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Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns

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ABSTRACT. The Asian elephant's foraging strategy in its natural habitat and in cultivation was studied in southern India during 1981–83. Though elephants consumed at least 112 plant species in the study area, about 85% of their diet consisted of only 25 species from the order Malvales and the families Leguminosae, Palmae, Cyperaceae and Gramineae. Alteration between a predominantly browse diet during the dry season with a grass diet during the early wet season was related to the seasonally changing protein content of grasses.

Crop raiding, which was sporadic during the dry season, gradually increased with more area being cultivated with the onset of rains. Raiding frequency reached a peak during October–December, with some villages being raided almost every night, when finger millet (*Eleusine coracana*) was cultivated by most farmers. The monthly frequency of raiding was related to the seasonal movement of elephant herds and to the size of the enclave. Of their total annual food requirement, adult bull elephants derived an estimated 9.3% and family herds 1.7% in quantity from cultivated land. Cultivated cereal and millet crops provided significantly more protein, calcium and sodium than the wild grasses. Ultimately, crop raiding can be thought of as an extension of the elephant's optimal foraging strategy.

KEY WORDS: Asian elephant, crop depredation, elephant ecology, *Elephas maximus*, feeding habits, foraging strategy, India.

INTRODUCTION

Depredation of crops by elephants occurs to varying extents throughout their present range in Africa and Asia, wherever cultivation abuts elephant habitat. In spite of the extensive research on African Elephant (*Loxodonta africana* Blumenbach), the interaction between elephants and agriculture has, surprisingly, received little attention from an ecological perspective. The work of Allaway (1979) is essentially descriptive rather than analytical. Studies on the Asian elephant (*Elephas maximus* L.) state the problem only briefly (McKay 1973, Olivier 1978) or give the economic implications of crop damage (Blair *et al.* 1979, Mishra 1971).

The present study was undertaken to understand crop raiding behaviour in relation to the elephant's life-history strategy (Sukumar 1985). An earlier paper described the elephant's movement and habitat utilization patterns (Sukumar 1989). This paper describes the elephant's feeding habits and shows how feeding on crops is related to its seasonal movement and optimal foraging strategy.

METHODS

The study was carried out during 1981-83 within a 1130 km^2 area in the Chamarajanagar, Kollegal and Satyamangalam Forest Divisions (11° 30′ N to 12° 0′ N and 76° 50′ E to 77° 15′ E) in southern India (Figure 1). A background description of the study area has been given elsewhere (Sukumar 1989). To study elephant feeding habits, three broad habitat types were defined in the study area. These were (a) short grass habitats with predominantly browse vegetation, (b) mixed tall grass and browse areas in deciduous forests and (c) predominantly tall grass habitats. Based on plant species composition, topography and location these were further divided into smaller homogeneous zones. The locations of the zones are shown in Figure 1. Direct observations of feeding by elephants were made in selected zones representing each of these broad habitat categories.

A scan sampling method was employed, the plant species being eaten by each visible member in a herd recorded at 5-minute intervals (Altmann 1974). Each record was scored as browsing or grazing and the species noted. In some zones where sufficient direct observations were not made, an indirect method was used to determine the proportion of different browse plants in the diet. Ten plots each measuring 0.5-2.0 ha, depending on plant density in the zone, were examined for signs of elephant feeding on trees and shrubs. The number of individuals of each plant species and the number of branches broken from each individual were recorded.

Calculations were made as follows. Data on feeding were lumped together for all zones categorized under the three broad habitat types for the three major seasons (dry, first wet and second wet) and under each category the proportions of browsing and grazing were determined. The seasonal density of elephants in these habitats has been separately estimated (Sukumar 1989). This was used to give appropriate weighting to the diet of the elephant population in the study area as follows:

$$F_w = \sum e_i f_i$$

where F_w = weighted proportion of browsing or grazing during the season by the elephant population in the study area.

e_i = proportion of elephants of study area within the i^{th} habitat type during the season.

f_i = proportion of browsing or grazing within the i^{th} habitat during the season.

To study the pattern of crop depredation by elephants 22 settlements comprising 10 enclaves of cultivation (total area 46 km^2) of various sizes within the study area and two settlements just outside the forest boundary (Figure 1) were regularly monitored from March 1981 to February 1982 and less intensively for another year for comparison. On certain nights direct observations were made on raiding elephants. Records of the name of the cultivator, date of

