

Food plants of forest elephants and their availability in the Kakum Conservation Area, Ghana

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Abstract

The diet of elephants in the Kakum Conservation Area, Ghana, was studied from July 2001 to June 2002. Elephants ate fruits and other components of 34 plant species. An examination of elephant dung piles yielded fruit fragments representing 29 species, while data on fresh feeding signs showed an extra 5 plant species, either browsed upon or barked. The quantity and diversity of fruits eaten showed seasonal differences. Fruit availability in the park correlated to forest fruits consumed but was inversely correlated to cultivated crops consumed. Fruit was most available in October, least available in June. Barking activities were high in closed-canopy areas and browsing in open-canopy areas.

Résumé

Le régime alimentaire des éléphants de l'Aire de Conservation de Kakum, au Ghana, a été étudié de juillet 2001 à juin 2002. Les éléphants mangent des fruits et d'autres parties de 34 espèces végétales. L'examen des crottes a permis de récolter des morceaux de fruits de 29 espèces tandis que les données sur les signes d'aliments frais désignaient cinq espèces végétales supplémentaires, soit broutées soit écorcées. La quantité et la diversité des fruits consommés présentaient des différences saisonnières. La disponibilité des fruits dans le parc était en corrélation avec les fruits de forêt consommés et inversement proportionnelle aux plantes cultivées consommées. Les fruits étaient surtout abondants en octobre, et moins abondants en juin. L'écorçage était fréquent dans les endroits où la canopée est fermée et le broutage plutôt là où la canopée est ouverte.

Introduction

Few studies have been conducted on the diet of forest elephants in Ghana (Short 1981; Martin 1982; Liebermann et al. 1987; all in Bia National Park, Ghana) or elsewhere in West Africa (Alexandre 1978 in Tai National Park, Côte d'Ivoire; Merz 1981; Theuerkauf et al. 2000 in Bossematie Forest Reserve, Côte d'Ivoire).

It has been suggested that West African elephants are a separate species from other African elephants (Eggert et al. 2003) hence more information is needed on their foraging ecology to properly develop management strategies for their conservation. More research on the dependence of these elephants on seasonal fruit resources is also important for their

long-term conservation (Dudley et al. 1992). This is especially true since their protection is high on the conservation agenda in the subregion (AfESG 1999) and particularly in Ghana (Ghana WD 2000).

Study area

The Kakum Conservation Area (KCA) is made up of Kakum National Park and the adjacent Assin Attandanso Resource Reserve (fig. 1). It encompasses an irregular block of forest measuring 366 km², consisting mainly of *Celtis zenkeri* and *Triplochiton scleroxylon* moist semideciduous vegetation, which is transitional to the more typical rainforest *Lophira alata*–*Triplochiton scleroxylon* association in the southern part of Kakum Reserve (Dudley et al. 1992).

Materials and methods

To equalize sampling effort, KCA was classified into 10 blocks approximately 36 km² each: Adiembra, Aboabo, Ahomaho, Afiaso, Asomdwee, Antwikwaa, Briscoe I, Briscoe II, Mfuom and Park Headquarters (fig. 1).

Dung examination

In each block, elephant trails were followed to locate undisturbed and relatively new elephant dung piles in categories A to B (Barnes and Jensen 1987). Distance between selected dung piles was more than 5 m to ensure that samples taken were independent deposits (Yumoto and Maruhashi 1995).

Dung piles were examined in situ; 30 dung piles per month, 3 per block, were meticulously examined by carefully sifting the piles and recording the number and type of seeds, fruit and leaf fragments, and seedlings (Short 1981; White et al. 1993; Muoria et al. 2001; Blake 2002). The frequency of occurrence of forest fruits and cultivated crop fragments in dung piles was also estimated for each month. Unidentified seeds, seedlings, fruit and leaf fragments were sent to the University of Cape Coast Herbarium for identification.

Dung components were broadly classified as seeds, fibre, leaf fragments and unidentified remains. Their abundance was quantified on a 4-point scale of relative abundance: up to 25% abundance of a particular component was considered 'rare' and given 1 point; 25–50%, 'few', 2 points; 50–75%, 'common', 3 points; more than 75%, 'abundant', a full 4 points (White et al. 1993). Monthly averages

