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Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique

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Abstract

The distribution and diet of the elephants of the Maputo Elephant Reserve were studied using dung counts, satellite tracking and faecal analysis. The results were compared with earlier data from before the civil war in Mozambique. The elephant population decreased during the civil war, but 180 animals still remain. Earlier studies described the elephants as preferring the grass plains. Currently, the elephants prefer the dense forest patches over the high quality forage found in the grass plains. Water salinity affected distribution; elephant dung piles were found closer to fresh water in the dry season. A total of 95 different plant species were identified in the faeces. The percentage of grass was relatively low compared with other studies, increasing at the beginning of the rainy season. At the end of the dry season, elephants concentrated on the few available browse species with young leaves, but generally preferred grass species to browse species. Diet composition was mainly affected by season and less by habitat. The elephants have changed their habitat preference in reaction to poaching, and probably increased the contribution of browse species in the diet. The presence of forest patches has been vital for the survival of the elephants.

Key words: browse, dung, food, grass, habitat, movements

Résumé

On a étudié la distribution et le régime alimentaire des éléphants de la Réserve á éléphants de Maputo en utilisant le comptages des crottes, le tracking par satellite et l'analyse des excréments. On a comparé les résultats avec des données recueillies avant la guerre civile au Mozambique. La population d'éléphants a baissé pendant la guerre civile mais il reste 180 animaux. Des études antérieures montraient que les éléphants préféraient les plaines herbeuses. Actuellement, ils préfèrent les îlots de forêt dense au fourrage de haute qualité qui se trouve dans les plaines herbeuses. La salinité de l'eau modifie la distribution; on trouvait les crottes d'éléphants plus près de l'eau douce en saison sèche. On a identifié un total de 95 espèces végétales différentes dans les excréments. Le pourcentage d'herbes était relativement bas par rapport aux études antérieures, il augmentait au début de la saison des pluies. A la fin de la saison sèche, les éléphants se concentraient sur les quelques espèces de buissons comestibles ayant des jeunes feuilles, mais ils préféraient généralement les espèces herbeuses aux buissons. La composition du régime était surtout affectée par la saison et moins par l'habitat. Les éléphants ont changé leurs préférences en matière d'habitat en réaction au braconnage et ont sans doute ainsi augmenté la contribution des espèces buissonnantes dans le régime alimentaire. La présence des îlots forestiers a été vitale pour la survie des éléphants.

Introduction

The elephants (*Loxodonta africana* (Blumenbach)) *of* the Maputo Elephant Reserve (MER) in Mozambique

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have been poached ever since the establishment of the Reserve in 1932 (Tello, 1973). Poaching activities increased further during the civil war (1978–92). Elephants also stepped on mines, lost parts of their trunks in snares, and suffered bullet wounds (Ostrosky, 1988b). Hall-Martin (1988) estimated that one out of eight elephants from the nearby Tembe Elephant Park (TEP) in South Africa (Fig. 1), had injuries from snares or bullet wounds acquired in Mozambique, and the border of the TEP was therefore closed with an electric fence (Ostrosky, 1988b). The poaching resulted in a declining population, estimated at 3.4–7.4% $year^{-1}$ (de Boer & Ntumi, unpublished). A small population still remains; 180 elephants were counted during a 2 day helicopter survey in February 1998 (I. Whyte, personal communication). People who fled the area during the civil war have returned and resumed farming, and the elephants now cause significant crop damage around the MER (De Boer & Baquete, 1998).

Little is known about the ecology of the elephants in the MER. Tello (1973) gave a brief description, indicating that the preferred habitat was the large open grass plains in the north of the MER, but at present, elephants are rarely encountered in these open grasslands. The aim of this study was to investigate the distribution and diet of the elephants, and to estimate the importance of the different habitats available to them.

Study area

The MER is situated in the south of Mozambique (26°25′S, 32°45′E, Fig. 1). The human population is concentrated on the west side, between Bela Vista and Salamanga (Fig. 1). The climate is characterized by a hot, rainy summer (October–March) and a colder, drier winter (April–September). Mean annual rainfall is 690–1000 mm (DNFFB, 1994). The soils are mainly sandy, with some more fertile, alluvial soils found around the Futi and Maputo rivers. The vegetation can be classified into six vegetation communities (modified from Tello, 1973; DNFFB, 1994; Hatton, 1995; Haandrikman, 1998; Vriesendorp, 1998).

Mangroves: the mangroves border the bay and surround the deltas of the Maputo river and Bembe canal, comprising mainly *Avicennia marina* Vierh. and *Rhizophora mucronata* Lam. trees.

Dune vegetation: pioneer vegetation (*Scaevola* spp., *Ipomoea* spp., *Canavalia* spp.) with dune thicket and forest (*Diospyros rotundifolia* Hiern, *Mimusops caffra* Mey. and *Sideroxylon inerme* L.).

Grass plains: dominated by grass genera such as: *Themeda, Tristachya, Trachypogon, Aristida, Hemarthia, Ischaemum and Paspalum*. Parts of the grasslands are inundated in the rainy season.

Forest: dry sublittoral forest thicket occurs on the older dunes, dominated by *Albizia* spp., *Afzelia quanzensis* Welw., *Garcinia livingstonei* Anders. and *Sideroxylon inerme* L.

Woodland: open woodland with *Afzelia quanzensis*, *Albizia* spp. and *Sclerocarya birrea* Hochst.

Riverine vegetation: the seasonal Futi river with reedbeds of *Phragmites* spp., *Juncus* spp. and *Cyperus* spp., fringed by riverine forest of *Ficus* spp., *Syzygium cordatum* Hochst. and *Kigelia africana* Benth.

