
Forest elephant group composition, frugivory and coastal use in the Réserve de Faune du Petit Loango, Gabon

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Abstract

Results of a 16-month study of forest elephant (*Loxodonta africana cyclotis* Matschie) group size and composition, coastal use and frugivory are presented from the Réserve de Faune du Petit Loango, Gabon (now the Parc National de Loango). Mean forest elephant group size was 2.2 (n = 140) including solitary animals, and 3.1 excluding solitaires. Elephants consumed fruits of at least 49 species, and of the 220 elephant dungpiles examined, 185 (84.1%) contained seeds and 203 (92.3%) contained the remains of fruits (seeds and/or pulp). The mean number of seed species per dungpile (\pm SD) was 2.01 ± 1.49 , and the mean number of fruit species was 2.28 ± 1.43 . Elephants used the coastal habitat more during warmer months, and during the afternoon than the morning. It is hypothesized that coastal habitat use is related to sodium intake through consumption of salt-coated vegetation.

Key words: elephant, forest, frugivory, Gabon, Loango, rain forest

Résumé

Cet article présente les résultats d'une étude de 16 mois portant sur la taille et la composition des groupes d'éléphant de forêt (*Loxodonta africana cyclotis* Matschie), sur leur fréquentation de la côte et leur consommation de fruits dans la Réserve de Faune du Petit Loango (aujourd'hui Parc National de Loango) au Gabon. La taille moyenne du groupe d'éléphants de forêt était de 2.2 individus (n = 140), y compris les animaux solitaires, et de 3.1, solitaires non compris. Les éléphants consommaient des fruits d'au moins 49 espèces différentes et, sur les 220 tas de crottes d'éléphant examinés, 185 (84.1%)

contenaient des graines et 203 (92.3%) contenaient des restes de fruits (semences et/ou pulpe). Le nombre moyen d'espèces de graines par tas de crottes (\pm SD) était de 2.01 ± 1.49 , et le nombre moyen d'espèces de fruits était de 2.28 ± 1.43 . Les éléphants fréquentaient plus les habitats côtiers pendant les mois plus chauds, et plus l'après-midi que le matin. On émet l'hypothèse que la fréquentation de l'habitat côtier est liée à l'absorption de sodium, par la consommation de la végétation couverte de sel.

Introduction

Direct observations of elephants in forested habitats are rare and potentially dangerous, but in certain regions of Central Africa there are open areas within forests ('bais'), some of which serve as mineral licks for a wide range of mammals and where elephants can be observed at a distance (e.g. Dzanga, C.A.R., Turkalo & Fay, 1995; Maya, Congo, Querouil, Magliocca & Gautier-Hion, 1999). Elephants may also be observed in savanna areas (e.g. Lopé, Gabon, White, Tutin & Fernandez, 1993) or coastal forest scrub (Petit Loango, Gabon, Morgan & Lee, 2003).

Forest elephants are physically smaller than their savanna counterparts (Morgan & Lee, 2003), and genetic studies suggest they be reclassified as a distinct species (Roca *et al.*, 2001). Forest elephants are thought to spend most of the time in small groups with a core social structure of a mother–calf pair (White *et al.*, 1993). Male forest elephants, like their savanna counterparts, are not associated with specific matriline, but are dispersed between the female groups, and, although young males occasionally join their maternal groups, they do not consistently remain within them (Turkalo & Fay, 1995). Very little is known about how family bonds, if they exist, are maintained in forests with large (potential) home ranges, and it has been suggested that forest elephants may rely more

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heavily on infra-sound (e.g. McComb *et al.*, 2000) as a means of social cohesion and social knowledge, as their high dispersion within low visibility habitats may have increased the need for alternative auditory and olfactory mechanisms for recognition and movement co-ordination.

Alexandre (1978) first documented the qualitative importance of fruit in the diet of forest elephants. Subsequent dietary studies have shown that the bulk of the diet is composed of leaves, woody material and bark (Merz, 1981; Short, 1981; White *et al.*, 1993) or grass (Tchamba & Seme, 1993). Despite this domination by stems and foliage throughout the year, forest elephants are undoubtedly important frugivores and seed dispersal agents (Lieberman, Lieberman & Martin, 1987; White *et al.*, 1993; Maurois, Chamberlain & Maréchal, 1997). Short (1983) noted large-scale elephant migrations in response to seasonal fruiting patterns in the Tai forest, Côte d'Ivoire, and White (1994) noticed seasonal movements in the Lopé Reserve, an area rich in *Sacoglottis gabonensis* (Baill.) Urb. fruits.