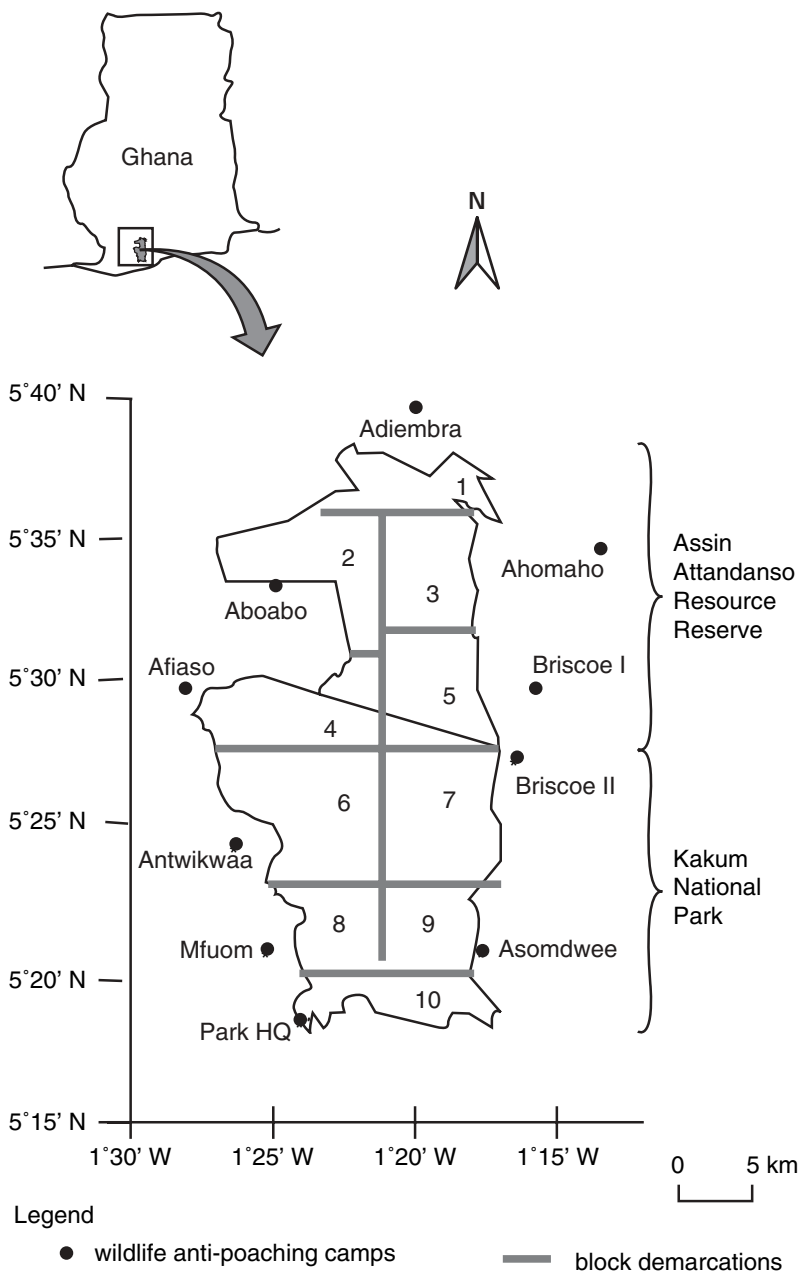


Figure 1. The Kakum Conservation Area showing the 10 classified blocks.

The rainfall pattern is bimodal: two rainfall seasons separated by a short dry spell in August. The major season is between March and July with a peak in June, and the minor season between September and November with a peak in October. There is also a main dry season from December to February or March, when many water-courses dry up.

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(nearest whole number) per dung component were computed by dividing the total points per component by number of dung piles each month.

An existing record (Nyame 1999) on the average seed content per fruit of each species was used to estimate fruit consumption per dung pile. Data were compiled for a large sample of fruits of the species (> 50 fruits), noting the average number of seeds per fruit per species.

Examination of feeding signs

Four blocks—Park Headquarters, Antwikwaa, Briscoe II and Ahomaho—were randomly selected out of the 10, based on a numbered system, and a strip transect for viewing elephant feeding signs was constructed in each. To increase the likelihood of observing elephant feeding signs and minimize vegetation damage when cutting new transects, viewing transects were constructed by linking up elephant trails. Thus were established four non-linear strip transects approximately 3.4 km long and 10 m wide.

Fresh feeding signs that could be attributed with certainty to elephants (directly by sight or indirectly by association with footprints or dung) were inspected monthly on transects, and species and parts consumed noted (White et al. 1993; Blake 2002). Vegetation type was classified as open or closed forest canopy based on the presence or absence of canopy gaps (> 5 m) within a 5-m radius from where the feeding activity was observed. Feeding was classified as leaf stripping, removing terminal twigs, or barking (Short 1981).

Fruit availability

Trees with diameter at breast height (dbh) greater than 0.01 m whose fruits are important elephant food sources (Merz 1981; Short 1981; White et al. 1993; Theuerkauf et al. 2000) were marked as encountered along and within 5 m of each side of the strip transects.

