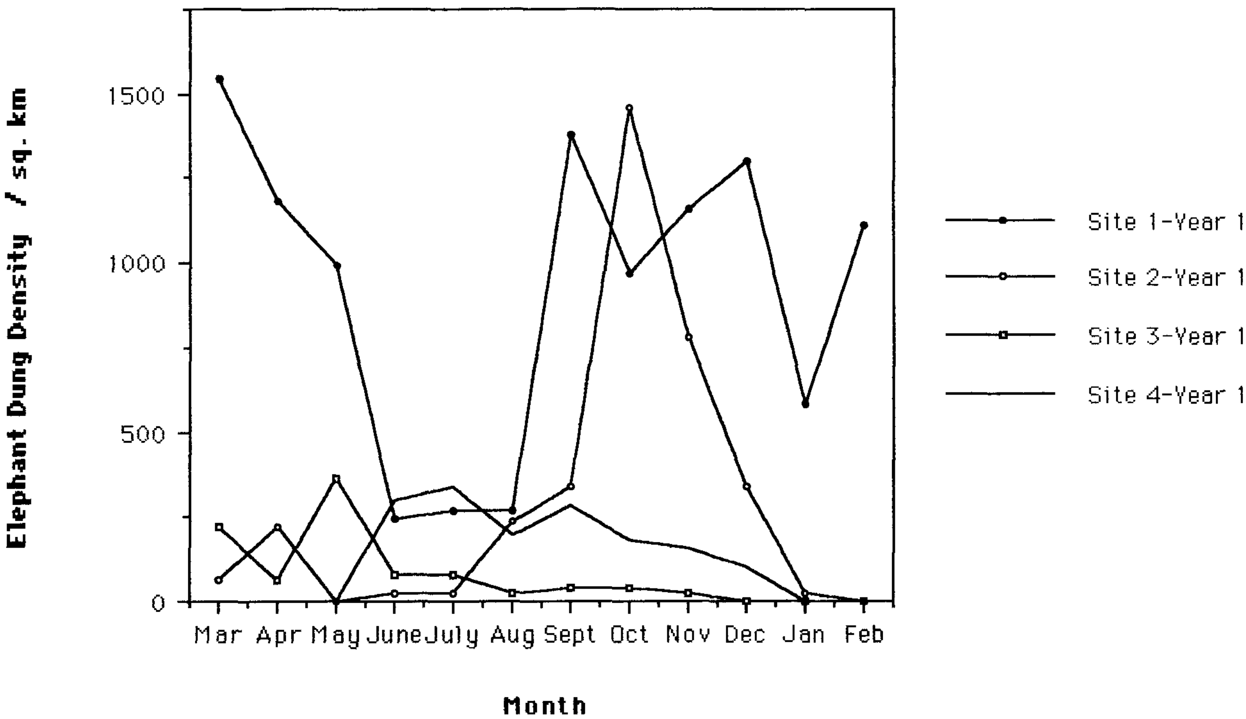
Table 5.7: Observed and expected frequencies of barking.

Girth Class (cm)	No. trees inspected	Number barked	% Barked	% Expected
10-20	2111	7	0.3	35.7
20-30	857	8	0.9	14.5
30-40	440	11	2.5	7.4
40-50	280	16	5.7	4.7
50-60	127	6	4.7	2.1
60-70	122	9	7.3	2.1
70-80	78	7	9	1.3
80-90	51	2	3.9	0.9
90-100	24	1	4.2	0.4
100-110	14	0	0	0.2
110-120	17	0	0	0.3
> 120	17	3	17.6	0.4

Seasonal movements.

Dung counts often differed markedly between sites in the same month, and between months at each site. Figure 5.3 shows plots of average dung pile density in Cites 1-4 each month for March 1989-February 1990 (see Chapter 6 for details of density calculation). Significant fluctuations in monthly elephant density, as indicated by dung, are apparent in all sites.

Figure 5.3: Elephant dung densities for Cites **1-4** (March 1989-February 1990).



This was most marked in Site 2, where a distinct peak was noted in October to December 1989. Here, the forest was characterised by *Sacoglottis gabonensis* (Humiriaceae) (Chapter *2)* which produces a fruit much sought after by elephants' (see above), and large quantities of ripe ***Sacoglottis gabonensis*** were observed to be falling to the ground at the time of the influx. *Sacoglottis gabonensis* occurred at an average density of 3.4 trees ha-1 and ranked fourth in terms of basal area (Chapter 2). Reitsma (1988) enumerated a 1-ha botanical plot nearby and found a higher density. ***Sacoglottis gabonensis*** is an emergent tree species rising above 45m. The fruit is an ellipsoid drupe, 3 to 4 cm by *2.5* cm, with a pulp about 1 cm thick around a rough stone. The fruit abscisses when ripe, and has a rich yeasty smell characteristic of many fruits favoured by elephants (see above). Two other trees which produce fruits often eaten by elephants were relatively common: *Hexalobus crispiflorus* (Annonaceae) and *Irvingia gabonensis* (Irvingiaceae); but Site 2 was otherwise poor in such species. In the four other study sites *Sacoglottis gabonensis* was absent or rare, and no other species producing fruits favoured by elephants occurred at comparable densities.