This study examined aspects of forest elephant ecology in the coastal area of the Réserve de Faune du Petit Loango, Gabon from September to November 1997, throughout 1998, and in May 1999. At this site, elephants can be clearly observed on the coastal scrub (Greth, 1997; Morgan, 2001). The aims of this study were to (i) assess frequency of and possible explanations for coastal habitat use by elephants; (ii) determine group size and composition; (iii) determine the importance of frugivory in the diet of forest elephants at Petit Loango.

Methods

The Réserve de Faune du Petit Loango (now within the Parc National de Loango) is situated on the south-west coast of Gabon. Vegetation analysis within the 20 km² study area indicated a complex mosaic of closed- and open-canopy forest, secondary forest, swamp areas, savannas, coastal scrub and *Sacoglottis gabonensis*-dominant forest. Climate at Petit Loango is described in detail elsewhere (Morgan, 2001). Total annual rainfall in 1998 was 2363 mm, and was strongly seasonal with six consecutive months with <70 mm rain (April–September). There was a minor dry season in January–February, which varies in intensity and duration inter-annually.

In order to minimize repeated measures of group composition on the same groups, individual elephants were identified following Moss (1993). Tusk size and shape, ear

features, and body shape, size and oddities were recorded with identification photographs of ear and full-body profiles wherever possible. Sex was determined for adult animals by head shape and genitalia. Adult age classes were ascribed by tusk diameter and body and head shape. For immature animals, height relative to that of the mother and to a lesser extent, tusk formation aided in age determination. Infants were defined as <2 years old and juveniles between 2 and 10 years of age. Group size counts included all individuals within 50 m of any other elephant. Only observations in open habitats (savannas and coastal scrub) were used in calculations of group size and composition.

Faecal analysis followed methods described for apes (Tutin & Fernandez, 1994). Elephant dungpiles were usually inspected *in situ* (n = 220), although randomly selected boli were taken to camp for further analysis (n = 51), where they were weighed, placed in a sieve of 1-mm mesh size, and agitated in water until the matrix was fully disturbed and the water ran clear. Remains were sun-dried and inspected. Elephants are known to be seeds predators on many species and thus broken seeds in dungpiles were also examined. A reference collection was maintained of every seed and undigested fruit pulp, and unidentified species were compared with fresh fruit specimens from phenological surveys.

Opportunistic surveys by foot (n = 81) or vehicle (n = 25) along the beach were used to document coastal habitat use by elephants. (These surveys represented optimal conditions for observing elephants on the coast, and do not necessarily reflect elephant 'density' within the study site.) Weather, time of day and tidal state were noted for each survey. All elephants were noted, with group size, composition, activity, response to observer and proximity to other groups and species. In the afternoon, the south-westerly winds allowed for slowly approaching elephants to within 5 m without detection, even when apparently in full sight of the animals. This supports the suggestion by several authors (White, Tutin & Fernandez, 1994; Van-Leeuwe & Gautier-Hion, 1998) that in addition to visual stimuli, forest elephants rely heavily on scent to detect threats.

Afternoon surveys were conducted from 15.00 hours and ended at the most southerly point at 17.30 hours. In July 1998 and May 1999 surveys were conducted throughout the daylight hours with the specific aim of locating elephants, and were extended to 15 km south of the study camp whenever time allowed (n = 19). For

approximately 1 h before and after low tide the beach was firm enough to allow driven surveys along the same path with a Toyota Landcruiser. A speed of 25 km h⁻¹ was maintained (slow enough to spot animals but not so slow as to sink into the sand) while two research assistants stood in the back and searched the coastal scrub for animals. When elephants were seen, the vehicle was stopped some way away and they were approached on foot. Reconnaissance surveys to the north were not successful because of continual detection by animals due to the strong prevailing winds. This work formed part of a larger study of mammal ecology (Morgan, 2001) and surveys were not equally distributed through months because of time constraints, mechanical problems, and the limiting nature of the tide. No surveys were conducted in September 1998. Foot and vehicle surveys and results from different census lengths were pooled and averaged per unit distance in order to increase sample size for analysis without statistically validating such pooling because of small sample size.

Monthly dungpile frequency surveys were conducted along the 5 km coastal transect running parallel to the sea at approximately 5–100 m from the sand at all points (Morgan, 2001). The total number of dungpiles seen along this transect each month was used as an additional index of coastal habitat use by elephants. Monthly surveys of all fallen fruits within a 1 m strip width along this transect were conducted to investigate a possible relationship with food availability along the coast (Morgan, 2001).