Fruit availability of marked species was monitored every two weeks by counting and recording the number of fresh fallen fruits within and along the strip transects (White et al. 1993; Chapman et al. 1994). Fruit availability was expressed as number of fruits per square kilometre.

Results

Dung examination

Three hundred and sixty elephant dung piles were examined yielding seeds and seedlings, fruits, and leaf fragments representing 29 species of which 26 were forest fruit trees (table 1) and three cultivated crops (*Carica*, *Dioscorea* and *Citrus* species)

There was a distinct seasonal difference in the quantity (Kruskal-Wallis one-way analysis of variance $H = 8.344$, $df = 3$, $p < 0.05$) and number of species ($H = 8.698$, $df = 3$, $p < 0.05$) that elephants consumed. The highest quantity (1688) and number of species (21) consumed occurred in the minor wet season, while these variables were least (quantity 60; number of fruit species 8) during the short dry period in August. Similarly, fruit density per dung pile was highest (18.8) in the minor wet season and least (2.0) during the short dry period (table 1). *Panda* was the most abundantly eaten species. *Desplatsia* and *Strychnos* species were eaten throughout the year while species of *Aningeria*, *Antiaris*, *Ficus*, *Milicia*, *Strombosia* and *Treculia* were eaten seasonally.

Elephant food contained more fibre during the major wet season (March to July) and a high proportion of seeds from minor wet season to early dry season (September to January). There were unidentified dung components in June (table 2).

Feeding signs

Thirteen species of plants were recorded either browsed or barked with eight previously registered during dung examination (table 3). Thus only five new species were added. Leaf and twig stripping (browsing) accounted for 58% of the feeding signs whereas barking formed 42%.

Apart from *Antrocaryon micraster*, all browsed tree species were saplings (dbh < 0.03 m). However, with the exception of *Musanga cecropioides*, barking activities occurred on bigger trees (dbh > 3 m). The stem of *Combretum oyemense*, a liana, was frequently chewed entirely. Elephants selectively browsed (95%) in open canopy forests (G -test of independence $G = 12.566$, $df = 1$, $p < 0.05$) and barked (87%) in closed canopy forests ($G = 8.014$, $df = 1$, $p < 0.05$). To sum up, elephants ate fruits and other components of 34 plant species including *Carica*, *Dioscorea* and *Citrus* species. Trees represented 85%, climbers 9%, and shrubs 6%.

Table 1. Type and quantity of forest fruit species (mean number of fruits per dung pile) found in dung piles in each season. Scientific names following Hutchison and Dalziel (1954–1972)

Family	Fruit species	Season				Total fruit consumed/ (percentage)
		Long wet (Mar–Jul)	Short dry (August)	Short wet (Sep–Nov)	Major dry (Dec–Feb)	
Anacardiaceae	<i>Antrocaryon micraster</i>	0	0	94 (1.0)	24 (0.3)	118 (3.7)
Chrysobalanaceae	<i>Parinari excelsa</i>	0	0	20 (0.2)	122 (1.4)	142 (4.5)
Euphorbiaceae	<i>Riciodendron heudelotii</i>	20 (0.1)	19 (0.6)	230 (2.6)	0	269 (8.4)
Euphorbiaceae	<i>Uapaca guineensis</i>	6 (0.04)	4 (0.1)	32 (0.4)	19 (0.2)	61 (1.9)
Guttiferae	<i>Mammea africana</i>	0	0	59 (0.7)	16 (0.2)	75 (2.4)
Irvingiaceae	<i>Irvingia gabonensis</i>	0	0	21 (0.2)	26 (0.3)	47 (1.5)
Irvingiaceae	<i>Klainedoxa gabonensis</i>	0	0	153 (1.7)	40 (0.4)	193 (6.1)
Loganiaceae	<i>Strychnos aculeata</i>	100 (0.7)	6 (0.2)	48 (0.5)	15 (0.2)	169 (5.3)
Mimosoideae	<i>Tetrapleura tetraptera</i>	7 (0.05)	4 (0.1)	41 (0.5)	39 (0.4)	91 (2.9)
Moraceae	<i>Aningeria robusta</i>	0	0	43 (0.5)	0	43 (1.3)
Moraceae	<i>Antiaris africana</i>	0	0	0	41 (0.5)	41 (1.3)
Moraceae	<i>Ficus capensis</i>	123 (0.8)	0	0	0	123 (3.9)
Moraceae	<i>Microdesmis puberula</i>	0	0	36 (0.4)	62 (0.7)	98 (3.1)
Moraceae	<i>Milicia excelsa</i>	186 (1.2)	0	0	0	186 (5.8)
Moraceae	<i>Musanga cecropioides</i>	8 (0.05)	0	4 (0.04)	0	12 (0.4)
Moraceae	<i>Myrianthus arboreus</i>	0	0	100 (1.1)	16 (0.2)	116 (3.6)
Moraceae	<i>Treculia africana</i>	25 (0.2)	0	0	0	25 (1.0)
Myristicaceae	<i>Pycnanthus angolensis</i>	4 (0.03)	2 (0.1)	34 (0.4)	12 (0.1)	52 (1.6)
Ochnaceae	<i>Strombosia glaucescens</i>	0	0	40 (0.4)	0	40 (1.3)
Olaceae	<i>Ongokea gore</i>	0	0	203 (2.3)	64 (0.7)	267 (8.4)
Palmae	<i>Raphia</i> sp.	89 (0.6)	13 (0.4)	50 (0.6)	24 (0.3)	176 (5.5)
Pandaceae	<i>Panda oleosa</i>	62 (0.4)	0	269 (3.0)	57 (0.6)	388 (12.2)
Sapotaceae	<i>Omphalocarpum ahia</i>	22 (0.1)	2 (0.1)	2 (0.02)	3 (0.03)	29 (1.0)
Sapotaceae	<i>Tieghemella heckelii</i>	0	0	47 (0.5)	114 (1.3)	161 (5.0)
Tiliaceae	<i>Desplatsia dewevrei</i>	47 (0.3)	10 (0.3)	162 (1.8)	11 (0.1)	230 (7.2)
Zygophyllaceae	<i>Balanites wilsoniana</i>	26 (0.2)	0	0	11 (0.1)	37 (1.2)
	Total	725 (4.8)	60 (2.0)	1688 (18.8)	716 (8.0)	(100)