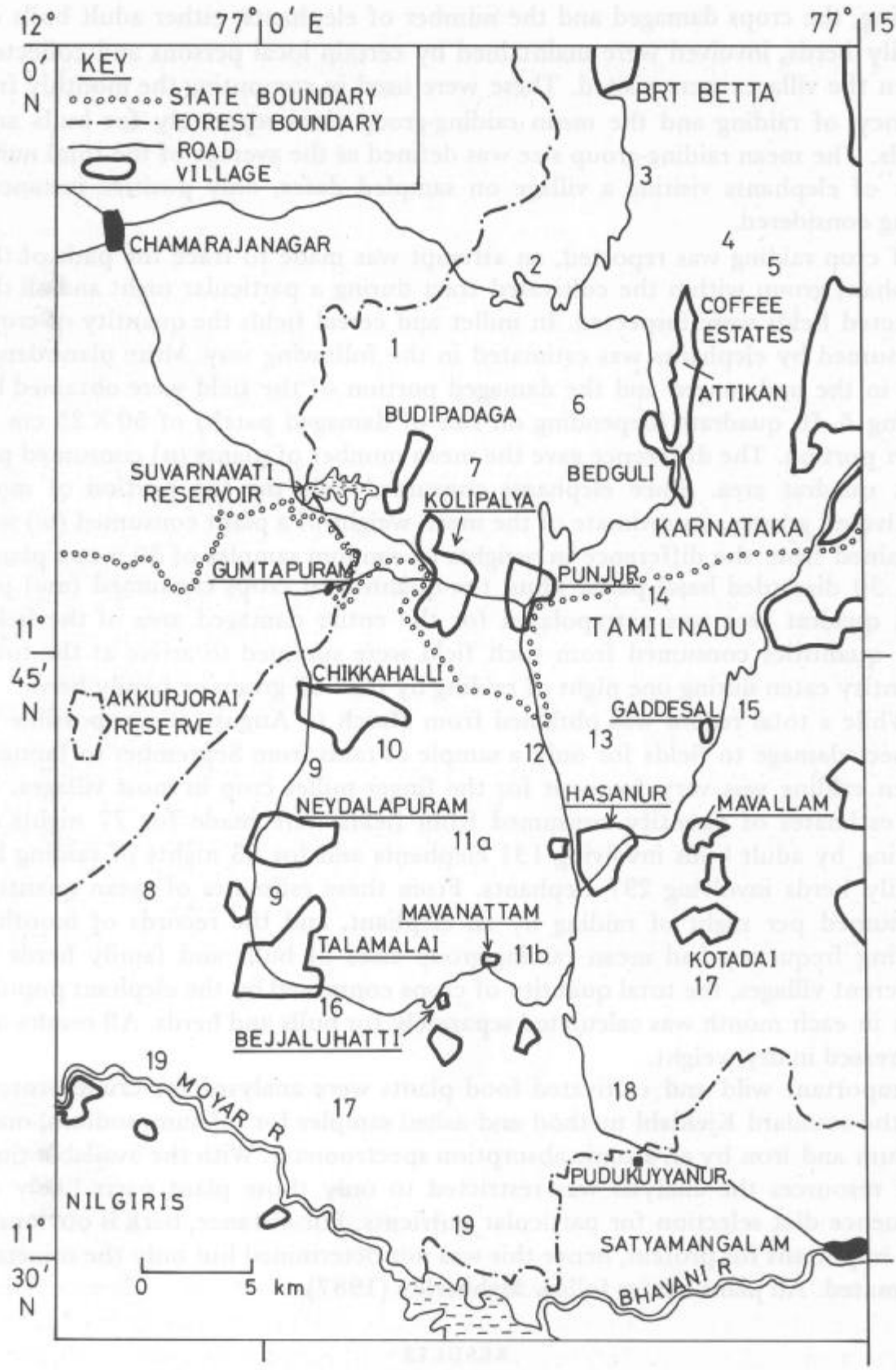

Figure 1. Map of the study area showing the enclaves of cultivation. The focal study villages are underlined. The numbers refer to locations of habitat zones.

raiding, the crops damaged and the number of elephants, either adult bulls or family herds, involved were maintained by certain local persons and collected when the villages were visited. These were used in computing the monthly frequency of raiding and the mean raiding-group sizes separately for bulls and herds. The mean raiding-group size was defined as the average of the total numbers of elephants visiting a village on sampled dates, only positive instances being considered.

If crop raiding was reported, an attempt was made to trace the path of the elephant group within the cultivated tract during a particular night and all the affected fields were inspected. In millet and cereal fields the quantity of crops consumed by elephants was estimated in the following way. Mean plant densities in the undamaged and the damaged portion of the field were obtained by laying 5–40 quadrats (depending on size of damaged patch) of 50 × 25 cm in each portion. The difference gave the mean number of plants (n) consumed per unit quadrat area. Since elephants consumed only the top portion of most cultivated grasses, an estimate of the mean weight of a plant consumed (w) was obtained from the difference in weights of random samples of 30 intact plants and 30 discarded basal parts. Thus, the quantity of crops consumed (nw) per unit quadrat area was extrapolated for the entire damaged area of the field. The quantities consumed from each field were summed to arrive at the total quantity eaten during one night of raiding by the bull group or family herd.

While a total record was obtained from March to August, it was possible to inspect damage to fields for only a sample of raids from September to January when raiding was very frequent for the finger millet crop in most villages. In all, estimates of quantity consumed from fields were made for 77 nights of raiding by adult bulls involving 131 elephants and for 33 nights of raiding by family herds involving 297 elephants. From these estimates of mean quantity consumed per night of raiding by an elephant, and the records of monthly raiding frequency and mean raiding-group sizes of bulls and family herds in different villages, the total quantity of crops consumed by the elephant population in each month was calculated separately for bulls and herds. All results are expressed in dry weight.

Important wild and cultivated food plants were analysed for crude protein by the standard Kjeldahl method and ashed samples for calcium, sodium, magnesium and iron by an atomic absorption spectrometer. With the available time and resources the analysis was restricted to only those plant parts likely to influence diet selection for particular nutrients. For instance, bark is obviously not important for protein, hence this was not determined but only the minerals estimated. All plant names follow Mabberley (1987).

RESULTS

Natural feeding habits

Wild plants eaten. Within the study area 112 plant species eaten by elephants in the wild were recorded. Though a generalist feeder, the most commonly

eaten plants were from only five botanical taxa - the order Malvales and the families Leguminosae (especially the sub-family Mimosoideae), Palmae, Cyperaceae and Gramineae. These taxa accounted for 76 (68%) of the recorded food species. In fact, just 25 species from these taxa constituted about 85% of the elephant's quantitative intake.

Elephants are both grazers and browsers. Grazing was primarily on the tall grasses *Themeda cymbaria, T. triandra* and *Cymbopogon flexuosus.* The portion of the grass consumed varies with season. After the first rains when the new flush appears, elephants remove the tender blades in small clumps without uprooting the plant. This was noticed during April-June. Later, when the grass attains a height of 0.5 to 1 m, entire clumps are uprooted with the trunk, dusted skilfully and the relatively fresh top portion of the leaves consumed, while the basal portion with the roots is discarded. When the grasses mature (October-March), after vigorous cleaning the succulent basal portion with the roots is consumed and the fibrous blades discarded. Short grasses were generally eaten only during the second wet season or later when they attained a height of about 0.5 m and began to flower.

From the bamboos, *Bambusa arundinacea* and *Dendrocalamus strictus,* various portions such as seedlings, culms and lateral shoots are consumed. When feeding on trees and shrubs, both leaves and twigs are taken as in species of *Acacia, Albizia, Grewia, Zizyphus* and *Ficus.* Elephants may select individuals within a species with the most fresh foliage, as was often observed when they fed on *Acacia pennata.* In the absence of leaves they still consume the twigs during the dry season. Thorn bearing shoots of many species of *Acacia* are consumed without any obvious discomfort. Elephants feed on the bark of certain plants such as *Acacia suma, Grewia tiliaefolia, Kydia calycina, Zizyphus xylopyrus, Tectona grandis* and *Eucalyptus* spp. Among the fruits consumed are those of *Limonia acidissima, Tamarindus indica* and *Careya arborea.* Leaves and fruits of the shrubby palm *Phoenix humilis* are eaten. Young plants may be uprooted with the forefeet, dusted, the basal soft stem chewed and the leaves discarded. Succulents such as *Sansieviera* and *Pandanus* are favoured, though these were not abundant in the study area.

Proportions of browse and grass in the diet. The proportion of time spent in browsing and grazing seasonally in each of the three broad habitat categories is given in Table 1. Based on the elephant occupancy in these habitat types, a weighted average proportion is also given.

(a) In the short grass zones, both during the dry season and first wet season a very high proportion of the diet (85-90%) was browse, while grazing was restricted to sedges and grasses growing along streams. Only after the short grasses had grown above 0.5 m during the second wet season were they consumed.

(b) In the mixed tall grass and browse forests there was only marginally more grazing than browsing during the dry months. But the new growth of grass after the first rains promoted significantly more grazing (73%) especially on *Themeda.*

Table 1. Proportion of time spent in browsing and grazing

Habitat type	Jan.-Apr. (dry) browse:grass	May-Aug. (I wet) browse:grass	Sept.-Dec. (II wet) browse:grass
1. Short grass habitat with predominantly browse vegetation	0.90:0.10 n = 575 e = 0.56	0.87:0.13 n = 260 e = 0.35	0.71:0.29 n = 205 e = 0.56
2. Mixed tall grass and browse habitat	0.45:0.55 n = 730 e = 0.40	0.27:0.73 n = 705 e = 0.62	0.40:0.60 n = 175 e = 0.40
3. Predominantly grassland habitat	0.19:0.81 n = 585 e = 0.04	+ e = 0.03	0.06:0.94 n = 260 e = 0.04
Weighted seasonal proportion in study area	0.69:0.31	0.46:0.54	0.56:0.44

n = Number of minutes of elephant feeding observed.
e = Proportion of elephant population of study area within the habitat type in 1982.
\+ Relatively few elephants were observed. Intermediate value of 0.12:0.88 has been taken.