Results

Sixty individual elephants were confidently identified during the study period, of which 49 (81.7%) were seen once, seven were seen twice (11.7%) and four (6.7%) were seen on more than two occasions. Mean group size where accurate compositions could be established ($n = 140$) was 2.17 including solitary animals, and 3.10 excluding solitaires (Table 1). These observations totalled 115 adult female elephants, 85 adult males, 62 juveniles and 42 infants (Fig. 1). Solitary animals were most common of all 'groups' encountered, followed by groups consisting of one female and a single offspring. The number of immature elephants per adult female was 0.90 (Table 1), a mean of 0.37 infants and 0.54 juveniles per adult female.

Of the 220 elephant dungpiles examined, 185 (84.1%) contained seeds, and 203 (92.3%) contained the remains of fruits (seeds and/or pulp). The mean number of seed

Table 1 Inter-site comparison of forest elephant group size and composition

	Petit Loango, Gabon ^a	Lopé, Gabon ^{b,j}	Dzanga bai, C.A.R. ^c	Tai, Côte d'Ivoire ^d	Maya bai, Congo ^e	Bossematié, Côte d'Ivoire ^f	Odzala, Congo ^g
Mean observed group size	2.2 ($n = 140$)	1.8 ($n = 383$) ^l		2.4 ($n = 38$)		3.0 ($n = 37$)	3.4 ($n = 32$)
Mean observed group size excluding solitaires	3.1 ($n = 78$)	3.3 ($n = 26$)		3.4 ($n = 22$)	3.5 ($n = 297$)	3.4 ($n = 31$)	4.5 ($n = 22$)
Mean identified group size excluding solitaires			2.6 ($n = 422$)		3.2 ($n = 128$)		
No. solitaires (as % of groups)	62 (44.3)	12 (31.6)	46 (9.8)	16 (42.1)	221	6 (16.2)	10 (31.3)
Solitaires as % of individuals	20.4	12.1	4.0	19.5	35.1	5.4	10.9
% male : female solitaires	88.7 : 11.3			57.1 : 42.9	91.4 : 8.6		
No. adults (as % of total)	200 (65.8)	61 (61.6)	495 (42.6)	71 (74.0)	401 (63.8)		
No. nonadults (as % of individuals)	104 (34.2)	37 (37.4)	668 (57.4)	25 (26.0)	228 (36.2)		
% male : female adults	42.5 : 57.5			36.6 : 63.4	49.4 : 50.6		
No. offspring per female	0.90, 0.97 ^h		0.74	0.64	1.12		

^aThis study; ^bWhite *et al.*, 1993; ^cTurkalo & Fay, 1995; ^dMerz, 1986; ^eQuerouil *et al.*, 1999; ^fTheuerkauf, Ellenberg & Guiro, 2000; ^gMaréchal, Maurois & Chamberlain, 1998; ^hexcluding solitary females; ⁱcomplete counts; ^jat salines; females and offspring only.

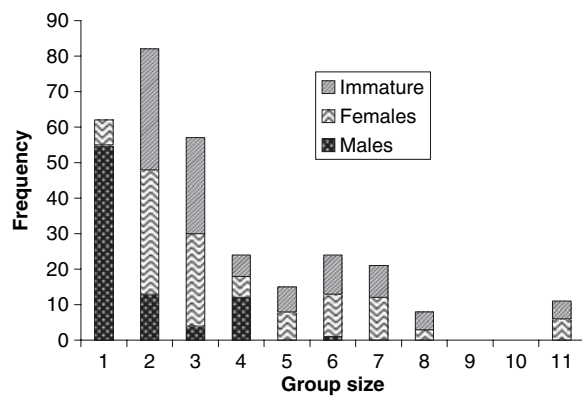


Fig 1 Individual and group sightings of elephants during afternoon surveys in relation to dungpile abundance on the coastal transect

species (\pm SD) per dungpile was 2.01 ± 1.49 , and the mean number of fruit species was 2.28 ± 1.43 . The remains of more fruit species than seed species were evident in faeces, probably due to avoidance of ingestion of large seeds and/or preference to the generally more digestible pulp.

Thirty-two species of seeds were found in fresh elephant dungpiles in 1998. Of these, nineteen could be described to species, 24 to genera, and 25 to family. Seven remain unidentified to family level. One additional fruit species was observed being eaten and sixteen further seed species were found in 'old' dungpiles, which were not systematically examined. Thus in total, elephants at Petit Loango eat fruits of at least 49 species (Table 2).