Table 2. Average abundance of seeds of forest fruit species, fibre, leaf fragments and unidentified remains in elephant dung piles in each month

Dung component	Month												Total points	Overall percentage
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun		
Seeds	1	1	2	3	3	3	3	2	1	1	1	1	22	32
Fibre	4	4	3	1	2	2	2	3	3	3	4	4	35	52
Leaf fragments	1	1	0	0	0	0	1	1	1	1	2	2	10	15
Unidentified remains	0	0	0	0	0	0	0	0	0	0	0	1	1	1

Fruit availability

Overall fruit availability showed a highly significant relationship with fruit consumption ($r^2 = 0.711, p < 0.05$) (fig. 2). Individually, *Panda* ($n = 7, r = 0.921, p < 0.005$), *Parinari* ($n = 4, r = 0.991, p < 0.01$) and *Tieghemella* ($n = 4, r = 0.984, p < 0.05$) species displayed significant correlations with the remaining fruit species being insignificant.

The forest fruits or cultivated crop species that elephants ate varied with fruit availability across

months (fig. 3). The highest fruit availability levels of the late minor wet season to the early dry season (October to January) resulted in the highest intake of forest fruits and reduced the consumption of cultivated crops. In contrast, in the major wet season (peak in June) consumption of cultivated crop species was highest and availability and consumption of fruit the least. Fruit availability correlated ($r = 0.908, p < 0.01$) to the presence of forest fruits in the dung piles but was inversely correlated ($r = -0.583, p < 0.05$) to the consumption of cultivated crops.

Table 3. Plant species browsed or barked by elephants. Fruits of species marked with asterisk (*) are also eaten. Scientific names following Hutchison and Dalziel (1954–1972)

Family	Tree species	Life form	Mean		Forest type	Activity observed	
			Dbh (m)	Feeding height (m)		Browsing	Barking
Anacardiaceae	<i>Antrocaryon micraster</i> *	tree	3.200	2.4	closed	1	2
Combretaceae	<i>Combretum oyemense</i>	liana	0.021	1.2	closed	–	6
Euphorbiaceae	<i>Uapaca guineensis</i> *	shrub	0.009	1.0	open	2	–
Loganiaceae	<i>Strychnos aculeata</i> *	liana	0.025	1.0	open	2	–
Meliaceae	<i>Entandophragma angolense</i>	tree	3.200	3.0	closed	–	2
Meliaceae	<i>Trichilia prieureana</i>	shrub	0.022	1.0	open	1	–
Mimosoideae	<i>Albizia zygia</i>	tree	0.021	1.0	open	1	–
Moraceae	<i>Aningeria robusta</i> *	tree	0.026	1.5	open	3	–
Moraceae	<i>Ficus capensis</i> *	tree	0.022	1.2	open	2	–
Moraceae	<i>Musanga cecropioides</i> *	tree	0.028	1.5	open	5	2
Moraceae	<i>Myrianthus arboreus</i> *	tree	0.012	2.0	open	2	–
Papilionoideae	<i>Baphia afzelia</i>	shrub	0.019	1.0	open	2	–
Sapotaceae	<i>Tieghemella heckelii</i> *	tree	3.600	2.6	closed	–	3