Therefore, the forest where *Sacoglottis gabonensis* was abundant presented an ideal opportunity to test to what extent fruit availability influences forest elephant movements. From July 1390 - June 1991 elephant densities and fruit production were monitored monthly to see if patterns of elephant movement could be explained.

Figure 5.4 shows plots of average dung pile density in all sites per month for July 1990-June 1991. In the 1990-1991 fruiting season a similar but less marked peak was observed in Site 2 in the October - December period. Figure 5.5 plots the availability of ripe and unripe *Sacoglottis gabonensis* fruits as measured on the fruit-fall transect (Chapter 3) and the number of elephant dung piles deposited in the previous month. *Sacoglottis gabonensis* availability in 1390-1991 was subjectively assessed to be less than in the previous year, and some trees failed to fruit in the October to December period, but produced a minor crop in March 1991. The number of fresh dung piles observed was positively correlated to the number of ripe *Sacoglottis gabonensis* fruits on the transect in 1990-1991 ($N=11$, $r_S = 0.619$, $P < 0.025$), and the number of fresh dung piles in 1983 - 1990 (when *Sacoglottis gabonensis* availability was subjectively assessed to show the same general pattern) was also correlated to *Sacoglottis gabonensis* availability in 1990-1991 ($N=11$, $r_S = 0.566$, $P < 0.05$).

Of 16 fresh dung piles searched for *Sacoglottis gabonensis* seeds in the study area during the fruiting season 10 contained seeds and the average number of seeds per dung pile was 41 (range 0-220)

Figure 5.4: Elephant dung densities for Sites 1-5 (July 1990-June 1991).