Elephants consumed more fruit species during the rainy months than during dry months ($r_s = 0.68$, $n = 12$, $P < 0.05$). The mean number of fruit species in dungpiles each month was also strongly correlated with rainfall (mean number of fruit species: $r_s = 0.86$, $P < 0.001$; seed species: $r_s = 0.86$, $P < 0.001$; $n = 12$ in both cases) (Fig. 2).

During 1998, the mean number of elephant groups and individuals recorded during combined foot and vehicle surveys was 0.21 and 0.48 km^{-1} respectively. Elephant groups and individuals were seen more frequently during the afternoon than during the morning (one-way ANOVA: $F = 12.32$, d.f. = 1,22, $P < 0.01$; $F = 13.02$, d.f. = 1,22, $P < 0.01$ for groups and individuals respectively). In reality, elephants started to emerge from the forest from approximately 16.00 hours onwards (B.J.M., pers. obs.). A single driven survey was conducted in May 1999 after dark, and within 7 km south of the camp six elephant groups were observed, totalling nineteen individuals.

Table 2 Fruit species consumed by forest elephants at Petit Loango

Anacardiaceae	<i>Fegimanra africana</i> Pierre
Annonaceae	<i>Annona glabra</i> L. <i>Hexalobus crispiflorus</i> A. Rich.
Apocynaceae	<i>Landolphia mannii</i> Dyer
Burseraceae	<i>Canarium schweinfurthii</i> Engl.
Celastraceae	<i>Salacia</i> sp.
Chrysobalanaceae	<i>Chrysobalanus icaco</i> L. <i>Magnistipula</i> sp. Engl.
Ebenaceae	<i>Diospyros abyssinica</i> F. White
Erythroxylaceae	<i>Erythroxylum mannii</i> Oliver
Euphorbiaceae	<i>Uapaca guineensis</i> Muell. Arg. <i>Ricinodendron heudlotti</i> Baill.
Flacourtiaceae	<i>Calancoma glauca</i> (P. Beauv.) Gilg <i>Casearia barteri</i> Mast.
Humiriaceae	<i>Sacoglottis gabonensis</i> (Baill.) Urban
Irvingiaceae	<i>Irvingia gabonensis</i> Baill. <i>Klainedoxa gabonensis</i> Pierre
Loganiaceae	<i>Strychnos</i> cf. <i>aculeata</i> Solered.
Moraceae	<i>Ficus</i> sp. 1 <i>Ficus</i> sp. 2 <i>Myrianthus arboreus</i> Beauv.
Myrtaceae	<i>Eugenia</i> cf. <i>staudtii</i> Engl. & V. Brehm <i>Eugenia fernandopoana</i> Engl. & Brehm <i>Syzygium guineense</i> (Willd.) D.C.
Olacaceae	<i>Coula edulis</i> Baill.
Palmae	<i>Borassus aethiopiun</i> Mart. <i>Phoenix reclinata</i> Jacq.
Pandaceae	<i>Panda oleosa</i> Pierre
Passifloraceae	<i>Barteria</i> cf. <i>salida</i> Bret.
Rubiaceae	<i>Nauclea</i> sp. <i>Psydrax subcordata</i> Bridson <i>Rothmannia macrocarpa</i> De Wild <i>Massularia acuminata</i> Bullock
Sapotaceae	<i>Manilkara lacera</i> (Bak.) Dubard <i>Manilkara</i> sp. 1 Adanson. <i>Manilkara</i> sp. 2 Adanson. <i>Tiegmella africana</i> Pierre <i>Baillonella toxisperma</i> Engl. <i>Adansonia digitata</i> L.
Bombaceae	<i>Mangifera indica</i> L.
Anacardiaceae	<i>Pentadesma butyracea</i> Sabine
Guttiferae	<i>Scytopetalum pierreanum</i> Pierre
Scytopetalaceae	<i>Solanum</i> sp.
Solanaceae	<i>Duboscia</i> sp. <i>Grewia coriacea</i> Mast.
Tiliaceae	<i>Vitex doniana</i> Sweet
Verbenaceae	<i>Cissus</i> cf. <i>dinklagei</i> Gilg. & Brandt.
Vitaceae	Indet. sp. 1 (found in faeces)
Unknown	Indet. sp. 2 (found in faeces)

Total no. fruit species consumed = 49.