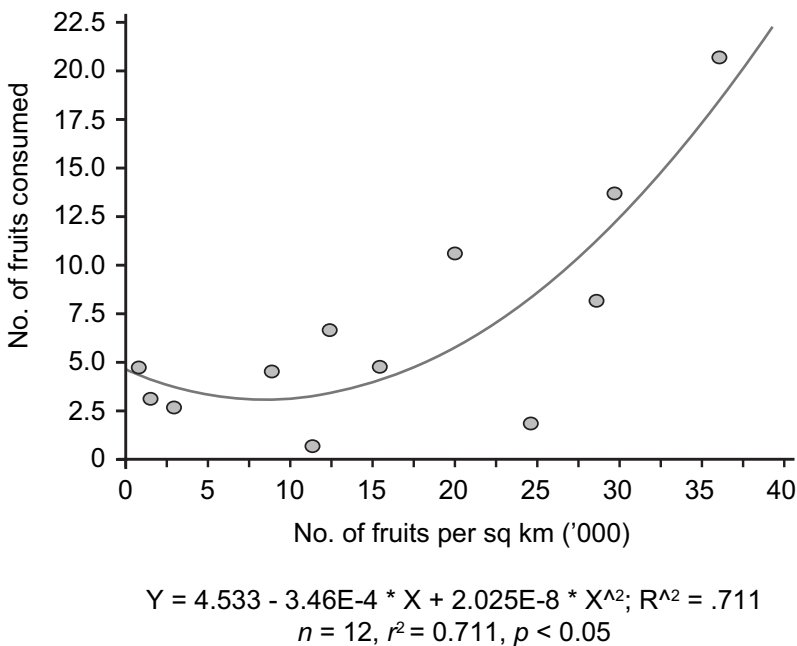


Figure 2. Relationship between fruit availability and elephant fruit consumption in the Kakum Conservation Area.

Discussion

Dung examination and fruit availability

The study enumerated 34 plant species in the diet of elephants at KCA. The bulk of the diet in number of

species and quantities eaten came from fruits, leaves, twigs and bark. Trees represented 85% of the species that elephants fed on in KCA. Similarly, White et al. (1993) reported that trees were 73.5% of consumption in Lopé Reserve, Gabon. Our sample of 360 dung piles in KCA is similar to the 311 dung piles that White et al. (1993) inspected at Lopé Reserve. However, soil and fungi, which elephants in Lopé Reserve were reported to have eaten, were not observed in the diet of elephants in KCA.

Differences in digestibility make difficult any detailed discussion of the relative quantities of plant parts that were ingested. However, the presence of seeds in all dung piles

shows the importance of fruits in elephant diet (Wing and Buss 1970; Short 1981; White et al. 1993 (in 82% of dung piles); White 1994; Muoria et al. 2001 (in 64.5% of dung piles)) and their significance as seed-dispersal agents (Alexandre 1978; Short 1981; Lieberman et al. 1987; White et al. 1993; Muoria et al.