Statistical tests:

(a) The proportions of browsing versus grazing in each habitat type during different seasons were tested for statistical significance by the z-test. Those which were significantly different at least at 10% level were the following:

Habitat 1 - dry/II wet ($P < 0.05$), I wet/II wet ($P < 0.10$).
Habitat 2 - dry/I wet ($P < 0.01$).
Habitat 3 - dry/II wet ($P < 0.01$).

(b) The proportions of browsing versus grazing in different habitats during each season were also tested for statistical significance. All the differences were significant ($P < 0.01$).

During the second wet season grazing on tall grass declined though the data are insufficient to prove this.

(c) In lowland grasslands, grazing obviously remained at a high level (>80%) throughout the year, though in view of the very restricted area the overall contribution of grass from here was low.

Overall, the importance of browse (69%) during the dry season is clear. Feeding on grass (54%) picks up during the first wet season. Once again after the second heavy rains feeding on browse (56%) increases in the natural habitat.

Proportion of different browse plants in the diet. Important browse plants which constituted at least 2% of the browse diet in a zone are given in Table 2. Only five representative zones where sufficient observations were made are shown. These include two tall grass habitats (Zones 3 and 11) and three short grass habitats (Zones 12, 18 and 19).

Feeding on cultivated crops

The crops cultivated. Agriculture in the region is mainly traditional, rain-fed cultivation. The perennial or semi-perennial plantation crops include coconut (*Cocos nucifera*), banana (*Musa paradisiaca*) and sugar cane (*Saccharum officinarum*), but these are grown on a small scale. Jackfruit (*Artocarpus integrifolia*) and mango (*Mangifera indica*) trees are found in some gardens. The

Table 2. Proportions of important browse plants consumed in different habitats.

Plant species	Zone 3	Zone 11	Zone 12	Zone 18	Zone 19
		Malvales			
1. *Kydia calycina*	56.1	R	–	–	–
2. *Helicteres isora*	12.6	–	–	–	–
3. *Grewia tiliaefolia*	17.9	9.9	2.3	–	–
		Leguminosae			
4. *Atylosia albicans*	–	5.3	–	–	–
5. *Tamarindus indica*	–	R	8.4	5.0	R
6. *Hardwickia binata*	–	–	–	–	7.5
7. *Dicrostachys cinerea*	–	–	R	9.0	R
8. *Mimosa rubicaulis*	–	3.0	R	–	–
9. *Acacia leucophloea*	–	R	3.4	14.4	15.0
10. *Acacia latronum*	–	–	–	13.1	R
11. *Acacia suma*	–	–	12.4	–	–
12. *Acacia sundra*	–	–	R	20.3	12.2
13. *Acacia ferruginea*	–	–	–	3.6	–
14. *Acacia torta*	R	14.4	5.6	–	–
15. *Acacia pennata*	–	10.6	26.4	–	–
16. *Albizia amara*	–	–	–	23.0	49.7
		Other dicots			
17. *Capparis sepiaria*	–	–	2.3	–	–
18. *Commiphora caudata*	–	–	–	R	2.0
19. *Zizyphus xylopyrus*	R	5.3	3.4	5.4	8.8
20. *Tectona grandis*	R	3.8	R	–	–
		Palmae			
21. *Phoenix humilis*	–	11.4	–	–	–
		Bamboos			
22. *Bambusa arundinacea*	3.0	6.8	14.6	–	–
23. *Dendrocalamus strictus*	R	10.6	R	–	–
Total percentage of above species (approximate)	92%	82%	81%	96%	96%
Sample size (n)	246	132	178	222	147

Only those species which constitute at least 2% of the browse diet in a zone have been included.
R: Recorded as eaten but in negligible quantity (below 2%) in the zone.
–: Not found in the zone or not recorded being eaten.

millets, cereals, pulses and oilseeds are cultivated in two fairly distinct crop seasons (Figure 2).

(a) Minor crop season: the cultivation of sorghum (*Sorghum vulgare*) and maize (*Zea mays*) begins after pre-monsoon showers during April–May. These rely mainly on the SW monsoon (first wet season) during June–July and the crop is ready for harvest by August. Only a small fraction (4%) of the cultivable land area was cultivated for these crops during this season in 1981. Gingelly (*Sesamum indicum*) is also grown during this period.

(b) Major crop season: the staple food crop of the people, ragi or finger

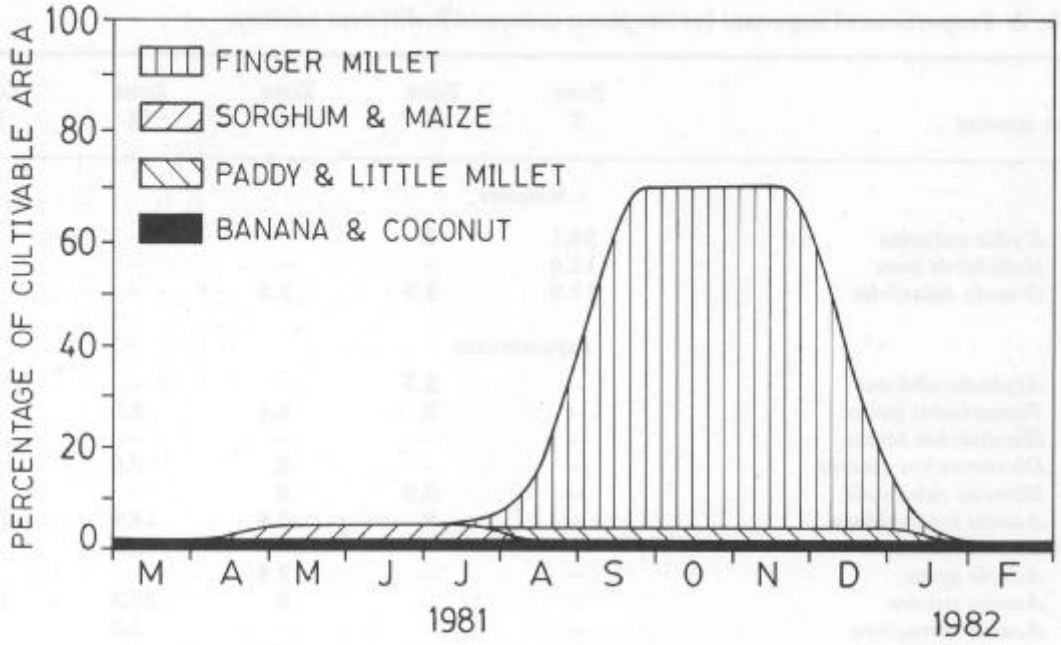

Figure 2. Cultivation of crops in the study villages between March 1981 and February 1982.

millet (*Eleusine coracana*) is usually sown during August-September before the end of the SW monsoon. It depends for its growth mainly on the NE monsoon (second wet season) during October-November and is ready for harvest in December-January. Most farmers also plant rows of niger (*Guizotia abyssinica*), an oilseed crop, along with finger millet. In 1981 finger millet was cultivated over 65% of the land area. Paddy (*Oryza sativa*) and little millet (*Panicum miliare*) were grown to a far lesser extent, occupying 1.5% and 0.5% of the area respectively. Among the legumes, horse gram (*Dolichos biflorus*) is cultivated mixed with other crops.