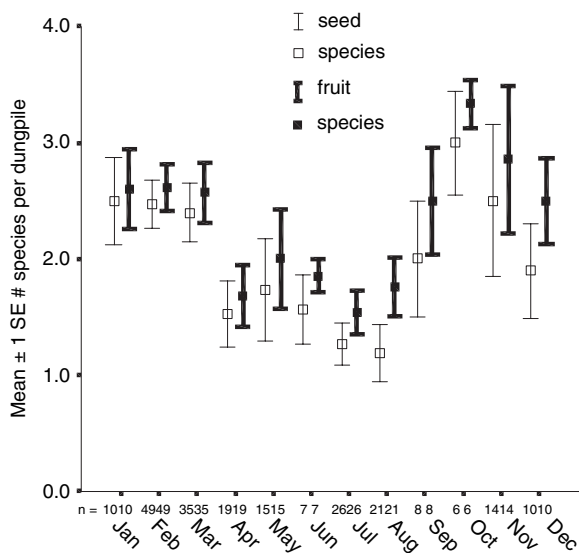


Fig 2 Mean number of seed and fruit species in elephant dungpiles

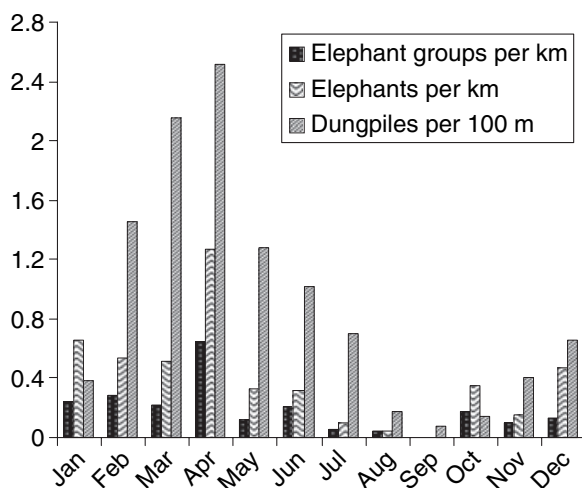


Fig 3 Group composition in terms of age and sex class

Elephants were encountered most frequently on coastal surveys between January and April and during December, and despite a large survey effort in July and August few animals were encountered during this time, at the height of the dry season (Fig. 3). Elephant group abundance on the coast was reflected in abundance estimations from faecal counts on the coastal transect (Fig. 3), although this relationship was not statistically significant ($r_s = 0.55$, $n = 11$, $P = 0.08$).

No statistical relationship between coastal habitat use and rainfall was apparent, but correlations between

coastal use and monthly temperature were strong, suggesting that elephants tended to visit the coast during the warmer months (elephant groups per kilometre versus temperature $r_s = 0.78$, $P < 0.005$; no. dungpiles versus temperature $r_s = 0.70$, $P < 0.05$, $n = 11$ for both cases).

Coastal dungpile abundance was high when fruitfall biomass along the coastal transect was high ($r_s = 0.62$, $n = 12$, $P < 0.05$), although there was a negative relationship between dungpile abundance and the number of fruit species available ($r_s = -0.81$, $n = 12$, $P < 0.001$). Specifically, more dungpiles were apparent when individual *Borassus aethiopicum* Mart. fruits were abundant ($r_s = 0.62$, $n = 12$, $P < 0.05$). However, elephant observations did not demonstrate this clear association, in that there were no statistically significant relationships between the number of elephants observed during coastal surveys and the number of fruit species, individual fruits or fruitfall biomass on the coastal transect.

Discussion

The exposed nature of the coastal habitat at Petit Loango, together with the open nature of the forest understorey (due to lack of terrestrial herbaceous vegetation, Morgan, 2001) allows excellent opportunities for observing forest elephants. Of 60 identified individuals (21 males, 28 females and eleven dependent offspring), 10.7% females and 33.3% males were seen on more than one occasion. These data should be treated with caution, however, as it is possible that individuals were seen several times before confident identifications were made, and occasionally elephants fled before re-identification was possible. At least 2100 individual elephants have been identified at Dzanga bai, comprising around 85% of visitors in 932 observation days (Turkalo, 1996). At Maya bai, Congo, 629 individual elephants have been identified, with 21% of identified males and 24% of identified females or female-offspring groups visiting the bai on more than 1 day (Querouil *et al.*, 1999).