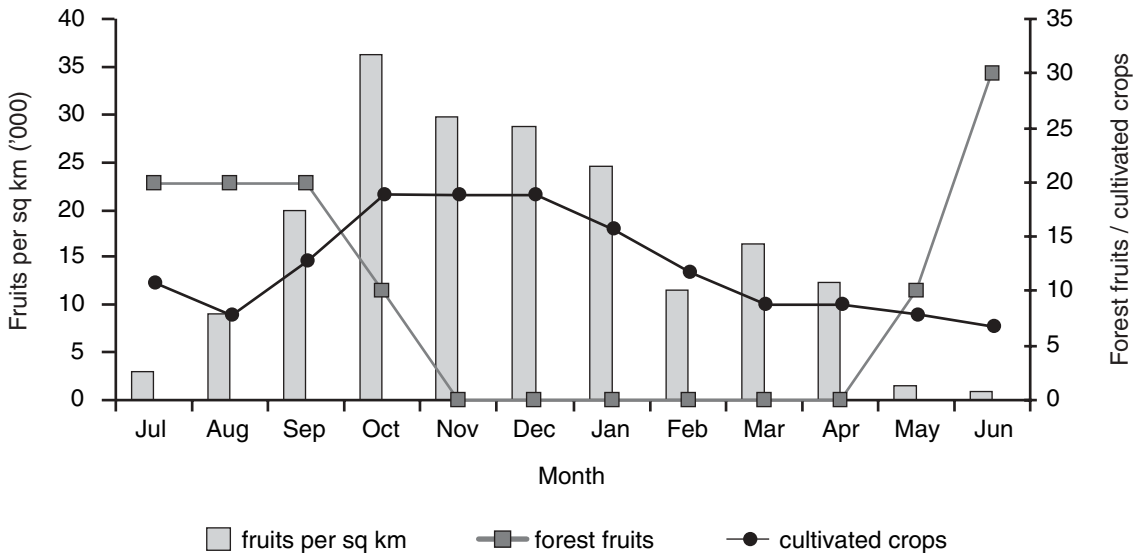


Figure 3. Frequency per dung pile of forest fruits and cultivated crop fragments in relation to fruit availability each month.

2001; Waithaka 2001; Blake 2002). In KCA elephants disseminated seeds of at least 29 species of forest trees in their dung piles. Other animal groups like birds, rodents, monkeys, duikers and antelopes also disperse many of these species; hence it may be that only a few tree species really depend directly on elephants for their survival (Hawthorne and Parren 2000). Possibly large mammals such as elephants may better disperse seeds by conveying them over a wider area than other animals (Yumoto and Maruhashi 1995). Also, plants with large seeds such as *Tieghemella* sp., *Panda* sp. and *Parinari* sp., which usually would not be swallowed by other animal groups, stand a better chance of avoiding 'seed shadow' by being dispersed at suitable places by elephants. Hawthorne and Parren (2000) also reported improved regeneration rates of *Panda* and *Balanites* species with passage through elephant gut.

Generally, elephants are known to feed on a wide variety of plant species (Barnes 1982; Yumoto and Maruhashi 1995; Dudley 1999). Research on forest elephant feeding ecology in Nouabalé-Ndoki National Park in northern Congo has shown that elephants have a general diet comprising more than 350 species (Blake 2002). At Lopé, the diet of elephants was also diverse and constituted 230 plant species with 73.5% from trees (White et al. 1993). Furthermore, the Lopé elephants barked trees from a wide range of 87 plant species (White et al. 1993). At KCA, however, elephants

had a rather narrow diet of 34 plant species with 85% from trees; they barked only 4 tree species. This may seem unusual considering the extent of plant diversity that occurs in tropical forests. However, elephants may be restricted in the range of foods they consume in KCA because the number of preferred species is limited (Short 1981).

There is a distinct difference in the quantity and number of fruit species (diversity) eaten seasonally (White et al. 1993). In KCA, the threshold fruit density (approximately 15,000 fruits/km²) influences elephant feeding behaviour. As fruit density increases beyond the threshold (from minor wet to early dry season), elephants consume the available fruits with increasing rapidity. During this period, they are probably less attracted to other sources of food and hence the absence of cultivated crops in their diet. Large quantities of seeds are present in the dung piles, which are low in fibre and leaf fragments. When fruit density falls below the threshold, elephants possibly use a different feeding strategy to compensate for the lack of fruit and tend to depend much more on supplementary food, including foliage and bark. Reduced consumption of fruits and increased consumption of supplementary foods is responsible for the decreased seed content but increased fibre and leaf fragment content of dung piles for the period. An increased level of cultivated crop fragments (suggesting an increase in crop-raiding activity) and the presence of uniden-

tified components in elephant dung piles all indicate a shift in elephant feeding behaviour (Danquah 2003).

Dudley et al. (1992) speculated that a reduction in the number of fruiting trees (due to logging) in KCA, has stimulated elephants to sometimes go outside the forest to raid crops, but they provided no evidence. Barnes et al. (1995) suggested that if the hypothesis were true, it would mean that yesterday's loggers are partly responsible for today's crop-raiding problems in KCA. Recently Danquah (2003) reported that due to logging there has been a significant reduction in tree densities of large timber species whose fruits elephants eat. Hence fewer trees than previously are likely to result in poor fruit availability, especially in minor fruiting seasons. There is an inverse correlation between fruit availability in the forest and consumption of cultivated crops, which provides the evidence to support Dudley et al. (1992). Elephants ate fewer cultivated crops outside the forest when fruit availability in the forest was high, and elephant crop-raiding activity increased during the major wet season with reduced fruit availability. It is likely that other factors act together with insufficient quantity of fruit to encourage elephants to raid farm crops. Seasonal migration of forest elephants (Short 1983) and changes in their use of habitat (Blake 2002) in response to fruit availability have been intimated as reasons for crop raiding.