Fauna

The herbivore population was destroyed during the civil war (DNFFB, 1994). Reedbuck (*Redunca arundinum* (Boddaert)), preferring the open grass plains, suffered the most. The smaller antelopes, such as red duiker (*Cephalophus natalensis* (Smith)), suni (*Neotragus moschatus* (von Dueben)) and common duiker (*Sylvicapra grimmia* (L.)), still occur in reasonable numbers.

Materials and methods

Dung density

In January and February 1996, dung densities were counted on foot on 20 linear strip transects (Barnes, 1996) per vegetation community. Because elephants were absent from the mangroves and dune vegetation, the measurements were made only in the forest, woodland and grass plains. The distance between a dung pile and the centre line of the transect was measured to the nearest cm. Transects were walked for an hour and total transect length was determined using a calibrated pedometer.

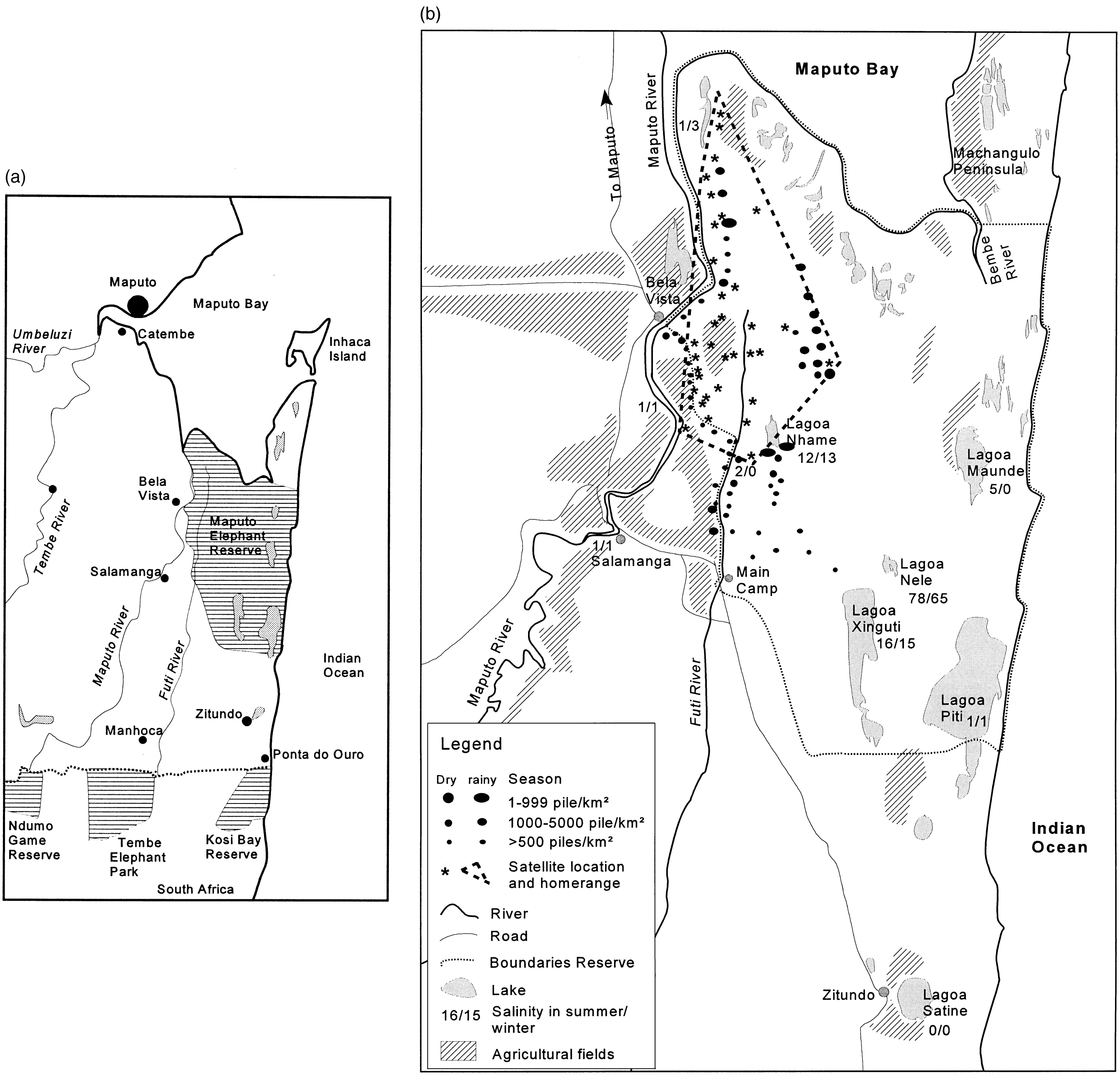

Fig 1 The location of the Maputo Elephant Reserve (a) and its main features (b). The different surface water salinities are given in ‰. The locations of the elephant tracked by the satellite are indicated, as well as its home range, following the minimum convex polygon (Harris *et al.*, 1990; Whyte, 1996). The relative abundance of dung piles on the roads which were included in the car survey is shown.

Dung piles were also counted on road strip transects from a car in the rainy season (April 1996) and dry season (August 1996). A total of 114 km was cleared of dung in the wet season, and 119 km in the dry season, 4 weeks prior to the survey. Dung piles were counted with reference to location and vegetation community.