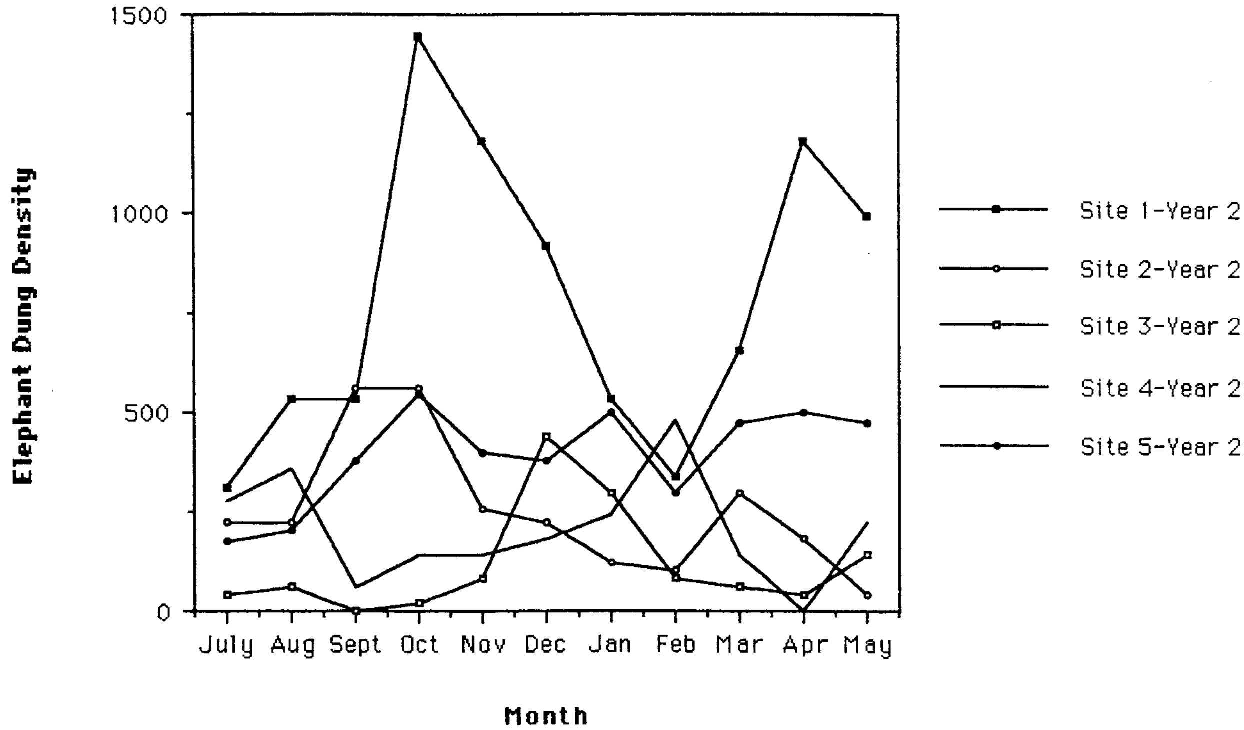
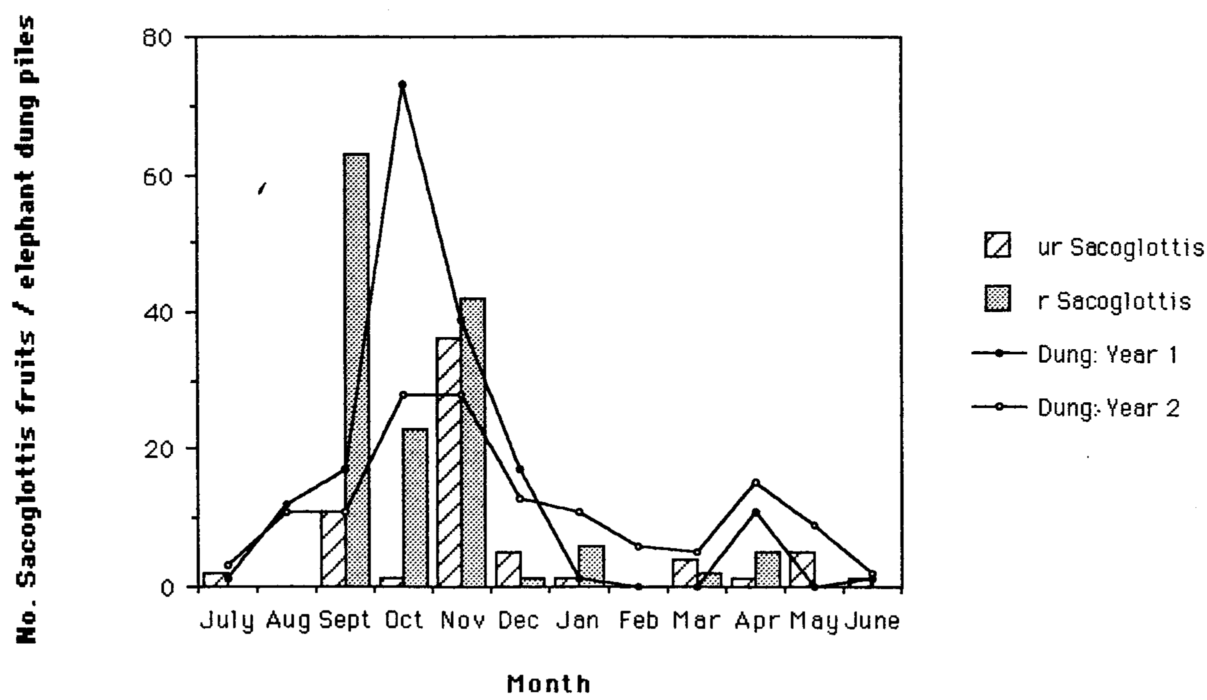


Figure 5.5: Elephant dung and *Sacoglottis gabonensis* fruit counts in Site 2.



Discussion.

Group size and composition.

The average group size of elephants in savanna habitats varies over time arid between areas and some of this variation can be related to food availability (Leuthold, 1976; Moss, 1988; Western & Lindsay, 1984). Moss (1988) found that group size in Amboseli National Park averaged 15.1 in a year during which there was a serious drought and food was scarce, but was 45.9 in a year when good rains fell and food was abundant, with maximum group sizes at this time of up to 550 individuals, where the majority of the total population for the area was present. Males were found singly, in short lived all-male groups (mean group size 3.8, range 2-25) or in association with females (Moss, 1988; Moss & Poole, 1983).

Complete counts in the forest at Lope were biased towards smaller groups, as for larger groups it was rarely possible to be sure that all individuals had been detected. For this reason, minimum estimates and counts obtained at salines are considered more reliable and give average group sizes of 2.5 and 2.6 respectively (range 1-8). Excluding lone individuals (assumed ta be males) average group sizes (family unit sizes) rise to 3.2 and 3.3 respectively. Group sizes recorded in the savanna, where complete counts were almost always possible, give a slightly higher average group size (2.8 individuals/group, 3.5/group excluding lone animals), due to the occurrence of 3 large groups (Table 5.1). The only comparable data for forest elephants (Merz, 1986c) gave average group size of 2.44 ±1.7, or 3.4 ±1.6 excluding solitary animals, for the Tai Forest, Ivory Coast (N=63, range 1-9).