The crops consumed. Finger millet makes the highest contribution among crops to the elephant's diet in the study area. During this season paddy and little millet fields are also visited, especially when these are harvested only after the finger millet crop. Selection was distinctly biased towards fields with robust plant growth, high density of standing crop and plants in inflorescence or grain stage. Elephants rarely utilized finger millet crops in the vegetative stage in fields they had to cross before reaching the target field. They also invariably consumed only the terminal portion of the plant bearing the inflorescence, while discarding the basal stem with the roots. On an average the terminal portion consumed formed 62% (SD = 10.5, N = 31 samples of 30 plants each) by weight of the finger millet plant. When feeding on sorghum and maize, the elephant is again selective in plucking the stalk bearing the inflorescence. However, in the absence of the spikes they may eat the terminal portion of the succulent stem and the leaves.

From young coconut trees, below 2 or 3 m in height, only the central rachis is pulled out and eaten. Taller trees are uprooted, usually by adult bull elephants, before the rachis is plucked. Banana stems are split and the fibrous pith

VILLAGE	MAR		APR		MAY		JUN		JUL		AUG		SEP		OCT		NOV		DEC		JAN		FEB	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
1. Hasanur	○	○	○	○	◔	○	◔	○	◔	○	○	○	◔	○	●	○	●	○	●	◔	◑	◔	○	○
2. Punjur	○	○	○	○	○	○	◔	◔	○	◔	○	○	◔	◔	◕	◕	◕	◕	◕	◑	○	○	○	◔
3. Kolipalya	○	○	○	○	○	○	◔	◔	○	◔	○	◔	◔	◔	●	◕	◕	◑	◔	◔	○	○	○	○
4. Gumtapuram	○	○	◔	○	◔	◔	◔	◔																
5. Chikkahalli	◔	◔	○	○	○	○	◔	○	○	○	○	○	◔	○	◕	◔	◔	◔	◔	◔	◔	◔	○	○
6. Neydalapuram	◔	○	○	○	◔	○	◔	○	◔	◔	○	○	◔	○	◔	○	◑	◑	◕	◑	◑	◔	○	○
7. Talamalai	◔	○	○	○	◔	○	○	○	◔	○	○	◔	○	○	◔	◔	●	◕	◕	◑	◔	◔	◔	◔
8. Bejjaluhatti	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
9. Mavanattam	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	◔	◔	◔	◔	○	○	○	○
10. Gaddesal	○	○	○	○	○	○	◑	○	◑	○	◔	○	○	○	○	○	○	○	○	○	○	○	○	○
11. Mavallam	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	◔	○	◔	◔	○	○
12. Pudukuyyanur	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	◔	◔	◔	◔	○	○

Number of days of raiding per month: ○ Absent; ◔ 1 - 5 days; ◔ 6 - 10 days; ◑ 11-15 days; ◕ 16-20 days; ◕ 21 - 25 days; ● > 26 days

Figure 3. Frequency of crop raiding by adult male (M) and family herd (F) elephants. Data was not gathered in Gumtapuram from July to February but some raiding occurred during October-December. Gaddesal did not cultivate finger millet during October-December.

consumed, as also occasionally the inflorescence spike or fruit bunch. Sugar canes are broken, chewed and consumed as a whole. A preference for mango trees was noticed from the time the flowers appeared until fruiting, such shoots being selectively eaten. Jackfruits are plucked or shaken off the trees, crushed with the foot and consumed.

Frequency and seasonality of raiding. Elephants usually enter cultivated land only after sunset and leave before sunrise, though some exceptions to this do occur. The frequency of crop raiding during different months in the year was, as could be expected, proportional to the area of land under cultivation. There were also differences in the raiding frequency pattern between adult bulls and family herds (Figure 3).

During the dry period from February to April, when most of the land was in fallow, raiding was sporadic. Solitary bulls made occasional incursions to feed on plantation crops such as coconut, banana, mango, jackfruit and sugar cane. From May to August, a few bulls and herds operated in the northern villages of Punjur, Kolipalya and Gumtapuram where some farmers cultivated sorghum and maize. During this season raiding was at a relatively low frequency, confined to less than 10 days in a month.

The frequency of raiding reached a peak during the finger millet crop season when a large area was under cultivation. Intensive raiding by both bulls and herds began during the last week of September, when the finger millet flowered in the fields of Punjur and Kolipalya, and continued until the harvest began in December. Hasanur was raided mostly by adult bulls from late September until mid-January with only a single herd raiding during the first week of December.

On the western sector at Chikkahalli, raiding was at a peak during October by mainly bulls and, to a lesser extent, by herds. Raiding gathered momentum in November at Neydalapuram and Talamalai, continued at a high frequency during December and decreased in January. The small settlement at Mavanattam was visited in late November and early December by some adult bulls and a couple of small herds. Gaddesal did not cultivate finger millet in 1981. Mavallam was visited only a few times late in the season by adult bulls. In the plains to the south, raiding by bulls and herds began in the bordering villages including Pudukuyyanur in late November or early December, but was generally at a low frequency. There was no raiding between March and October in this region.

Mean raiding-group size of bulls and herds. Table 3 gives the mean raiding-group sizes or number of adult bulls and elephants in family herds visiting a village in a day during each month. While raids by just one bull per day were the most common event in all the villages, up to six bulls were recorded on certain days during October–November at Hasanur. In all the villages the raiding-group sizes of bulls were highest during the finger millet season. The largest family herd sizes recorded were in the village of Kolipalya during June, July and October. Between 15 and 25 elephants raided the fields here on many occasions. In general, sizes of raiding herds were between three and 10 elephants with a mean size of 7.9 for all villages.

Quantity consumed from crop fields. (a) Adult bulls: the mean quantity of crops consumed by an adult bull elephant per day of raiding was calculated for two distinguishable strata of cultivation (based on differences in plant productivity and biomass per unit area due to rainfall and on the intensity of feeding by elephants). This was 43.9 kg per elephant per day at Punjur and Hasanur (N = 40 days of raiding involving 73 bulls) and 30.1 kg in all other villages (N = 37 days of raiding involving 58 bulls).

The upper limit to the weight of crops that an adult bull consumed in one night's feeding (12 hours) was between 70 and 75 kg of finger millet, recorded a number of times at Hasanur, Punjur and Kolipalya. Figure 4 shows the total quantity of crops consumed by adult bulls from 10 study village enclaves each month. In the vicinity of these villages about 15 bulls were present during March–August and 20 bulls during September–February. From the estimate that an average adult bull weighing 4000 kg requires 60 kg fodder (1.5% of its body weight) each day (Laws *et al.* 1975), the total quantity of crops consumed each month has been converted into percentage of the monthly food requirement of the bull population (Figure 5). The contribution of crops in the diet, which remained relatively low at 1–4% between March and September, suddenly increased to a very significant 22–30% during October–December when finger millet was cultivated. For the entire year it was estimated that cultivated crops formed 9.3% of an average adult bull's diet. Certain habitual crop raiders derived a much higher proportion of their food from cultivation.