Satellite tracking

A sub-adult cow was anaesthetized with M99 (Ebedes, du Toit & van Rooyen, 1996) in the MER in May 1996, and fitted with a collar incorporating a PTT satellite transmitter (Telonics ST-14). The equipment permitted tracking of the elephant on a 24 h on/48 h off basis (Tchamba, Bauer & Iongh, 1995; Thouless, 1996; Whyte, 1996). Only 4 months of data were collected, because the elephant was killed by poachers in September 1996. Each location was accompanied by a location-class (accuracy) of the location, and by the number of consecutive messages transmitted by the PTT.

Diet analysis

An epidermis reference collection was made (Field, 1972; Soane, 1980; Bhadresa, 1986) of different plant parts comprising leaves, fruits and roots of plants occurring in the study area. Microscope slides were prepared for each plant species and photographed at different magnifications.

The diet was studied using faecal analysis (Stewart & Stewart, 1970; Soane, 1980; Bhadresa, 1986). Faecal samples were collected in the early rainy season (November 1993), late rainy season (March 1994) and the late dry season (September 1995), in the three main vegetation communities (Tello, 1973): forest, woodland and grass plains. Six different, fresh faecal samples were collected in each month per vegetation community (Field, 1972). The point-intercept method was used for the identification of epidermic fragments (Bhadresa, 1986). A total of 100 different epidermic fragments were identified per sample. Plant species were classified in three major growth form categories: (i) tree and shrub (ii) grasses and (iii) herbs (dicotyledons with little or no lignification). The epidermis fragments of *Androstachys johnsonii* Prain could not be distinguished from *Sclerocarya birrea* and the two species were therefore taken together in the analysis.

Habitat parameters

A vegetation map describing plant biomass was used for the interpretation of data obtained via the satellite tracking study (East African Technical Services, 1990). Average salinity of lakes, rivers and pools was calculated from nine readings per site, using a refractometer. The elephant dung distribution was analysed in relation to salinity.

Statistical analysis

Dung density was calculated from transect width and perpendicular distance between a dung pile and the centre line of the transect. Faecal density was calculated after correction for detection probability, which was computed by 'Distance' (Buckland *et al.*, 1993; Laake *et al.*, 1994). Significant differences in dung density among the habitats were determined by the absence of overlap of the 95% confidence limits (Buckland *et al.*, 1993). Dung decomposition was assumed to be similar in the three habitats.

Dung counts on roads, road length and width, also enabled an estimation of elephant density, using the formula of Jachman (1984):

$$E = D/(R \times T \times L \times W)$$

E = elephant density ($n\,\mathrm{km}^{-2}$); D = dung number; R = defecation rate: 20 and 14 per day for rainy and dry season, respectively (average from Jachman & Bell, 1984 and Ruggiero, 1992); T = accumulation period (days); L = road length (km); W = average road width (km).

The formula includes several uncertainties and density studies based on dung counts can be severely biased (e.g. Jachman & Bell, 1984; Jachman, 1984; Barnes *et al.*, 1991; Fay, 1991; Barnes, 1993, 1996). It was therefore only used as a relative measurement of density. Density differences were tested with a Kruskal–Wallis test.

A table of the relative occurrence of forage species in the different habitats was constructed, based on Tello (1973), Hatton *et al.* (1995), Maria (1997), C. Boane (personal communication) and J. Hatton (personal communication). The diet composition was compared with forage availability by comparing the relative occurrence of forage species in the diet with its relative occurrence in the field. The expected proportions of plant species in the diet was calculated by multiplying the relative occurrence in the field with the total number of identified epidermic fragments. Diet preference was calculated by a technique similar to the forage-ratio calculation of Krebs (1989). A plant species was considered preferred if it was taken at twice the expected value in the diet (relative occurrence).

The importance to the diet of the three different habitats was analysed by comparing species proportion with relative occurrence. This was done by multiplication of the two factors and the resulting scores were added for each habitat. Diet preference was tested by comparing total scores with relative occurrence. Difference between expected and observed diet composition was tested with a χ^2-test, after which a non-parametric multiple comparison test was carried out (Wonnacott & Wonnacott, 1990). A Principal Component Analysis (Ludwig & Reynolds, 1988) was used to analyse similarity between the faecal samples.

Results

Dung densities – foot transect

Total transect length was less in the denser forest, which is difficult to penetrate. The detection curves for the three different habitats were similar, but different models were used for the detection curve. A uniform model with two cosine adjustment factors was calculated by the program 'Distance' for the detection curve in the forest and the woodland, and a half-normal function with two cosine adjustments for the grass plain data. Transect length, detection probability and calculated dung densities are given in Table 1. Significantly higher densities, 4600 dung piles km^{-2}, were obtained in the forest. The woodland and the grass plains had lower densities of 1300–1400 dung piles km$^{-2.}$

Dung densities – road counts

Dung density followed a negative binomial distribution and could not be transformed to a normal distribution

Table 1 Elephant dung pile density as calculated from the transect data in January–February 1996, and the road counts

	Habitat		
	Forest	Woodland	Grass plains
Foot transect – data			
Total transect length (m)	4640	9367	7808
Mean transect length (m)	232	468	390
Total number of transects	20	20	20
Total number of dung piles	56	30	19
Average perpendicular distance (m)	0.91	0.74	0.74
Detection probability (*P*)	0.47	0.47	0.41
Dung pile density (n km^{-2})	4600	1400	1300
95% confidence interval	3100–6600	800–2500	600–2900
Road count – rainy season			
Road length (km)	28.6	54.1	19.1
Road area (km^2)	0.058	0.109	0.039
Dung piles (n)	266	132	4
Dung pile density (n km^{-2})	4604	1208	104
Elephant density (n km^{-2})	7.1	1.9	0.2
Road count – dry season			
Road length (km)	35.7	84.1	12.0
Road area (km^2)	0.072	0.170	0.024
Dung piles (n)	464	204	0
Dung pile density (n km^{-2})	6434	1201	0
Elephant density (n km^{-2})	14.8	2.8	0

after transformation with an inverse hyperbolic sine (Zar, 1984). No difference was found in dung density between seasons ($H_{1,333} = 0.086$; $P > 0.05$), but the three habitats produced different dung densities ($H_{2,332} = 28.822$, $P < 0.001$). The highest dung density was obtained in the forest, with an average of 11.0 elephant km^{-2}, whilst the grass plains had the lowest density at 0.1 elephant km^{-2} (Table 1).