There was no significant difference between counts in the savanna and those at salines, suggesting that there was no tendency to form larger groups in the open savanna. Accurate counts of large groups are almost impossible in the forest, and salines are rarely large enough to accommodate 10 individuals, so group sizes recorded in the savanna are considered to be most representative of the normal pattern of elephants at Lopé. This suggests that a single mother and her offspring is by far the most frequent family unit for forest elephants at Lope, and that males are generally solitary. This conclusion is reinforced by the data from known family groups which were stable, and composed of a female with one or more offspring, and occasionally other adults (possibly also offspring). These groups were seen to fuse with other similar units, but associations of more than four or five elephants did not seem to be common or stable.

Small groups consisting of a single adult female with her offspring are only rarely encountered in savanna areas, although their incidence increases during times of severe environmental stress (Moss, 1988). The smaller family unit observed for forest elephants may have serious implications for the survival of younger elephants where poaching is a problem. Females are increasingly becoming targets for poachers in areas where males (who bear larger tusks) are scarce due to heavy hunting (e.g., Poole & Thomsen, 1989). The death of any adult member of a family may affect the survival and social relationships of other members of even quite large groups (Poole, 1989), but where the family unit consists of just one female with her young, the chances of the offspring surviving the death of their mother are very low.

Local and temporal variations in the rate of encounters with elephants at Lopé were great, suggesting that family units co-ordinate their movements to some extent in response to seasonal availability of fruit (e.g., *Sacoglottis gabonensis*). Studies in east and southern Africa have revealed coordinated movements of elephant groups that are out of visual and olfactory contact (Martin, 1978; Poole *et al.*, 1988). These groups appear to maintain contact by using infrasonic calls, which allow communication over distances of up to five km {Payne *et al.*, 1986; Poole *et al.*, 1988). As studies of forest elephants progress we may find that related family units tend to remain close enough to use infrasonic calls to enable them to coordinate movements.

Large aggregations of elephants such as those seen in east and southern Africa did not occur in Lopé Nor was there any tendency to form larger groups in the savanna, even at the beginning of the wet season, when a flush of new grass created conditions resembling those in east and southern Africa. This suggests that there is a fundamental difference in the social organisation of forest and savanna elephants.

It has been suggested that average group size (and density) of elephants decreases in poorer quality habitat (Leuthold 1976; Olivier 1978). However, average densities in the SEGC study area (Site 1) were over 2 elephants km^{-2} (Chapter 6), which is higher than in many savanna areas (e.g., Laws *et al.*, 1975), suggesting that the tropical rain forest in Lope is not a poor quality habitat for elephants. Elephant population density at Lopé is higher- than that reported for other tropical forest areas, where densities average about 0.2 - 0.6 individuals km-2 (Barnes et al., in press; Fay, 1991; Merz, 1981; Merz & Roth, 1986; Short, 1983) but the Lopé population is well protected from poaching (see also Chapter 6).

Western & Lindsay (1934) discussed reasons for large group formation. Large aggregations formed in response to heavy predation (by humans) (Laws et al., 1975), but the characteristically tight formations that were adopted in areas of heavy poaching bear little resemblance to looser aggregations formed naturally (Western & Lindsay, 1984). It seems unlikely that forest and savanna races of elephant would have sufficiently different evolutionary experience of predation for this to be the reason for present differences in social organisation. Moss (1981) and Poole (1982) have suggested that there are social and reproductive benefits to be gained from formation of large aggregations, but similarly it is unlikely that this would be so for one race and not the other.

If the smaller group size observed at Lope is typical of forest elephants as a whole, it could be due to the importance of fruit in the diet. Elephant movements seem to be related to fruiting patterns (Short, 1983; this study). Small family units are perhaps better able to exploit a patchily available resource such as ripe fruit than are larger groups. Observation of a tendency for larger associations of elephants in areas where favoured fruits were temporarily super-abundant supports this, but insufficient data are available at present to draw any conclusions.

Diet seed dispersal and ecological role in the forest

The diet of elephants at Lopé was diverse, including a minimum of 306 items (Table 5.4). The bulk of the diet, both in terms of number of species and quantities eaten, came from leaves and bark (70% of all items recorded), but it was not possible to quantify the amounts of each species eaten. Trees accounted for 73% of the species fed upon, which is similar to the figure for elephants in the Tai National Park in Ivory Coast (Merz, 1981), but contrasts sharply with the findings of Short (1981) in the Bia National Park, Ghana, where woody lianes made up the majority of plants browsed.