Average group size at Petit Loango was similar to other study sites (Tables 1 and 3), with the largest group consisting of eleven individuals – six females, three juveniles and two infants. Maximum group size at Lopé was ten (White *et al.*, 1993) and Turkalo & Fay (1995) noted that stable groups varied from two (mother with one offspring) to nine (three adult females with six offspring). A stable group of five (two females with two juveniles and one infant) was the largest female/offspring group recorded

Table 3 Forest elephant group size and composition at Petit Loango

Group size	No. groups	No. female/offspring groups	No. male-only groups	No. mixed groups
1	62	7	55	
2	40	33	6	1
3	19	15		4
4	6	3	3	
5	3	3		
6	4	3		1
7	3	3		
8	1	1		
9	1	1		
11	1	1		
Total (%)	140 (100.0)	70 (50.0)	64 (45.7)	6 (4.3)

during this study, and was seen twice. Querouil *et al.* (1999) stated that groups of more than six individuals were never seen twice with the same composition, and considered them to be made up of separated family units. Larger aggregations of around 100 animals witnessed at Maya and Dzanga bai (Turkalo & Fay, 1995; Querouil *et al.*, 1999), are probably examples of tertiary groupings, where elephants are attracted to an area for mineral salts and where social interactions are facilitated.

Herbaceous material including leaves, grass, woody materials and bark were found in dungpiles, but were not identified to species level. Nonvegetable matter including fungi, soil and small stones were also recorded. This study concurs with findings from other study sites that forest elephants consume fruits throughout the year (at least 49 species), and 92.3% of 220 dungpiles contained fruit remains. At Lopé, at least 72 fruit species are consumed (White *et al.*, 1993), and fruit remains were found in 82% of 311 dungpiles. Short (1981) noted 35 species from dungpiles in Bia National Park, Ghana (93% of dungpiles contained fruit remains), with a mean of 4.6 species per dungpile in the dry season, compared with a maximum of 3.0 in October at Petit Loango (Fig. 2). At Taï, Côte d'Ivoire, Alexandre (1978) recorded 37 species dispersed by elephants, and in a later study at the same site Merz (1981) counted 44 fruit species. Differences in the numbers and species of fruit eaten between sites are likely to be at least partly dependent on species diversity within the area, which is liable to vary widely as a result of differences in soil conditions, climate, historical factors and human disturbance. However, some fruit species are available

throughout much of Central Africa – *Klainedoxa gabonensis* Pierre (Irvingiaceae) and *Panda oleosa* Pierre (Pandana-ceae) fruits are eaten by elephants in Gabon (this study; White *et al.*, 1993), Congo (Maurois, Chamberlain & Maréchal, 1997), Côte d'Ivoire (Alexandre, 1978) and in Ghana (Lieberman *et al.*, 1987).

That forest elephants migrate to areas of high fruit availability (Short, 1983; White, 1994) is also indicative of the importance of fruit in the diet. Petit Loango is unique in its high density of *Sacoglottis gabonensis* trees and other important fruit species (Morgan, 2001), and a longer study is likely to confirm that the high elephant density is largely due to the year-round abundance of fruit at this site.

The high dungpile abundance on the coastal transect in April (25 km⁻¹ transect, Fig. 3) is comparable with a one-off maximum count of 35 dungpiles per kilometre on large, well-used elephant paths linking geophagical clearings in Congo (Querouil *et al.*, 1999), giving some indication of the intense use of the coastal area in Petit Loango. There are several nonexclusive explanations for this phenomenon: cool sea winds may give relief from heat and biting insects; elephants may be attracted to some food source; or the salt-laden winds leave quantities of sodium on vegetation that attract elephants.

Coastal surveys indicate that elephants use this habitat more during cooler months. Forest elephants may have greater problems with thermoregulation under high ambient heat conditions than savanna elephants, given their smaller ear surface areas for heat dissipation, and larger surface area to body volume ratio. At Dzanga the majority of elephants visited the bai during the late afternoon and night (Turkalo & Fay, 1995), and the largest elephant aggregations at Maya bai, were observed during late afternoon and at sunrise (Querouil *et al.*, 1999). Forest elephants may use open areas more at night due to poaching pressure in some areas, although this is probably not the reason at Petit Loango. Strong onshore winds affect the coast from midday to dusk, and biting insects are less common, which may also be an explanation for daily observations of forest buffalo (*Synceus caffer nanus* Sparrman) walking along, standing, or lying at the water's edge.

The second explanation, of fruit 'inducements' in the coastal area was the accepted wisdom by villagers before this study, specifically with regard to *Borassus* fruits (Greth, 1997). Elephants are known to favour these fruits elsewhere, and may gorge themselves when fruits are plentiful (Sikes, 1971). However, while dungpile censuses indicated elephant habitat use in relation to the total biomass of all

fallen fruits and the number of *Borassus* fruits on that transect, the frequency of elephant observations along the coast showed no conclusive relationships with any index of fruit presence. In reality, elephants spent the majority of their time foraging on coastal creepers and grasses at the coast, and during many hours of elephant observations over 16 months, *Borassus* fruits were observed being eaten only twice (despite fruit presence on the ground throughout the year), once when a solitary adult male pushed a fruit-laden palm and dislodged fruits. Furthermore, it is unlikely that *Borassus* fruits could be a major attractant for elephants given the low density of trees at the site (zero inland, 2.0 trees ha⁻¹ at the coast, B.J.M., unpublished data), and the fact that *Borassus* is a dioecious species. We suggest an alternative explanation for this phenomenon relating to usage of the coast as a semi-permanent 'salt lick'.