Table 3. Mean raiding-group size of adult bulls and family herds.

Village	Adult bulls												Family herds											
	Mar 1981	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan 1982	Feb	Mar 1981	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan 1982	Feb
1. Hasanur	0	0	1.0	1.0	1.4	0	2.2	3.4	4.5	3.1	1.0	0	0	0	0	0	0	0	0	0	0	9.5	4.0*	0
2. Punjur	0	0	0	1.0*	0	0	1.0	2.4	1.5	1.9	0	0	0	0	0	5.0	7.0	0	8.5	7.0	6.8	6.8	0	8.0*
3. Kolipalya	0	0	0	1.0*	0	0	1.0*	2.1	2.3	2.0	0	0	0	0	0	15.7	15.0*	4.7	6.5	14.3	6.6	4.0	0	0
4. Gumtapuram	0	1.0	1.3	1.0	–	–	–	–	–	–	–	–	0	0	5.0	11.5	–	–	–	–	–	–	–	–
5. Chikkahalli	1.0	0	0	1.0*	0	0	1.0*	2.3	2.0	1.0*	1.0	0	4.0*	0	0	0	0	0	0	4.0	7.5	7.5	12.5	0
6. Neydalapuram	1.0	0	1.0	1.0	1.0	0	1.0*	1.0*	1.5	2.0	2.3	0	0	0	0	0	7.0	0	0	0	8.8	8.4	3.0	0
7. Talamalai	1.0	0	1.0*	0	1.0*	0	0	1.5	1.3	1.3	1.0	1.0	0	0	0	0	0	10.0*	0	6.0	6.4	13.3	6.5	4.0*
8. Bejjaluhatti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9. Mavanattam	0	0	0	0	0	0	0	0	1.0*	0	0	0	0	0	0	0	0	0	0	0	5.0	4.0*	0	0
10. Gaddesal	0	0	0	1.0	1.5	2.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11. Mavallam	0	0	0	0	0	0	0	0	0	1.0*	2.0	0	0	0	0	0	0	0	0	0	0	0	3.0*	0
12. Pudukuyyanur	0	0	0	0	0	0	0	0	0	1.0*	1.0	1.0*	0	0	0	0	0	0	0	0	0	4.3	6.2	0

Total sample sizes are 258 days of raiding for adult bulls and 120 days of raiding for family herds.
* Based on only one instance of raiding during the month. – Data not gathered.

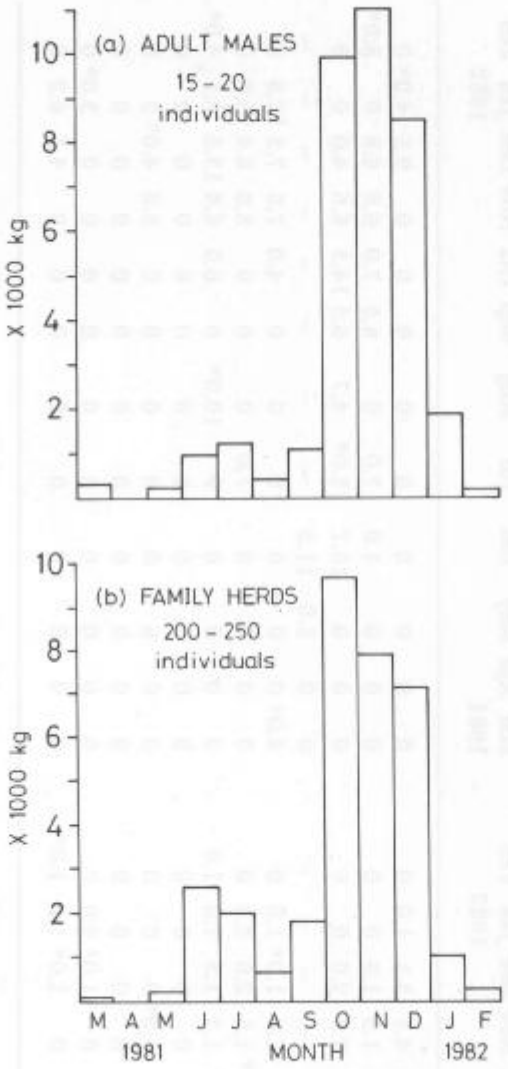

Figure 4. Quantity of crops consumed by elephants from ten study villages (excluding Gumtapuram and Pudukuyyanur).

For instance, one well identified bull (MA-6) foraged about 20% of its annual requirement from crop fields.

Family herds: The mean quantity of crops consumed per day of raiding by an elephant belonging to a family herd was 24.2 kg at Punjur and Kolipalya (N = 18 days of raiding involving 169 elephants) and 10.8 kg in all other villages (N = 15 days of raiding involving 128 elephants).

The highest quantity consumed was 52 kg per elephant per day by a herd of nine elephants from a finger millet field. Figure 4 shows the total quantity of crops consumed by family herds from the study villages each month. It was estimated that about 200 elephants were present during March-August and 250 elephants during September-February in the forest region around the villages. An average elephant in a family group, weighing 1575 kg would require 23.6 kg of food every day. The proportion of crops in the total diet of family herds was about 4-5% during October-December and insignificant during other months

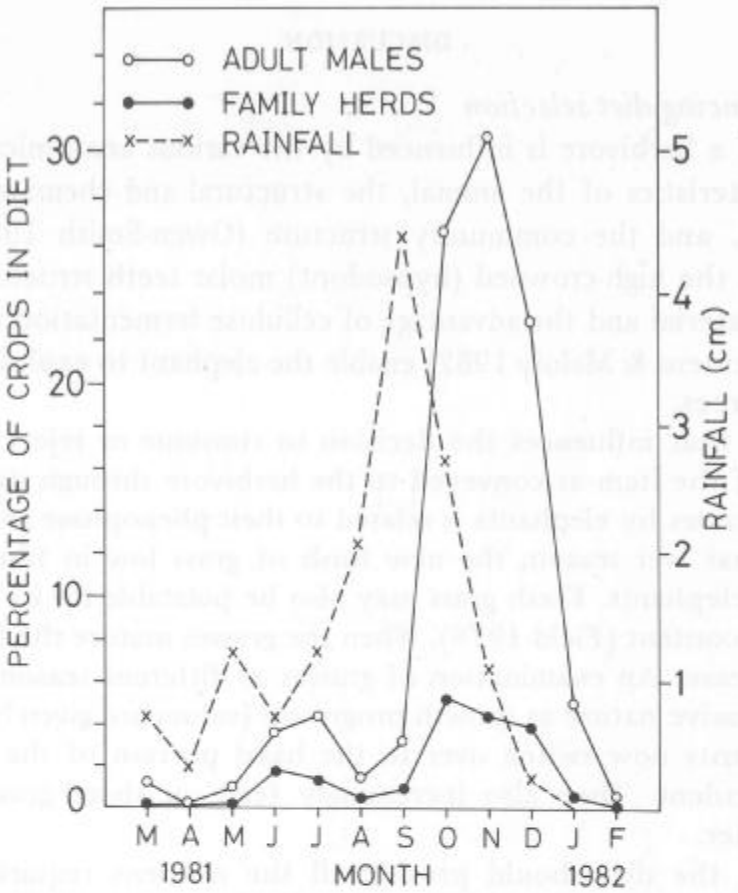

Figure 5. Proportion of crops in the total diet of elephants.