Dudley et al. (1992) did not record elephants eating citrus, yet this study found citrus seeds in elephant dung piles. Recently established citrus plantations close to the south-eastern edge of KCA might have influenced this elephant adaptation. Barnes et al. (2003) reported strong correlation between distance from the boundary of KCA to maize farms and frequency of elephant crop raids, yet this study did not record maize seeds in dung, possibly due to their high digestibility. Farmers also complained of emerging cases of elephants eating cocoa fruits, but no cocoa seeds were found in the dung sampled. It is also possible that elephants involved in this act are few and that the study missed their dung piles. Nonetheless, the large-scale expansion of cocoa farms around almost all sides of the park suggests the potential of elephants adapting to cocoa fruits growing in close proximity to the park. This is a serious signal to park management to discourage farming and destruction of forest close to the conservation area to avert the problem of elephants adapting to new sources of food outside protected areas.

Seeds of *Strychnos aculeata* and *Desplatsia dewevrei* were found regularly in dung piles throughout the study period. Short (1981) also found *Strychnos aculeata* in dung throughout the year. Apart from longer fruiting periods, these fruits possess extra hard outer coats and are able to persist on the forest floor for a long time without decaying. Such characteristics enable them to serve as a source of fruit for a long time, even when their fruiting season is long past. Nevertheless, elephants relied heaviest on *Panda oleosa*, *Parinari excelsa* and *Tieghemella heckelli*. Such species fruit for only short periods and deteriorate rapidly and thus are available only briefly. Therefore, consumers with relatively small home ranges such as small primates may experience reduced fruit resources, unlike elephants, which have large home ranges and will move within them to find these fruits.

Feeding signs

Entandophragma and *Tieghemella* species found barked by Short (1981) in Bia National Park, Ghana, were also barked in KCA. *Antrocaryon micraster*, which occurs in both locations, was barked only in KCA. Barking of trees is likely to have a very severe effect on tree species that occur in low densities since barking formed a significant proportion of feeding activity. This aspect of elephant feeding behaviour, which is targeted at bigger trees, should be of great concern to park management. Short (1981) reported that *Guibourlia ehia* became vulnerable to termite attack after being barked. Struhsaker et al. (1996) observed that elephant damage to larger trees in the form of bark damage exposes the wood to attack by beetles and fungi. Elephants, however, browsed much more on saplings than on bigger trees (Struhsaker et al. 1996). Barnes (1982) argued that the anatomy of the elephant's digestive system makes it more sensitive than a ruminant to toxic secondary plant compounds; hence, elephants avoid eating larger, more mature plants. Elephants perpetuate clearings and secondary forests by continuously browsing and trampling on immature plant communities (Struhsaker et al. 1996).

Generally it is accepted that forest elephants prefer secondary forests that follow logging to primary parts of rainforests (Barnes et al. 1991; Struhsaker et al. 1996) because of the abundance of palatable browse species. Barnes et al. (1991) also found elephants in Gabon abundant in secondary forests if there was no hunting. Theuerkauf et al. (2000), however, argued that the

assumption that forest elephants prefer secondary forest might not be valid under certain habitat conditions. According to Theuerkauf et al. (2001), in heavily exploited forests that were too degraded to offer optimal conditions for elephants, such as in the Bossematie Forest Reserve, elephants rather preferred parts of the forest with high canopy cover, obtaining fruits from the remaining mature trees. Dudley et al. (1992) also stated that the fruiting trees on which forest elephants depend for both fruits and bark are more abundant in primary forest and therefore elephants prefer such habitats. However, this study found no evidence to reject either claim. Our results indicate that elephants tend to bark more trees and browse plants in closed-canopy primary forests than in open-canopy secondary forests (Short 1981). Similarly, White et al. (1993) and Merz (1981) indicated that resources in secondary forests combined with resources of the primary forest offer the forest elephant the best possible living conditions. Barnes (1982) noted that because elephants lack a rumen they do not benefit from the synthesis of amino acids and vitamins by rumen bacteria. Hence one can assume that in KCA, elephants eat both vegetation types to provide the necessary range of nutrients and achieve good nutrition.