Salinity

No significant difference was detected between summer and winter salinity measurements ($P > 0.05$), but large differences were detected in the different surface waters (Fig. 1). Highest salinities were measured in Lagoa Nele (65–94‰), Lagoa Xinguti (10–20‰) and Lagoa Nhame (10–16‰). The mean coefficient of variation per site was < 10%. Dung was found significantly closer to fresh water in the dry season than to saline water (contingency table, $\chi^2 = 22.7$, df = 1, $P < 0.05$). Dung was randomly distributed in the rainy season ($\chi^2 = 6.6$, df = 1, $P > 0.05$).

Satellite tracking

A total of 164 satellite messages were received, allowing calculation of the location on 34 occasions (Fig. 1). The PTT was operational for a total of 63 days, averaging 1.6 locations per 24 h. A minimum of 237 km was travelled during this period at a mean minimum speed of 0.4 km h$^{-1.}$ The minimum convex polygon (Fig. 1) gives a total range of 129 km^2, but this is difficult to interpret due to the short study period. The vegetation community distribution within the animals' home range was compared with the received locations within this area. Locations were not randomly distributed over the different vegetation communities ($\chi^2 = 20.127$, df = 4, $P < 0.01$). Significantly more locations (59%) were received from the forest than from other vegetation communities (multiple comparison test, $P < 0.05$). No significant relationship was found between the day or night and vegetation type ($\chi^2 = 1.49$, df = 2, $P > 0.20$).

Faecal analysis

Table 2 gives the proportions of plant species found in the diet. The proportion is generally below 3% per plant species, with few exceptions. Species found in the diet and contributing more than 2% were: *Andropogon* spp., *Bridelia micrantha* Baill., *Combretum* sp., *Dichrostachys cinerea* Wight & Arn, *Parinaria capensis* Harv., *Phragmites communis* Steud, *Sclerocarya birrea*, *Sesuvium portulacastrum* L., *Setaria* spp., *Strychnos innocua* Del., *Terminalia sericea* Burch, and *Ziziphus mucronata* Willd. Seventeen species were identified as preferred (Table 2).

A total of 95 different species was identified, of which 66% were browse species (Table 3). The broadest diet was found in the late rainy season with a total of 90 species, the narrowest diet in the early rainy season with 56 species.

The results indicated that the elephants of the MER are browsers, their diet mainly consisting of tree and shrub species. Diet composition fluctuated little, and differences among habitats or seasons in their tree, grass or herb composition was normally < 10%. The biggest difference was found in the contribution of the grasses which constituted 37% of the diet in the early rainy season, 27% in the late rainy season and 14% in the dry season. Dung samples collected in the three habitats were similar in their plant composition. A high proportion of tree species was found in dung collected on the treeless grass plains (63%).

The species composition of the different habitats ('abundance' in Table 2) influenced faecal sample composition. Total abundance scores were computed for each habitat and totalled 117 for forest, 94 for woodland and 60 for the grass plains, a ratio of 2.0 : 1.6 : 1.0. Table 4 shows that the faecal samples had a relatively higher proportion of grass plain species, and a lower proportion of forest species. The multiple comparison test showed significant differences between all plant species at $P < 0.01$ (df = 1). The highest contribution of grass plain species was found for faecal samples collected in the late dry season and in the forest. Forest plant species were under-represented in all faecal samples.

The Principal Component Analysis (Fig. 2) indicated that samples from different seasons were taken together and that habitat did not influence the pattern. Table 2 also shows that samples collected in different habitats are more similar than samples collected in different seasons.

Table 2 Plant species' composition (%) of faecal samples collected in different seasons and habitats. Plant type consists of the following plant categories: T = trees and shrubs, G = grass, H = non-lignified herbaceous vegetation, C = cultivated plants. The plant species' relative abundance in the three different habitats is given as follows: 0 = absent; 1 = rare; 2 = common; 3 = abundant. The total score per plant species is used to calculate expected proportion (E) after which plant preference (P) is calculated, by comparing the 'mean' with the 'E' column: preference (+), avoidance (–) or indifference (0) (see Methods). N.I. = not identified.