(Figure 5). For the entire year, cultivated crops contributed only 1.7% of the total food requirements of family herds.

Chemical composition of food plants

Crude protein and mineral values (dry weight) of wild and cultivated plants consumed by elephants are given in Appendix I. The protein content of browse leaves (range 6.0–18.0% dry season, 13.0–25.5% wet season) was higher than that of wild grass leaves (3.2–4.8% dry season, 6.8–9.9% wet season) during all the seasons. The basal portion of grass clumps had a lower protein content (1.6–3.8%) than the upper leaves. The range of protein values was higher in cultivated grasses (5.3–13.0%) than in wild grass leaves but lower than in browse leaves.

Calcium content was lower in plants of Gramineae (0.8–10.8 mg g^{-1}) than in those of other families (17.7–57.2 mg g^{-1}). In this regard, the higher calcium value of *Eleusine coracana* (7.4–10.8 mg g^{-1}) than of all other cultivated and wild grasses (0.8–4.6 mg g^{-1}) was significant. Sodium (0.11–0.36 mg g^{-1}) and magnesium (0.53–2.12 mg g^{-1}) values did not vary much in most plants, except for sodium during the flowering stage of *Eleusine coracana* (0.94 mg g^{-1}). The iron content was more variable (0.03–0.48 mg g^{-1}) but no clear pattern could be discerned.

DISCUSSION

Factors influencing diet selection

The diet of a herbivore is influenced by the various anatomical and physiological characteristics of the animal, the structural and chemical constitution of the plants, and the community structure (Owen-Smith 1982). The prehensile trunk, the high-crowned (hypsodont) molar teeth structured for grinding fibrous material and the advantage of cellulose fermentation in the caecum and colon (Clemens & Maloiy 1982) enable the elephant to exploit a wide range of plant resources.

The factor that influences the decision to consume or reject a plant is the palatability of the item as conveyed to the herbivore through its senses. Selection of tall grasses by elephants is related to their phenophase and palatability. During the first wet season, the new flush of grass low in fibre and silica is preferred by elephants. Fresh grass may also be palatable for its higher soluble carbohydrate content (Field 1976). When the grasses mature the fibre and silica contents increase. An examination of grasses at different seasons reveals their increasing abrasive nature as growth progresses (values are given by Field 1971, 1976). Elephants now switch over to the basal portion of the grass tussock which is succulent. They also increasingly feed on short grasses which are relatively tender.

Ultimately, the diet should provide all the nutrient requirements of the animal. Ungulates show a positive selection of plant species and plant parts with the highest protein value (Field 1976) or minerals such as sodium (Belovsky 1981). An elephant requires daily 0.3 g of digestible protein per kg of its body weight (McCullagh 1969). This may translate into a minimum level of 5-6% crude protein in plant material for maintenance. The elephant's strategy of alternating seasonally between grass and browse is related to their protein content (see Appendix I for values). Fresh growth of tall grass during the first wet season (May-August) had a crude protein of 8-10% dry weight. Leaves of *Themeda cymbaria* had 10% protein in May and this altered only slightly to 8% by November when the grass was mature at the end of the second wet season. By the dry season (February) it dropped considerably to 3% protein. *Themeda* bases had less protein with 4% in the wet season and 1.6% in the dry period. *Cymbopogon flexuosus* also showed a similar trend though with a narrower range. Clearly the elephant's preference for grass leaves during the first wet season supplied it with over 8% protein. But they avoid the leaves with high protein (7-8%) and switch over to the bases (2-4%) during the second wet season. This could be due to two reasons - the unpalatable nature of the siliceous leaves and the presence of soluble carbohydrates in the more succulent basal portion (Field 1971, 1976).

During the dry season the protein level in the grass bases falls below 2.5% which is insufficient for maintenance. Browse plants have high crude protein levels even in the dry period. The range of values is 8-10% in the Malvales and 10-20% in the Leguminosae such as *Acacia* and *Albizia*. It is not known how

much of the browse protein is unavailable because of interference by secondary compounds. Elephants showed a clear preference for browse in the dry season.

Feeding on bark may help maintain an optimum fibre:protein ratio to ensure proper digestion of protein (Laws *et al.* 1975), supply essential fatty acids (McCullagh 1973) or minerals such as manganese, iron, boron, copper and calcium (Bax & Sheldrick 1963, Dougall *et al.* 1964, Laws *et al.* 1975). One study found no relationship between degree of debarking and mineral content of plants (Anderson & Walker 1974).

As might be expected the calcium content of dicot bark (range 18–57 mg g^{-1}) was much higher than that of grasses (1–5 mg g^{-1}). Though a diet of only grass could provide sufficient intake of calcium for elephants, it is not known how much of it is physiologically unavailable. Also it is not necessary for an animal to be deficient in a particular nutrient to consume foods rich in that nutrient. Supplementing the diet with bark could certainly increase its calcium intake to a safe level.

Elephants are known to be prone to sodium deficiency (Benedict 1936, Olivier 1978) and to prefer water and soils rich in sodium (Weir 1973). All the wild plants analysed had a relatively low sodium content though, as will be discussed later, certain cultivated crops had significantly higher amounts.

Plant secondary compounds may also influence nutrition (Freeland & Janzen 1974, Rosenthal & Janzen 1979). Among the food plants of the elephant, the various species of *Acacia* have a high tannin content. Bark of *A. pennata* contains 9% tannin, while that of *A. leucophloea* may be up to 21% tannin (Wealth of India 1948), both of which are commonly consumed by elephants. Further studies are needed to see whether the degree of debarking and the tannin content are seasonally related. Presence of latex in plants of Moraceae and Anacardiaceae does not prevent elephants from feeding on them (also see Olivier 1978). It is well known that hydrogen cyanide (HCN) concentrations are highest in immature tissues of plants included in the families Gramineae and Leguminosae (Conn 1979). Elephants perhaps avoid toxicity by feeding on these plants only after they have grown sufficiently for HCN levels to be negligible.

Causes of crop raiding

Raiding of agricultural fields by elephants can be explained in terms of proximate factors such as contact with cultivation, especially in fragmented habitats, in the course of their movement for foraging or drinking. However, in ultimate terms crop raiding can be thought of as an extension of their natural optimal foraging strategy.