Sodium levels are typically low in tropical forests, are not accumulated in the majority of plant species (Klaus & Schmid, 1998), and are readily leached from areas with even moderate precipitation. Petit Loango is characterized by very pale, sandy, leached soils, similar to those reported for a coastal site in Cameroon (McKey *et al.*, 1978). Leaching is accelerated by high and spasmodic rainfall, which tends to filter out small particles of clay, organic matter and minerals which end up in watercourses and are lost from the system (Robbins, 1993). Most of the streams and coastal lagoons at Petit Loango are very dark in colour, supporting this scenario (see also Anderson, 1981). Sodium is known to be a limiting factor for many herbivore populations (Freeland, Calcott & Geiss, 1985), and the majority of geophagical studies consider sodium to be the primary element attracting mammal species (Klaus, Klaus-Hügi & Schmid, 1998). Weir (1972) hypothesized that sodium is one factor determining savanna elephant distributions in South Africa by studying artificial waterholes. While there is no information on sodium levels in vegetation at Petit Loango, the strong onshore afternoon winds at Petit Loango coat the vegetation with a thick layer of salt (B.J.M., pers. obs.).

The bays of C.A.R. and Congo are visited throughout the year by elephants, possibly as a host of minerals are available and requirements vary through the year. At Petit Loango elephants might be predicted to visit the coastal area less frequently during the driest months due to more concentrated salt build-up (with little or no rain to wash vegetation), satisfying sodium requirements in fewer visits, a pattern confirmed by this study. Alternatively, dry

season foods may contain higher levels of sodium so fewer visits are necessary, or animals may be attracted to resources that are far from the sea, making frequent visits to the coast costly (also see Klaus & Schmid, 1998).

We hypothesize that elephants are attracted to the coast for multiple reasons, including the presence of *Borassus* fruits, the lack of biting insects and the potential for social interactions between possible elephant family units. However, investigations of sodium levels in vegetation and soils at coastal and inland areas of Petit Loango, and comparisons with vegetation and soil studies at other sites including bays may demonstrate that it is the salt-coated vegetation that attracts elephants to coastal Petit Loango in such numbers at particular times of the year.

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References

- ALEXANDRE, D.Y. (1978) Le rôle disseminateur des éléphants en forêt de Taï, Côte d'Ivoire. *Rev. Ecol. (Terre et Vie)* **32**, 47–72.
- ANDERSON, A.B. (1981) White-sand vegetation of Brazilian Amazonia. *Biotropica* **13**, 199–210.
- FREELAND, W.J., CALCOTT, P.H. & GEISS, D.P. (1985) Allelochemicals, minerals and herbivore population size. *Biochem. Syst. Ecol.* **13**, 195–206.
- GRETH, A. (1997) Gamba, la plage des éléphants. Panda – La Revue du WWF France. *Avril 1997*, 19–21.
- KLAUS, G. & SCHMID, B. (1998) Geophagy at natural licks and mammal ecology: a review. *Mammalia* **62**, 481–497.
- KLAUS, G., KLAUS-HÜGI, C. & SCHMID, B. (1998) Geophagy by large mammals at natural licks in the rain forest of the Dzanga Na-