Short (1981) recorded bark feeding in Bia but noted that it was highly selective, with only 20 species of tree affected, and only seven regularly fed upon; in Tai, Merz (1981) identified 22 tree species whose bark was eaten. Wing and Buss (1970) list eight species that were heavily utilised in Kibale forest, Uganda, and Short (1981) noted that some species fed upon in Kibale, and in Murchison Falls National Park in Uganda (Field, in Laws *et al.,* 1975), were not used in Bia, although they were present. Merz (1981) stated that the bark of *Coula edulis* and *Sacoglottis gabonensis* were favoured foods, but at Lope these species were rarely fed upon, though common. There also seem to be regional differences within Gabon: at Lope *Scytopetalum klaineanum,* a common tree, was not barked, but at Doussala, in southeast Gabon, most individuals were fed upon heavily (J.M. Reitsma, personal communication), and *Symphonia globulifera,* which was only rarely fed upon in Lopé, is a favoured species in other parts of the country (unpublished data).

Grubb (1974) suggested that the chemical make-up of a plant varies with the soil chemistry (see also Gartlan et *al.,* 1980). Perhaps regional variations in bark feeding are related to differences in the chemical composition of the bark. Alternatively they could be due to differing dietary requirements of elephants living in different areas, or to cultural differences in taste preference or experience (see also Short, 1981). Bark was not eaten by Asian elephants living in rain forest in Malaya (Olivier, 1378).

Savanna plant species, including grasses, were poorly represented in the diet of elephants at Lope. This was due, in part, to sampling bias, as most data were collected in the forest and few observations of elephants feeding in the savanna were made. Grass was rarely distinguishable in dung (it was recorded only once in systematic searches of 311 fresh dung piles in the forest), but it is possible that its importance increased at the beginning of the rainy season in September, as elephants were often observed feeding on young shoots that were abundant at this time (but see above).

Fruit was an important part of the diet in this tropical forest habitat. Fruit of at least 71 species was eaten at Lopé and the remains of at least one species of fruit were found in *82%* of dung piles. The correlation between the number of species of ripe fruit on transects and the number of fruit species per dung pile, indicates that elephants are opportunistic frugivores. This is also supported by the wide range of sizes, shapes, colours and types of fruit eaten by elephants.

Other studies in African rain forests confirm the importance of fruit in the diet of forest elephants: Merz (1981) recorded 44 species of fruit eaten by elephants in Tai, and noted that fruit remains can form up to 35% of faecal dry weight; Alexandre (1977) recorded 37 species that were fed upon and subsequently dispersed in Tai; and Short (1981; 1983) found that 93% of dung piles inspected in Bia contained fruit remains, and listed 35 fruit species that were eaten, nine of which he considered to be major components of the diet. In East Africa, Wing & Buss (1970) recorded fruit eating by savanna elephants resident in Kibale Forest, Uganda, where one species, *Balanites wilsoniana* was present in 44% of dung piles inspected (this species is a preferred food in Gabon where it occurs, but was not found in the Lope, unpublished data). Olivier (1976) found that elephants in rain forest habitat in Malaya rarely ate fruit: Fruits from eight genera were present in dung, but only one species, *Mangifera* sp., was relatively common. It is interesting to note that of 13 genera whose fruit have been recorded 3s foods in Malaya (Khan, 1977; Olivier, 1978) five were also represented in the diet of elephants at Lope (*Mangifera*, *Santiria*, *Irvingia*, *Ficus* and *Parkia*).

Elephants in Lope disperse the seeds of all but one of the fruit species eaten and for 23 species they are the sole known dispersers. The fruits of many tropical forest trees show a range of morphological characters that encourage dispersal of their seeds by a particular agent (Howe & Vande Kerckhove, 1979; Janson, 1983; Van der Pijl, 1972). Characters of fruit with seeds dispersed solely by elephants are abscission on ripening; strong smell; and dull green or brown colouration (see also Alexandre, 1977; Gautier-Hion et *al.*, 1985a; Janzen and Martin, 1982; Short, 1981). Seed size of "elephant fruits" was less consistent: some of the fruit having very large seeds which even gorillas (the next largest frugivore at Lopé) never, or very rarely, swallow (e.g., *Baillonella toxisperma, Tieghemella africana, Mammea africana*, *Klainedoxa* spp., *Irvingia* spp.); but others have smaller seeds, (e.g. *Swartzia fistuloides*, *Tetrapleura tetrandra, Duboscia macrocarpa*- see Table 5.45. Even the mechanically unprotected seeds ingested by elephants, (e.g., *Pentadesme butyracea, Parkia bicolor)* often passed through the gut intact and elephants at Lopé were known to predate (i.e., crunch up) the seeds of only one species, *Coula edulis* (but see Alexandre, 1977). Since this study was undertaken, *Celtis tessmannii* fruited at SEGC, and attracted large numbers of elephants, but few seeds were found intact in the dung, suggesting that they were destroyed during feeding (C.E. G. Tutin, personal communication). It was striking how rarely elephant feeding on fruit led to damage and the delicacy with which tiny fruit (e.g., *Antidesma vogelianum*) were selectively removed was remarkable.