(a) Raiding in relation to movement patterns. In the first instance, elephants probably come into contact with cultivated land in the course of their natural seasonal movement. There is evidence that the movement pattern seen today is as close to a natural situation as possible in spite of habitat changes due to human impact. From the observations of Sanderson (1878) more than a hundred years back it can be seen that elephants were following the same strategy as that seen in recent years. Elephants used to move from the moist deciduous

forests of the hills (Zone 3) in September into lower elevation habitats such as around Punjur and Kolipalya even when the former village was very small and the latter did not exist (discussed in Sukumar 1989).

A comparison of the frequency of raiding in each village with the overall strategy of movement and the density of elephants in the zones adjoining these villages show an obvious correlation. This can be illustrated with a few examples. From September when elephants began moving southwards from Zone 3 into Zone 7, raiding began first in the villages of Punjur and Kolipalya. Some herds also moved further south into Zones 8, 9 and 10. There was sequential raiding at Chikkahalli, Neydalapuram, Talamalai and Mavanattam corresponding with the movement of herds into adjacent zones during October–November. Hasanur was totally free of raiding by herds until the end of November, although the finger millet crop was in a highly preferred stage during October–November, because no herds were present in its vicinity. Similarly, in the southern plains (Zone 18), raiding in villages such as Pudukuyyanur adjoining the forest boundary was confined to between late November and February, in spite of crops being grown practically all year round due to better irrigation. This correlates with the presence of elephants in the adjacent forests only from November to February.

In contrast to family herds, many adult bulls seem to be habitual crop raiders. Certain bulls took up position for long periods near villages, regularly raiding the fields at night and retreating into the forest during the day. For instance, an adult bull (MA-6) spent the entire period from June to early January near Hasanur, raiding whatever crops were available, after which it headed west towards Talamalai where it continued its depredation.

(b) Competition for water. Often village ponds and small irrigation reservoirs are used by elephants at night. Since water is relatively scarce in the region, a need for utilizing water from agricultural land increases the frequency of an elephant's contact with crops. In the process the traversed fields may be damaged. Elephants seem able to smell water and move towards a large water body or an area receiving rain (Allaway 1979, Leuthold 1977). Herds of elephants which traversed the fields of Gumtapuram and Kolipalya often headed towards the Suvarnavati Reservoir, the largest water body in the area. Small ponds in the villages of Gaddesal, Hasanur, Talamalai and Chikkahalli were used by bulls and herds at night. These visits were often combined with attempts to feed on available crops. Whether elephants damage crops in their passage to water or whether the utilization of ponds is merely opportunistic in the course of raiding crops cannot be deduced with certainty. Both these situations may be true depending on the specific requirements and motivational status of the animals concerned.

(c) Reduction of natural habitat. While a large and compact natural habitat allows an unimpeded movement, with cultivation making inroads there is often little room left for manoeuvrability by these far ranging mammals. The larger the size of a cultivated enclave, and the longer its perimeter abutting the forest

the higher the frequency of raiding that can be expected simply due to the higher probability of an elephant making contact with its boundary. As expected the frequency of raiding was, in general, directly proportional to the size of the cultivated enclave. The situation may be aggravated when the passage from one habitat to another becomes narrow. For instance, the traditional movement has been hampered by the settlements of Kolipalya and Punjur. Since the steep hills to the east of Punjur are not much used, most of the elephants are forced to move through the narrow 1.5 km wide corridor between these two enclaves. This funnelling effect increases their contact with cultivation.

(d) Degradation of habitat. Degradation of the natural habitat is often mentioned as the primary cause of crop raiding. Here, the term degradation is used to describe any exploitation of the habitat that reduces the elephant's food resources. A qualitative ranking of habitat types around the villages when compared with the intensity of raiding showed no clear pattern. Villages such as Kolipalya, Chikkahalli and Neydalapuram placed in more degraded habitats did not have a higher frequency of raiding than similar sized tracts at Punjur, Hasanur and Talamalai which, in part, adjoin more favoured elephant habitats. Thus, elephants inhabiting an area with a clear surplus of natural food resources would still resort to crop raiding. While a degraded area in the vicinity of a village might provide motivation for entering cultivation, the tendency for elephants to avoid below optimum habitats might be a counter force taking them into more frequent contact with cultivated tracts situated in the more favoured natural habitats.

(e) Palatability and nutritive value of crops. Ultimately, if a crop raiding strategy is to confer some benefit to the elephant it must provide a higher plane of nutrition than foraging on wild plants. Since humans have selected their food crops primarily on considerations of sensory quality, digestibility, absence of toxins, productivity and, in recent times, for their nutritive value, it is not surprising that many such crops are also attractive to elephants especially as they are analogous to their wild counterparts.

The elephant's natural preference for plants of Gramineae, Palmae and Leguminosae could also be extended to the analogous cultivated plants. When it encounters a cultivated grass field, the elephant would naturally treat it as any wild grass species. While feeding on wild palms, elephants are known to select only the central rachis (Olivier 1978). In the cultivated coconut palm and oil palm also only the central rachis is consumed. Similar selection for wild and cultivated Leguminosae, Anacardiaceae and Moraceae occurs.

Cultivated crops, as a whole, have higher palatability and nutritive value than their wild counterparts. During the second wet season the wild grasses *Themeda* and *Cymbopogon* are very fibrous and siliceous, while the succulent finger millet plants are much more edible. Sucrose in sugar cane could appeal to the elephant's palate. Cultivated crops are also either low in or devoid of secondary compounds.

The crude protein content of finger millet in inflorescence stage (8.3%) and grain stage (5.3%) or paddy (10%) is not different from that in the leaves of tall grasses (6.8–8.0%) during the second wet season. However, at this time elephants do not consume the leaves but the basal portion of wild grasses which has only 2.0–3.8% protein. Hence, feeding on cultivated grasses provides it with substantially more protein.

The calcium content is also higher in finger millet inflorescences (10.8 mg g^{-1}) and grain stage (7.4 mg g^{-1}) than in the basal portion of wild grasses (0.8–2.3 mg g^{-1}). The sodium content of finger millet in inflorescence stage (0.94 mg g^{-1}) is strikingly higher than that of any other wild food plant including barks analysed (range 0.10–0.28 mg g^{-1}). Paddy in the mature stage also has a relatively high sodium content of 0.36 mg g^{-1}. As mentioned earlier this could be important to elephants which are likely to be deficient in sodium.

Elephants may respond to the nutrients associated with the phenological stage of a cultivated grass. From the time of pollination, which usually occurs two or three days after flowering, there is a sudden influx of sucrose and amino-acids from the leaf into the developing seed for about 15 days. After this the grain begins to dry. It may be significant that peak raiding of finger millet fields occurs during the inflorescence stage.

The higher propensity of adult male elephants to raid crops than female herds may have its origin in the higher variance in male reproductive success in this polygynous mammal, leading to selection pressures favouring a risky strategy in the males to derive better nutrition for enhancing reproductive success (Sukumar & Gadgil 1988).

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LITERATURE CITED

ALLAWAY, J. D. 1979. Elephants and their interactions with people in the Tana river region of Kenya. Ph.D. thesis, Cornell University, Ithaca.

ALTMANN, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49:227–267.

ANDERSON, G. D. & WALKER, B. H. 1974. Vegetation composition and elephant damage in the Sengwa Wildlife Research Area, Rhodesia. *Journal of the South African Wildlife Management Association* 4:1-14.