- tional Park, Central African Republic. *J. Trop. Ecol.* **14**, 829–840.
- LIEBERMAN, D., LIEBERMAN, M. & MARTIN, C. (1987) Notes on seeds in elephant dung from Bia National Park, Ghana. *Biotropica* **19**, 365–369.
- MARÉCHAL, C., MAUROIS, C. & CHAMBERLAIN, C. (1998) Size (and structure) of forest elephant groups (*Loxodonta africana cyclotis* Matschie, 1900) in the Odzala National Park, Republic of Congo. *Mammalia* **62**, 297–300.
- MAUROIS, C., CHAMBERLAIN, C. & MARÉCHAL, C. (1997) Aperçu du régime alimentaire de l'éléphant de forêt, *Loxodonta africana cyclotis*, dans le Parc National d'Odzala. République du Congo. *Mammalia* **61**, 127–130.
- MCCOMB, K., MOSS, C., SAYIAELE, S. & BAKER, L. (2000) Unusually extensive networks of vocal recognition in African elephants. *Anim. Behav.* **59**, 1103–1109.
- MCKEY, D., WATERMAN, P.G., MBI, C.N., GARTLAN, J.S. & STRUHSACKER, T.T. (1978) Phenolic content of vegetation in two African rain forests: ecological implications. *Science* **202**, 61–64.
- 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**, 299–305.
- MERZ, G. (1986) Movement patterns and group size of the African forest elephant *Loxodonta africana cyclotis* in the Tai National Park, Ivory Coast. *Afr. J. Ecol.* **24**, 133–136.
- MORGAN, B.J. (2001) Ecology of mammalian frugivores in the Réserve de Faune du Petit Loango, Gabon. PhD Thesis, University of Cambridge, Cambridge.
- MORGAN, B.J. & LEE, P.C. (2003) Forest elephant (*Loxodonta africana cyclotis*) stature in the Réserve de Faune du Petit Loango, Gabon. *J. Zool. (Lond.)* **259**, 337–344.
- MOSS, C. (1993) Getting to know a population. In: *Studying Elephants* (Ed. K. KANGWANA). African Wildlife Foundation, Nairobi, Kenya.
- QUEROUIL, S., MAGLIOCCA, F. & GAUTIER-HION, A. (1999) Structure of population, grouping patterns and density of forest elephants in north-west Congo. *Afr. J. Ecol.* **37**, 161–167.
- ROBBINS, C.T. (1993) *Wildlife Feeding and Nutrition*. Academic Press, New York.
- ROCA, A.L., GEORGIADIS, N., PECON-SLATTERY, J. & O'BRIEN, S.J. (2001) Genetic evidence for two species of elephant in Africa. *Science* **293**, 1473–1477.
- SHORT, J.C. (1981) Diet and feeding behaviour of the forest elephant. *Mammalia* **45**, 177–185.
- SHORT, J.C. (1983) Density and seasonal movements of forest elephant *Loxodonta africana cyclotis*, Matschie) in Bia National Park, Ghana. *Afr. J. Ecol.* **21**, 175–184.
- SIKES, S.K. (1971) *The Natural History of the African Elephant*. Weidenfeld & Nicholson, London.
- TCHAMBA, M.N. & SEME, P.M. (1993) Diet and feeding behaviour of the forest elephant in the Sanchou Reserve, Cameroon. *Afr. J. Ecol.* **31**, 165–171.
- THEUERKAUF, J. & ELLENBERG, H. & GUIRO, Y. (2000) Group structure of forest elephants in the Bossematié Forest Reserve, Ivory Coast. *Afr. J. Ecol.* **38**, 262–264.
- TURKALO, A. (1996) Studying forest elephants by direct observation in the Dzanga clearing: an update. *Pachyderm* **22**, 59–60.
- TURKALO, A. & FAY, J.M. (1995) Studying forest elephants by direct observation: preliminary results from the Dzanga clearing, Central African Republic. *Pachyderm* **20**, 45–54.
- TUTIN, C.E.G. & FERNANDEZ, M. (1994) Faecal analysis as a method of describing diets of apes: examples from sympatric gorillas and chimpanzees at Lopé, Gabon. *Tropics* **2**, 189–197.
- VANLEEUWE, H. & GAUTIER-HION, A. (1998) Forest elephant paths and movements at the Odzala National Park, Congo: the role of clearings and Marantaceae forests. *Afr. J. Ecol.* **36**, 174–182.
- WEIR, J. (1972) Spatial distribution of elephants in an African NP in relation to environmental sodium. *Oikos* **23**, 1–13.
- WHITE, L.J.T. (1994) *Sacoglottis gabonensis* fruiting and the seasonal movements of elephants in the Lopé Reserve, Gabon. *J. Trop. Ecol.* **10**, 121–125.
- WHITE, L.J.T., TUTIN, C.E.G. & FERNANDEZ, M. (1993) Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lopé Reserve, Gabon. *Afr. J. Ecol.* **31**, 181–199.
- WHITE, L.J.T., TUTIN, C.E.G. & FERNANDEZ, M. (1994) Behavioural and dietary similarities of elephants and apes in the Lopé Reserve, Gabon: should forest elephants be re-classified as apes? In: *Current Primatology*, Vol. 1: Ecology and Evolution (Eds B. THIERRY, J. R. ANDERSON, J. J. ROEDER and N. HERRENSCHMIDT). Université Louis Pasteur, Strasbourg, France.

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