		Faecal composition							Relative plant abundance					
		Season			Habitat									
Plant species	Type	Early rain	Late rain	Late dry	Forest	Wood-land	Grass plain	Mean	Forest	Wood-land	Grass plain	Total	E	P
Acacia davyi	T	–	0.3	< 0.1	0.2	–	0.1	0.1	2	1	0	3	1.1	–
Acacia karroo	T	0.8	1.8	1.4	0.6	1.4	2.1	1.4	3	0	0	3	1.1	0
Acacia kraussiana	T	3.0	0.2	0.6	–	1.1	2.7	1.3	0	1	0	1	0.4	+
Acacia sp.	T	2.8	0.9	0.3	0.8	1.6	1.6	1.3	2	1	0	3	1.1	0
Acacia xanthophloea	T	–	0.2	0.3	0.1	0.4	–	0.2	1	0	0	1	0.4	–
Afzelia quanzensis	T	1.6	0.9	< 0.1	1.1	0.6	0.8	0.8	3	1	0	4	1.5	0
Albizia adianthifolia	T	3.2	0.2	–	0.7	1.2	1.5	1.1	2	1	0	3	1.1	0
Albizia versicolor	T	–	0.4	–	0.4	–	–	0.1	2	1	0	3	1.1	–
Aloe bainesii	T	1.9	0.6	–	0.2	2.1	0.2	0.8	0	1	0	1	0.4	+
Aloe sp.	T	0.1	1.3	0.3	0.5	1.2	< 0.1	0.6	0	1	0	1	0.4	0
Andropogon eucomus	G	4.4	2.9	0.1	2.3	2.9	2.3	2.5	0	3	3	6	2.2	0
Andropogon gayanus	G	2.9	5.3	–	2.6	3.4	2.3	2.7	0	3	3	6	2.2	0
Annona senegalensis	T	–	0.3	0.4	< 0.1	0.7	–	0.2	0	3	0	3	1.1	–
Apodytes dimidiata	T	0.1	1.0	–	0.2	0.8	0.2	0.4	2	1	0	3	1.1	–
Aristida canescens	T	0.6	0.4	–	0.2	0.7	< 0.1	0.3	0	2	1	3	1.1	–
Aristolochia sp.	H	–	0.8	–	0.2	0.6	–	0.3	2	0	0	2	0.7	–
Artabotrys brachypetalus	T	0.6	0.5	< 0.1	0.3	0.6	0.3	0.4	1	0	0	1	0.4	0
Asparagus plumosus – bulb	H	–	< 0.1	–	–	–	< 0.1	< 0.1	3	1	0	4	1.5	–
Balanites manghamii	T	0.3	0.7	0.3	0.7	0.6	< 0.1	0.4	2	0	0	2	0.7	0
Boscia albitrunca	T	–	0.2	–	0.1	< 0.1	< 0.1	< 0.1	1	1	0	2	0.7	–
Brachylaena discolor	T	1.3	0.7	–	0.3	0.4	1.4	0.7	2	2	0	4	1.5	–
Bridelia micrantha	T	2.3	< 0.1	4.3	3.1	1.9	1.7	2.2	1	0	0	1	0.4	+
Canthium locuples	T	–	0.2	0.2	–	< 0.1	0.4	0.1	2	0	0	2	0.7	–
Capparis tomentosa	T	1.4	1.6	0.3	1.0	0.8	1.4	1.1	1	0	0	1	0.4	+
Chloris gayana	G	< 0.1	0.6	2.1	1.7	0.6	0.4	0.9	0	0	2	2	0.7	0
Clerodendrum glabrum	T	–	1.1	< 0.1	0.3	0.4	0.5	0.4	1	0	0	1	0.4	0
Combretum imberbe	T	0.7	0.8	0.4	0.1	1.4	0.4	0.6	2	1	0	3	1.1	0
Combretum sp.	T	0.6	5.6	0.4	1.2	1.8	3.5	2.2	2	1	0	3	1.1	0
Commiphora neglecta	T	1.6	2.1	–	1.3	0.9	1.4	1.2	2	1	0	3	1.1	0
Crinum delagoense	H	–	–	3.8	0.8	2.0	1.0	1.3	1	1	0	2	0.7	0