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References

- [AfESG] African Elephant Specialist Group. 1999. Strategy for the conservation of West African elephants. AfESG, Ouagadougou.
- Alexandre DY. 1978. Le rôle disseminateur des éléphants en forêt de Tai, Côte d'Ivoire. *La Terre et la Vie* 32:47–72.
- Barnes RFW. 1982. Elephant feeding behaviour in Ruaha National Park, Tanzania. *African Journal of Ecology* 20:123–136.
- Barnes RFW, Azika S, Asamoah-Boateng B. 1995. Timber, cocoa and crop-raiding elephants: a preliminary study from southern Ghana. *Pachyderm* 19:33–38.
- Barnes RFW, Barnes KL, Alers MPT, Blom A. 1991. Man determines the distribution of elephants in the rainforests of north-eastern Gabon. *African Journal of Ecology* 29:54–63.
- Barnes RFW, Boafo Y, Nandjui A, Dubiure UF, Hema EM, Danquah E, Manford M. 2003. *An overview of crop raiding by elephants around the Kakum Conservation Area. Parts 1 and 2.* Elephant Biology and Management Project, Africa Program, Conservation International, USA. Unpublished.
- Barnes RFW, Jensen KL. 1987. How to count elephants in forests. *IUCN African Elephant Specialist Group Technical Bulletin* 1:1–6.
- Blake S. 2002. The ecology of forest elephant distribution and its implications for conservation. PhD dissertation, University of Edinburgh, Edinburgh.
- Chapman CA, Wrangham R, Chapman LJ. 1994. Indices of habitat wide fruit abundance in tropical forests. *Biotropica* 26:160–177.
- Danquah E. 2003. Feeding behaviour of the forest elephant and logging impact on fruit production in the Kakum Conservation Area. MPhil dissertation, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana. Unpublished.
- Dudley JP, Mensah-Ntiamoah AY, Kpelle DG. 1992. Forest elephants in a rainforest fragment: preliminary findings from a wildlife conservation project in southern Ghana. *African Journal of Ecology* 30:116–126.
- Dudley JP. 1999. Seed dispersal of *Acacia erioloba* by African bush elephant in Hwange National Park, Zimbabwe. *African Journal of Ecology* 37:375–385.
- Eggert LS, Eggert JA, Woodruff DS. 2003. Estimating population sizes for elusive animals: the forest elephants of Kakum National Park, Ghana. *Molecular Ecology* 12:1389–1402.
- Ghana. Wildlife Division. 2000. *Strategy for the conservation of elephants in Ghana.* Wildlife Division, Forestry Commission, Accra.
- Hawthorne DN, Parren MPE. 2000. How important are forest elephants to the survival of woody plant species in the Upper Guinea forests? *Journal of Tropical Ecology* 16:33–150.
- Hutchison J, Dalziel JM. 1954–1972. *Flora of tropical West Africa.* Crown Agents, London.

- Lieberman D, Lieberman M, Martin C. 1987. Notes on seeds in elephant dung from Bia National Park, Ghana. *Biotropica* 19:365–369.
- Martin C. 1982. Management plan for the Bia conservation areas. IUCN/WWF Project 1251. Wildlife Division, Forestry Commission, Accra, Ghana, Unpublished.
- Merz G. 1981. Recherches sur la biologie de nutrition et les habitats préférés de l'éléphant de forêt *Loxodonta africana cyclotis* Matschie, 1900. *Mammalia* 45:299–312.
- Muoria PK, Gordon I, Ouge NO. 2001. Elephants as seed dispersal agents in Arabuko-Sokoke Forest, Kenya. *Pachyderm* 30:75–80.
- Nyame J. 1999. Field notes: types of trees and fruits in the Kakum Conservation Area. Kakum Ecological Centre, Kakum, Cape Coast, Ghana. Unpublished.
- Short J. 1981. Diet and feeding of forest elephants, Bia National Park. *Mammalia* 45:177–186.
- Struhsaker TT, Lwanga JS, Kasenene JM. 1996. Elephants, selective logging and forest regeneration in the Kibale Forest, Uganda. *Journal of Tropical Ecology* 12:45–64.
- Theuerkauf J, Ellenberg H, Waitkuwait WE, Muhlenberg M. 2001. Forest elephant distribution and habitat use in the Bossematie Forest Reserve, Ivory Coast. *Pachyderm* 30:37–43.
- Theuerkauf J, Waitkuwait WE, Guiro Y, Ellenberg H, Porembski S. 2000. Diet of forest elephants and their role in seed dispersal in the Bossematie Forest Reserve, Ivory Coast. *Mammalia* 64:447–460.
- Waithaka J. 2001. Elephants as seed dispersal agents in Aberdare and Tsavo National Parks, Kenya. *Pachyderm* 30:70–74.
- White LJT. 1994. *Sacoglottis gabonensis* fruiting and the seasonal movements of elephants in the Lope Reserve, Gabon. *Journal of Tropical Ecology* 10:121–125.
- White LJT, Tutin CEG, Fernandez M. 1993. Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie, 1900, in the Lopé Reserve, Gabon. *African Journal of Ecology* 31:181–199.
- Wing LD, Buss IO. 1970. *Elephants and forests*. Wildlife Monograph 19. Wildlife Society, Washington, DC. 92 p.
- Yumoto T, Maruhashi T. 1995. Seed dispersal by elephants in a tropical rainforest in Kahuzi-Biega National Park, Zaire. *Biotropica* 27(4):526–530.