Seeds of a variety of species were seen germinating in elephant dung and it seems likely that the surrounding matrix of fibrous dung favours germination (see Alexandre, 1977). Germination of *Balanites wilsoniana* was significantly more likely after passage through elephants (Chapman *et al.,* in press[b]; Lieberman *et al.,* 1987). There can be no doubt that elephant seed dispersal plays a critical role in the dynamics of tree regeneration at Lope. Alexandre (1977) found that certain elephant dispersed species were not regenerating in areas of Tai where elephants had been eliminated by poaching.

Repeated bark feeding by elephants produced a characteristically bulbous and distended base of trunks of species such as *Detarium macrocarpum, Pentadesma butyracea, Antrocaryon klaineanaum* (Plate 5.2). Other species were less resistant and tree deaths occurred after extensive bark stripping in some species (e.g. *Hylodendron gabunense*, *Chlorophora excelsa*, *Ficus mucuso*), although this was generally a rare occurrence. The bark of many tree species commonly eaten by elephants has structural properties that preclude large amounts being removed. Bark fibres of trees adapted to elephant feeding tend to break easily when prized away from the wood, and it is therefore not possible to remove large strips. The result was that elephants rarely removed areas of bark greater than about 100 cm^2 from these species. Some tree species that were only rarely fed upon lacked this adaptation, and long strips of bark were occasionally removed (e.g., on an individual of *Paraberlinia bifoliolata,* which was not generally eaten, bark damage extended to a height of about 7 metres, where strips had been pulled off).

Wounds tended to heal quickly, generally by regrowth inwards from the edges of the scar, although in the case of *Petersianthus macrocarpus*, a species that was never seen without signs of feeding, regeneration occurred from numerous pores on the bared wood, an adaptation that speeds the healing process. It seems that in some cases, buttress roots serve to protect the tree's bark by rendering it inaccessible to elephants' tusks, and bark on buttresses appears structurally different, generally being very thin. This is supported by the enormous quantities of bark stripped from freshly fallen trees of buttressed species such as *Hylodendron gabunense* and *Ceiba pentandra* (which is also protected mechanically by sharp spines when young). Another example of structural features providing protection from elephant feeding was seen at two individuals of the epiphytic strangling fig, *Ficus thonningii,* which fell during the study and were completely stripped of bark: both trees were inaccessible to elephants when standing. Similarly, aerial roots and/or spines may contribute to protecting the pith of some monocotyledons such as **Pandanus candelabrum** and various palms.

Elephants tended not to eat the bark of trees that do not attain a diameter >*30* cm, which suggests that smaller species may be protected chemically. The selection pressure on smaller tree species to invest in secondary compounds will be high, as **it** is easy for elephants to push over small trees, and they would probably do so to feed on bark that would otherwise be out of reach.

The leaves of most mature trees are inaccessible to elephants, but trees of up to about 40 cm dbh were pushed over, either being uprooted or snapped, **by** elephants feeding on leaves. This seemed particularly destructive as often only a small number of leaves were eaten, but as noted above, few trees were affected. Campbell (1991) showed that elephants act as gap builders and maintainers along trails in the forest at Oveng, Gabon. In contrast, elephants ate most, or all, of the leaves of many large victims of natural tree-falls during the course of the study. Again, this suggests that leaves of small trees of many species may be protected **by** secondary compounds, making them distasteful to elephants and other terrestrial herbivores, whereas leaves of certain large trees are less chemically protected, or perhaps have different defences, to deter a different set of herbivores. Leaves of herbaceous understorey plants, especially of the Zingiberaceae and Marantaceae, are important foods for elephants and while their feeding is destructive on a local scale, the regenerative powers of these plants (through vegetative reproduction) are remarkable (see Bullock, 1981).

Elephant densities in Lope were high (Chapter 6) and elephant feeding on leaves and bark had detrimental effects on individual plants, as smaller trees were pushed over, and accessible branches pulled down. However, data from botanical transects showed that elephant mortality accounts for only 0.01% mortality of trees > 10 cm dbh per year, compared to overall natural mortality of about 1-2 % (Hladik, 1982; Reitsma, 1988; Williamson & White, unpublished data). Elephants feeding at salines led indirectly to the death of mature trees which fell after being undermined. In these areas clearings up to about 0.25 ha had been created by the activity of elephants over the years. In Congo, clearings up to 4-5 ha have been recorded (Léonard, 1951) within which characteristic vegetation associations can be identified. However, these openings are localised, and overall elephants do not seem to warrant the "bulldozer" label they have been given in the past (Kortlandt, 1984).