Crotalaria monteiroi	T	< 0.1	0.6	< 0.1	0.5	< 0.1	0.2	0.2	0	1	0	1	0.4	0
Cymbopogon excavatus	T	0.8	1.7	0.3	1.1	1.3	0.4	0.9	0	0	2	2	0.7	0
Cynodon dactylon	G	1.5	3.1	0.6	1.3	2.5	1.3	1.7	0	1	3	4	1.5	0
Dialium schlechteri	T	0.3	0.8	0.7	0.4	1.1	0.2	0.6	2	0	0	2	0.7	0
Dialium s. – fruit	T	1.2	1.7	–	1.9	0.7	0.3	1.0	2	0	0	2	0.7	0
Dichrostachys cinerea	T	2.9	3.0	1.1	1.7	2.6	2.7	2.3	2	3	0	5	1.8	0
Digitaria longiflora	G	3.7	0.3	–	0.9	1.6	1.4	1.3	0	2	3	5	1.8	0
Echinochloa pyramidalis	G	2.4	0.9	–	1.2	0.8	1.3	1.1	0	0	3	3	1.1	0
Eragrostis ciliaris	G	–	1.4	–	0.4	0.2	0.7	0.5	0	1	3	4	1.5	–
Euclea natalensis	T	0.3	0.9	–	0.2	0.7	0.3	0.4	2	1	0	3	1.1	–
Euclea sp.	T	–	0.2	–	0.1	< 0.1	–	< 0.1	2	1	0	3	1.1	–
Eugenia capensis	T	–	–	3.6	0.5	0.3	2.7	1.2	0	1	0	1	0.4	+
Euphorbia kunthii	T	–	–	0.4	–	0.4	< 0.1	0.1	1	1	0	2	0.7	–
Euphorbia tirucalli	T	2.1	–	1.5	0.7	1.5	1.4	1.2	1	1	0	2	0.7	0
Fagara capensis	T	–	0.2	–	0.2	< 0.1	–	< 0.1	2	0	0	2	0.7	–
Festuca arundinacea	G	–	0.2	< 0.1	0.2	–	0.1	< 0.1	0	0	1	1	0.4	–
Ficus capensis	T	–	0.1	0.2	0.1	0.2	–	< 0.1	2	0	0	2	0.7	–
Ficus sycomorus	T	0.8	2.7	–	0.8	0.8	1.8	1.1	1	0	0	1	0.4	+
Ficus sp. 1	T	1.6	3.8	–	1.2	1.3	2.9	1.8	2	0	0	2	0.7	+
Ficus sp. 2	T	–	0.6	2.4	0.9	0.3	1.7	1.0	2	0	0	2	0.7	0
Garcinia livingstonei – fruit	T	0.1	0.8	0.8	0.6	0.6	0.7	0.6	2	2	0	4	1.5	–
Grewia caffra	T	0.7	1.3	1.2	0.6	1.2	1.3	1.0	2	0	0	2	0.7	0
Hyparrhenia dissoluta	G	2.6	1.9	0.4	0.9	2.4	1.5	1.6	0	0	2	2	0.7	+
Hyparrhenia sp.	G	2.7	0.2	–	1.4	0.9	0.6	1.0	0	0	2	2	0.7	0
Indigofera podophylla	T	–	0.3	< 0.1	0.3	–	–	0.1	1	3	2	6	2.2	–
Ischaemum arcuatum	G	–	0.2	–	< 0.1	< 0.1	< 0.1	< 0.1	0	1	2	3	1.1	–
Mangifera indica	TC	0.6	–	–	0.2	0.3	0.1	0.2		around settlements				
Manihot esculenta	HC	–	0.3	0.2	0.2	0.2	0.1	0.2		agricultural fields				
Mimusops caffra	T	–	0.5	0.7	0.3	0.3	0.6	0.4	3	0	2	5	1.8	–
Ozoroa obovata	T	–	0.1	1.0	0.4	0.3	0.3	0.4	2	1	0	3	1.1	–
Panicum maximum	G	0.2	0.3	–	< 0.1	0.4	–	0.1	2	1	1	4	1.5	–
Panicum sp.	G	–	0.2	–	–	< 0.1	0.1	< 0.1	2	1	2	5	1.8	–
Parinari capensis	T	–	0.3	6.4	6.1	0.6	0.1	2.2	0	0	3	3	1.1	+
Phoenix reclinata	T	–	< 0.1	0.8	< 0.1	0.3	0.5	0.3	1	2	1	4	1.5	–
Phragmites communis	G	2.7	0.9	8.2	4.3	4.5	3.0	3.9	0	0	3	3	1.1	+
Phyllanthus reticulatus	T	–	0.1	0.2	0.2	< 0.1	< 0.1	< 0.1	1	0	0	1	0.4	–
Rubus sp.	H	–	< 0.1	–	–	< 0.1	–	< 0.1	0	0	1	1	0.4	–
Rhus microcarpa	T	1.0	0.6	< 0.1	0.8	0.4	0.4	0.6	1	0	0	1	0.4	0
Rhus natalensis	T	–	0.2	1.2	0.6	0.3	0.6	0.5	1	1	0	2	0.7	0
Rhus sp.	T	–	< 0.1	0.4	< 0.1	0.4	–	0.1	1	0	0	1	0.4	–
Salacia kraussii	H	1.9	1.2	4.1	2.1	2.1	3.1	2.4	1	3	0	4	1.5	0

Table 2 *continued*

		Faecal composition							Relative plant abundance					
		Season			Habitat									
Plant species	Type	Early rain	Late rain	Late dry	Forest	Wood-land	Grass plain	Mean	Forest	Wood-land	Grass plain	Total	E	P
Sansevieria hyacinthoides	H	< 0.1	0.2	–	0.2	< 0.1	–	< 0.1	2	0	0	2	0.7	–
Sansevieria h. – rhizome	H	0.3	1.5	–	0.3	0.8	0.6	0.6	2	0	0	2	0.7	0
Sapium ellipticum	T	2.6	1.3	1.2	1.8	1.6	1.8	1.7	2	1	0	3	1.1	0
Scilla sp. – root	H	< 0.1	0.3	–	0.2	0.1	< 0.1	0.1	1	0	0	1	0.4	–
*Androstachys johnsonii**	T								plantation					
*Sclerocarya birrea**	T	0.2	1.6	16.5	5.5	5.8	6.9	6.1	2	3	0	5	1.8	+
Sclerocarya birrea – fruit	T	0.1	4.3	–	1.4	1.6	1.4	1.5	2	3	0	5	1.8	0
Scutia myrtina	T	0.4	0.4	–	0.3	0.3	0.3	0.3	1	0	0	1	0.4	0
Sesbania sesban	T	–	< 0.1	–	–	< 0.1	–	< 0.1	0	0	1	1	0.4	–
Sesuvium portulacastrum	H	5.9	0.4	0.7	2.6	1.8	2.7	2.4	0	0	1	1	0.4	+
Setaria chevalieri	G	7.5	0.5	0.7	4.6	2.8	1.3	2.9	1	0	0	1	0.4	+
Setaria holstii	G	1.6	3.6	1.4	2.8	2.4	1.4	2.2	1	0	0	1	0.4	+
Sporobolus subtilis	G	–	0.6	–	0.3	0.2	–	0.2	1	2	3	6	2.2	–
Strychnos innocua	T	9.2	5.6	0.4	6.7	3.8	4.8	5.1	3	3	0	6	2.2	+
Strychos madagascariensis	T	–	1.2	0.8	1.1	0.3	0.6	0.7	2	3	0	5	1.8	–
Strychos spinosa	T	–	0.4	0.1	0.4	–	0.1	0.2	2	3	0	5	1.8	–
Syzygium cordatum	T	–	0.7	0.5	0.2	0.6	0.4	0.4	1	3	2	6	2.2	–
Syzygium cordatum – fruit	T	–	0.5	–	0.4	–	0.1	0.2	1	3	2	6	2.2	–
Terminalia sericea	T	< 0.1	0.7	2.1	0.5	1.0	1.4	1.0	0	1	0	1	0.4	+
Themeda triandra	G	3.3	2.2	–	1.3	1.6	2.6	1.8	0	2	2	4	1.5	0
Triraphis schlechteri	G	< 0.1	0.2	< 0.1	0.2	< 0.1	< 0.1	< 0.1	1	0	0	1	0.4	–
Vangueria infausta	T	1.7	1.8	–	0.7	1.2	1.6	1.2	1	2	0	3	1.1	0
Vangueria tomentosa	T	0.6	2.1	0.9	1.0	1.1	1.6	1.2	1	2	0	3	1.1	0
Vigna sinensis	H	–	1.0	–	0.2	0.7	0.1	0.3	0	1	0	1	0.4	0
Xylotheca kraussiana	T	–	0.2	–	–	< 0.1	0.2	< 0.1	1	1	0	2	0.7	–
Zea mays	HC	–	< 0.1	–	< 0.1	–	–	< 0.1	agricultural fields					
Ziziphus mucronata	T	5.1	1.0	0.8	3.0	1.9	2.1	2.3	2	1	0	3	1.1	+
Unidentified #1	T	–	0.3	–	0.1	< 0.1	0.2	0.1	2	0	0	2	0.7	–
Monocotyledons – N.I.		0.6	1.8	12.8	5.4	4.7	5.0	5.0	1	2	3	6	2.2	+
Dicotyledons – N.I.		0.5	2.1	8.8	4.3	3.8	3.3	3.8	3	2	1	6	2.2	0
Total percentage		100.0	100.0	100.0	100.0	100.0	100.0	100.0					100.0	
Total identified fragments		1800	1800	1800	1800	1800	1800	5400						
Total score									117	94	60	271		