Elephant diet at Lope overlapped extensively with many sympatric mammal species. A parallel study of the feeding ecology of western lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) at Lopé allows comparison of their respective diets. Gorillas at Lope are the most frugivorous population of this genus yet studied (Williamson *et al.*, 1990; Tutin *et al.*, 1991a): the fruit of at least 91 species is eaten and 96% of 4,301 gorilla faeces analysed over a 7-year period contained the remains of at least one species of fruit. Of 75 species identified to family, whose succulent or fibrous pericarp/mesocarp was found to be eaten by gorillas over a seven year period (Tutin *et al.*, 1991b), 49 (65%) were recorded as elephant foods during this one-year study. Most were probably eaten by elephants. Chimpanzees are more frugivorous than gorillas: although the diversity of species eaten (N=96) and the frequency of fruit remains in faeces (98%) are similar, fruit dominates chimpanzee diet even when fruit availability is low during the annual 3-month dry season (Tutin *et al.*, 1991a). This is not the case for either gorillas or elephants: elephant diet is dominated by foliage and bark throughout the year and gorilla diet is dominated by non-fruit foods duririg the dry season (Williamson, 1988). Body size certainly limits the degree of dependency on fruit (Dubost, 1980) and the elephants' digestive physiology is adapted to a bulky, high-fibre diet (Janis, 19765; Olivier, 1978).

Chimpanzees and gorillas are also important dispersers of seeds (Tutin *et al.*, 1991b). In addition to the 23 tree species whose seeds are dispersed solely by elephants, 21 additional species depend entirely on elephants and one, or both, species of ape to disperse their seeds (see Table 5.3). The relatively large body sizes of these three species make them excellent seed dispersers, as they ingest large quantities and carry the seeds considerable distances from the parent plant. Many species dispersed solely by elephants and apes are commercially exploited in Gabon and other areas of west and central Africa, so the continued presence of elephants and apes may be vital for regeneration of commercial species in logged forest (e.g., *Tieghemella africana*, *Baillonella toxisperma*, *Gambeya africana*, *Swartzia fistuloides*). Other fruits that rely upon elephants for the dispersal of their seeds are also important for humans (e.g., the seeds of *Irvingia* spp. and

Baillonella *toxisperma* are used by many peoples to make oils used in cooking and the flesh in seed pods of *Tetrapleura tetraptera* is used as a flavouring).

The few species of fruit eaten by elephants but not by apes share a common character of falling to the ground when ripe (see Table **5.4)**. Chemical analysis of gorilla foods (Rogers *et* al., 1990) showed that gorillas have eclectic tastes, but tend to avoid fruits high in lipids. Gorillas tolerate high concentrations of secondary compounds such as tannins but prefer sugary drupes over fibrous fruit (Rogers et al., 1990; Tutin et *al.,* 1991b). Chemical analysis of the exclusive elephant foods might reveal why apes apparently find them unpalatable.

Despite extensive overlap in diet, little direct competition for food appears to occur between gorillas and chimpanzees (Tutin *et al.,* 1991a). No indication was obtained of competition between apes and elephants as, while many fruit foods are shared, the apes have an obvious advantage in their ability to climb. Apes will collect and eat fruit from the ground but more often climb to harvest directly from the canopy, taking almost ripe fruit from species that absciss on ripening, such as *Irvingia* spp.,. *Mammea* ***africana*** *Duboscia macrocarpa*. Incidental observations suggest that elephants are sometimes attracted to trees where a group of gorillas is feeding, or has recently fed, (e.g. *Gambeya* spp., *Diospyros* spp.) to eat the fruit and fruit parts that fall to the ground. However, it was not possible to determine whether elephants were attracted by the sound of fruit dropping or by the smell of the freshly processed fruit.

It is clear from these data and those of other studies of frugivorous communities, that the feeding behaviour of animals may exert selective pressure on many features of plant morphology and, perhaps physiology. A clear example is the timing of abscission of fruit: to depend wholly on elephant dispersion, the fruit must be accessible! Wheelwright & Orians (1982) suggested that specialisation by a plant to a single species of disperser is unusual, and it does seem a risky evolutionary strategy. However, the fact that 23 tree species depend solely on elephant dispersal of seeds at Lope suggests that in some tropical communities . such co-evolved relationships are relatively common. Similarly, elephant feeding on leaves and bark is likely to have exerted selective pressures, favouring structural or chemical defences that minimise damage to the plant and reduce the risk of mortality.

Seasonal movements

Elephants living in savanna regions in Africa tend to migrate in response to vegetation changes induced by rainfall patterns (e.g., Bosman & Hall-Martin, 1986; Leuthold, 1976; Moss, 1988; Sikes, 1971; Western & Lindsay, 1984). Little is known about forest elephants but some generalisations of relevance to their biology are possible:

1) Tropical rain forests vary greatly in cornposition and may exhibit strong seasonality (e.g., Whitmore, 1984).

2) Fruit is an important part of forest elephant diet (Alexandre, 1978; Lieberman et al, 1987; Merz, 1931; Short, 1981; this study)

3) Densities fluctuate locally, and even regionally, perhaps in response to fruit availability (Short, 1983).