*Species lumped together because of identification characteristic similarities.

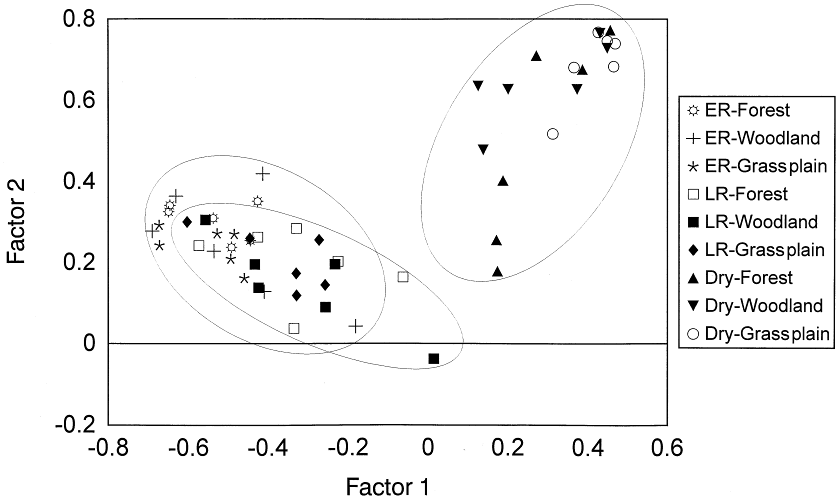

Fig 2 The composition of the faecal samples collected in three different habitats and three different periods as ordinated by a principal component analysis. ER = early rainy season; LR = late rainy season; DRY = dry season.

Discussion

Habitat

The results from the dung counts, and the satellite tracking study, both indicate that the forest of the MER is the preferred elephant habitat. This confirms our own observations; elephants are rarely encountered on the extensive grass plains. The old records and distribution maps from Tello (1973), Matias & Carter (1980) and Hall-Martin (1988), clearly showed the preference of the MER elephants for the grass plains and the delta of the Futi river. Habitat preference has changed and the forest patches are now selected in preference to these open areas. The high nutritional fodder quality of the grass plains and flood plains near the river, especially in the rainy season, is considered to be the main reason

Table 3 Relative frequency (%) and total number of different plant species of elephant faecal samples collected in different seasons and in different habitats.

	Season			Habitat			
Plant categories	Early rain	Late rain	Late dry	Forest	Woodland	Grass plain	Total
Relative frequency (%)							
Trees	53.9	62.8	55.7	55.6	53.7	63.0	57.5
Grass	36.8	27.4	14.0	27.8	29.5	20.9	26.1
Herbs	8.2	5.9	8.8	6.9	8.4	7.7	7.6
Monocotyledons, N.I.	0.6	1.8	12.8	5.4	4.7	5.0	5.0
Dicotyledons, N.I.	0.5	2.1	8.8	4.3	3.8	3.3	3.8
Number of species (*n*)							
Trees	35	58	43	57	58	53	62
Grass	16	21	10	20	20	19	21
Herbs	4	11	5	10	10	9	12
Total	56	90	58	87	88	81	95

N.I. = not identified.

Table 4 Relative occurrence of different plant species in elephant dung collected in different seasons and in different habitats, together with expected relative occurrence calculated from the plant abundance data given in Table 2. Total χ^2 and probability are based on the original faecal samples (df = 2)

Faecal sample	Forest plants	Woodland plants	Grass plain plants	Total χ^2	*P*
Expected	1.0	1.0	1.0		
Season					
Early rain	0.8	1.1	1.2	39.383	< 0.001
Late rain	0.9	1.1	1.0	16.748	< 0.001
Late dry	0.8	0.9	1.6	212.954	< 0.001
Habitat					
Forest	0.8	1.0	1.4	84.382	< 0.001
Woodland	0.8	1.1	1.3	62.509	< 0.001
Grass plain	0.9	1.1	1.1	19.319	< 0.001

for elephants breaking the fence in the TEP (Hall-Martin, 1988). The change in habitat preference from open, high-quality pastures to dense forest can be explained by increased disturbance, particularly poaching. The elephants are seeking refuge in the forest, which is almost inaccessible to poachers. The presence of the dense forest patches in the MER, with an area < 10% of the total area of the MER, is essential for the survival of the elephants.

Elephant density

The elephants are concentrated on the western part of the MER, and for several years none have been sighted in the eastern part. This utilization pattern limited their movements to roughly 50% of the total area of the MER. An estimated 180 elephants (0.45 elephants km^{-2}) still live in the MER, distributed over 400 $km^{2.}$ This density is roughly the same as the allowed maximum stocking rate and elephant density of the TEP (Hall-Martin, 1992) and the Kruger National Park (Trollope *et al.*, 1998). The vegetation damage in the TEP, where 75% of the trees are damaged by elephants and tree mortality is high (W. Matthews, personal communication), indicates a relatively high elephant pressure. The effects elephants can have, especially on the tree component of the vegetation has been well documented in other studies (Laws, 1970; Van Wijngaarden, 1985; Prins & van der Jeugd, 1993; Campbell *et al.*, 1996; Page, 1996; Struhsaker, Lwanga & Kasenene, 1996; Tafangenyasha, 1997; Trollope *et al.*, 1998), but the vegetation in the MER does not show evidence of high elephant pressure. This discrepancy between calculated high elephant density which is not reflected in a high level of vegetation damage, can be explained by two factors. Firstly, the MER is not fenced and the elephants move in and out freely, decreasing the pressure on the resources within the Reserve. Secondly, the elephants of the MER are mainly composed of breeding herds. Males have been observed to push over and debark trees more than females (Spinage, 1994; Dublin, 1995). The high incidence of damaged trees which have been pushed over in the TEP can therefore be partly explained by the high percentage of bulls, estimated at more than 60% (Hall-Martin, 1988; I. Whyte, personal communication).

Seasonal distribution

Elephants tend to concentrate near fresh water sources during the dry season and hence the density of dung piles is lower around saline lakes. Surface water is not a restricting factor for elephants in the rainy season, but in the dry season the main water source is the Futi River. Ostrosky (1987, 1988a, 1989) described a seasonal movement of bulls from the TEP in the dry season to the north in the direction of the MER, and regular movement of breeding herds visiting the Maputo River flood plains in the rainy season. Differences in seasonal distribution, other than that associated with water salinity, could not be confirmed by the study.

Diet composition

The diet composition reflects habitat preference, a relatively high percentage of browse (> 60%) and low percentage of grass (31%). The percentage of grass taken is lower than records from other areas (Laws, 1970; Skinner & Smithers, 1990; Kabigumila, 1993; Spinage, 1994; Paley & Kerley, 1998), although the MER is characterized by extensive, high quality grasslands. Moreover, faecal studies tend to overestimate the percentage of monocotyledons to dicotyledons (Pulliam & Nelson, 1980; Gordon & Illius, 1994, 1996).

Season was the important factor in the ordination of the faecal samples. Species composition was relatively unaffected by the habitat in which the dung pile was found (Jarman, 1971; Meissner *et al.*, 1990). The long digestive process, and the opportunistic feeding pattern masks the species composition of each habitat. This also explains the occurrence of, for example, the reed *Phragmites communis* in the faecal samples found in the forest, or the typical forest species such as *Ficus* spp. in the grass plain samples. The decreasing proportion of grass from the early rainy season to the late rainy season and the dry season can be explained by a decrease in palatability and nutrient concentration (Sukumar, 1989, 1990) and is also reported from other areas (Jarman, 1971; Kabigumila, 1993; Spinage, 1994; Dublin, 1996; Osborn, 1996). The smaller diet of the elephant in the early rainy season and the late dry season is explained by the fodder quality and availability. In the early rainy season, elephants select high quality grass species and concentrate on these species during the first part of the growth season (see also Skinner & Smithers, 1990; Sukumar, 1990). With the advance of the rainy season, the grasses decrease in quality (Sukumar, 1990; Kabigumila, 1993) but ample green vegetation is available, increasing the number of plant species in the diet. The late dry season is characterized by an absence of green herbaceous species and several tree species have lost their leaves. The elephants then concentrate before the start of the rains on a limited number of browse species with flowers and young leaves, such as *Sclerocarya birrea* (Jarman, 1971; Coetzee *et al.*, 1979; Sukumar, 1990).

Table 4 indicates that the grass plain species are selected relative to their availability. Elephants have started to use forests more than in the past, and the high percentage of browse in the diet must be seen as a cost related to protection from poachers. This could lead to an unfavourable diet in which the necessary bulk, provided by the grasses, cannot be attained (Laws, 1970; Skinner & Smithers, 1990). The percentage of grass in the diet is relatively low, especially in the rainy season. Grass is normally preferred to browse, because of the higher palatability and lower concentration of secondary compounds (Rosenthal & Berenbaum, 1979; Cooper & Owen-Smith, 1985; Gordon & Illius, 1994, 1996). The apparent habitat change since the 1970s can therefore only be understood by the increasing human disturbance in the area, which has consequently led to a less favourable diet.

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