4) Group composition differs from that of savanna elephants; their smaller group sizes are possibly related to the importance of fruit in their diet (see above).

Composition of the forest in Site 2 was unusual in that the fruit of one of the dominant tree species, **Sacoglottis gabonensis** is highly palatable to elephants, but few of the other commoner trees produced such fruits. In the 1990-1991 study period the crop of ***Invingia gabonensis*** failed completely, so only one other relatively common tree, *Hexalobus crispiflorus* , produced fruit that might have attracted elephants. ***Hexalobus crispiflorus*** fruited in April 1990, at the same time as Sacoglottis gabonensis produced a minor crop. Therefore, it was possible to test whether the availability of ***Sacoglottis gabonensis*** fruits determined elephant densities.

Sacoglottis gabonensis is common throughout the coastal sedimentary basin of west and central Africa (Letouzey, 1968; de Saint Aubin, 1968) but was only discovered recently in Lope, which is outside this range (Reitsma, 1988; Williamson, 1988). At Lope it is common in an isolated area of forest estimated to cover at least 200 km2 *(C.* Wilks, personal communication; unpublished data), within which it is one of the dominant tree species (Chapter 2). Outside this area it is either absent, or occurs as scattered individuals along savanna edges, until the beginning of the sedimentary basin, about 120 km to the west. Therefore, though locally abundant, it is a limited resource in Lope.

of all elephants from an area of about *3000* km2.

In other study areas it was not possible to correlate elephant density with overall fruit availability, although elephant numbers often seemed to be locally elevated when favoured tree species were fruiting (e.g., when **Gambeya subnuda** fruited in Site 4 elephants were encountered more often than usual, an?, in 1989-90: *Irvingia gabonensis* attracted elephants into the SEGC main study **area).** This may be because tree species producing fruits favoured by elephants generally occur at low density and the ground phenology undertaken was not extensive enough to demonstrate patterns of fruit production by these rarer species (Chapter **3).**

If a greater sampling effort had been possible it is likely that relations between elephant numbers and fruit availability would have shown up in other study sites. Data from Site 2 is so clear-cut because: 1) ***Sacoglottis gabonensis*** is a dominant species; 2) it produces a fruit favoured by elephants; **3)** it has quite a short fruiting season during which large quantities of fruit are available throughout the study area; **4)** elephants respond *en masse* Thus, the pattern is easily detected. This is the first time forest elephant movements have been correlated with fruit production in an area, but this pattern is unlikely to be unique to Sacoglottis gabonensis. Short (1983) suggested that elephants migrate into parts *of* Bia National Park, Ghana, where *Mammea africana* (Guttiferae) occurs at higher densities, in order to feed on its fruit, and similar shifts in range have been noted in Korup National Park, Cameroun (B Powell, personal communication). Observation of elephants *in* Lope suggest that elephants sometimes move directly between fruiting trees when foraging, and their trails often connect individual trees of preferred species.

Therefore, elephants' response to *Sacoglottis gabonensis* fruiting probably illustrates a general feature of their biology: That their movements are geared towards maximising the availability of favoured fruit species. Barnes ***et al.*** (1991) showed that man determines the distribution of elephants in the rain forests of northeastern Gabon, where elephant densities increase with increasing distance from roads and villages. Elephants in Lopé are not subject to the same human pressures. Densities vary between sites as A result of differences in forest composition (Chapter *6)* and within sites in response to fruiting patterns. When elephant censuses are being undertaken in limited areas the possibility of large changes in density in a short time should **be** borne in mind.

Future studies should aim to evaluate whether forest elephants in the central African forests undertake migrations of Y similar scale to those observed in *some savanna* elephant populations and to assess to what extent these movements *are* likely to he disrupted by human activity Elephant migration in savanna areas has been reduced greatly by human encroachment on habitat, to the point where some populations demonstrate only vestigial migratory gestures (Buechner *et* al., 1963; Sikes, 1966) Migration is a vital adaptation to surviving in a seasonally patchy environment and has enabled elephants to exploit every habitat available in Africa, even where these habitats could not support a permanent population (Sikes, 1971) Where elephants have been confined to limited protected areas, artificially elevated densities of permanently resident elephants have often resulted in severe habitat degradation (e.g , Buechner & Dawkins, 1961; Laws, 1970; Laws et al, 1975)

There is no evidence that forest elephants cause similar habitat modification, although they certainly play an important role in forest ecology (Jones, 1955; Kortlandt, 1984; Laws, 1970; Martin, 1991; Western, 1989; Wing & Suss, *1970)*, but if traditional migratory routes are eliminated by human activity and forest elephant communities are isolated into contracting home ranges, this possibility cannot *be* ruled out in the future