BAX, P. N. & SHELDRICK, D. L. W. 1963. Some preliminary observations on the food of elephants in the Tsavo Royal National Park (East) of Kenya. *East African Wildlife Journal* 1:40-53.

BELOVSKY, G. E. 1981. Food plant selection by a generalist herbivore: the moose. *Ecology* 62:1020-1030.

BENEDICT. F. G. 1936. *The physiology of the elephant.* Carnegie Institute, Washington.

BLAIR, J. A. S., BOON, G. G. & NOOR, N. M. 1979. Conservation or cultivation: the confrontation between the Asian elephant and land development in peninsular Malaysia. *Land Development Digest* 2:27-59.

CLEMENS, E. T. & MALOIY, M. O. 1982. The digestive physiology of three East African herbivores: the elephant, rhinoceros and hippopotamus. *Journal of Zoology* (London) 198:141-156.

CONN, E. E. 1979. Cyanide and cyanogenic glycosides. Pp. 387-412 in Rosenthal, G. A. & Janzen, D. H. (eds). *Herbivores: their interactions with secondary plant metabolites.* Academic Press, New York.

DOUGALL, H. W., DRYSDALE, V. M. & GLOVER, P. E. 1964. The chemical composition of Kenya browse and pasture herbage. *East African Wildlife Journal* 2:86-121.

FIELD, C. R. 1971. Elephant ecology in the Queen Elizabeth National Park, Uganda. *East African Wildlife Journal* 9:99-123.

FIELD, C. R. 1976. Palatability factors and nutritive values of the food of buffaloes (*Synercus caffer*) in Uganda. *East African Wildlife Journal* 14:1-15.

FREELAND, W. J. & JANZEN, D. H. 1974. Strategies in herbivory by mammals; the role of plant secondary compounds. *American Naturalist* 108:269-289.

LAWS, R. M., PARKER, I. S. C. & JOHNSTONE, R. C. B. 1975. *Elephants and their habitats.* Clarendon Press, Oxford.

LEUTHOLD, W. 1977. Spatial organization and strategy of habitat utilization of elephants in Tsavo National Park, Kenya. *Zeitschrift für Saugetierkunde* 42:358-379.

MABBERLEY, D. J. 1987. *The plant book: a portable dictionary of higher plants.* Cambridge University Press, Cambridge, U.K.

McCULLAGH, K. G. 1969. The growth and nutrition of the African elephant. II. The chemical nature of the diet. *East African Wildlife Journal* 7:91-98.

McCULLAGH, K. G. 1973. Are African elephants deficient in essential fatty acids? *Nature* (London) 242:267-268.

McKAY, G. M. 1973. The ecology and behavior of the Asiatic elephant in southeastern Ceylon. *Smithsonian Contributions to Zoology* 125:1-113.

MISHRA, J. 1971. An assessment of annual damage to crops by elephants in Palamau District, Bihar. *Journal of the Bombay Natural History Society* 68:307-310.

OLIVIER, R. C. D. 1978. On the ecology of the Asian elephant. Ph.D. thesis, University of Cambridge, Cambridge.

OWEN-SMITH, N. 1982. Factors influencing the consumption of plant products by large herbivores. Pp. 359-404 in Huntley, B. J. & Walker, B. H. (eds). *Ecological studies, Vol. 42: Ecology of tropical savannas.* Springer-Verlag, Berlin.

ROSENTHAL, G. A. & JANZEN, D. H. (eds). 1979. *Herbivores: their interactions with secondary plant metabolites.* Academic Press, New York. 718 pp.

SANDERSON, G. P. 1878. *Thirteen years among the wild beasts of India.* W. H. Allen, London. 387 pp.

SUKUMAR, R. 1985. Ecology of the Asian elephant (*Elephas maximus*) and its interaction with man in south India. PhD. thesis, Indian Institute of Science, Bangalore.

SUKUMAR, R. 1989. Ecology of the Asian elephant in southern India. I. Movement and habitat utilization patterns. *Journal of Tropical Ecology* 5:1-18.

SUKUMAR, R. & GADGIL, M. 1988. Male-female differences in foraging on crops by Asian elephants. *Animal Behaviour* 36:1233-1235.

WEALTH OF INDIA. 1948. Vol. I. Council for Scientific and Industrial Reesarch, New Delhi.

WEIR, J. S. 1973. Exploitation of water soluble soil sodium by elephants in Murchison Falls National Park, Uganda. *East African Wildlife Journal* 11:1-7.

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Appendix I. Nutritive value of food plants

(A) Crude protein

Plant species (a)	Plant parts (b)	Month and season (c)	Crude protein % dry matter (d)
		Wild browse plants	
Kydia calycina	leaves	Feb., dry	8.8
	leaves	Dec., II wet	15.6
Grewia tiliaefolia	leaves	Feb., dry	10.4
	leaves	Aug., I wet	14.5
	leaves	Dec., II wet	13.0
	bark	Aug., I wet	3.6
Zizyphus xylopyrus	leaves	Feb., dry	7.6
Acacia pennata	leaves	Feb., dry	17.6
Acacia torta	leaves	Mar., dry	11.3
	leaves	Aug., I wet	14.9
Acacia suma	leaves	Jan., dry	17.7
	leaves	Aug., I wet	25.5
Acacia leucophloea	leaves	Mar., dry	12.0
Albizia amara	leaves	Feb., dry	18.0
Phoenix humilis	leaves	Feb., dry	6.0
Bambusa arundinacea	leaves	May., I wet	14.5
Dendrocalamus strictus	leaves	Dec., II wet	14.4
		Wild grasses	
Themeda cymbaria	leaves	Feb., dry	3.2
	bases	Feb., dry	1.6
	leaves	May, I wet	9.9
	leaves	June, I wet	9.5
	leaves	Aug., I wet	9.3
	bases	Aug., I wet	2.2
	leaves	Nov., II wet	8.0
	bases	Nov., II wet	3.8
Themeda triandra	leaves	Feb., dry	3.8
Cymbopogon flexuousus	leaves	Feb., dry	4.8
	bases	Feb., dry	2.5
	leaves	June, I wet	8.4
	bases	June, I wet	3.2
	leaves	Nov., II wet	6.8
	bases	Nov., II wet	2.0
		Cultivated grasses	
Sorghum vulgare	vegetative stage	June, I wet	13.0
	inflorescence stage	July, I wet	11.6
Zea mays	vegetative stage	June, I wet	7.9
	entire cob	July, I wet	12.0
Eleusine coracana	vegetative stage	Sept., II wet	11.2
	inflorescence stage	Oct., II wet	8.3
	grain stage	Nov., II wet	5.3
Oryza sativa	inflorescence and grain stage	Nov., II wet	10.4
	basal portion of stem	Nov., II wet	9.8

(B) Mineral content

Plant species (a)	Plant part (b)	Month and season (c)	All values in mg g^{-1} dry matter: Total ash (d)	Calcium (e)	Sodium (f)	Magnesium (g)	Iron (h)
		Wild browse plants					
Kydia calcyina	bark	Feb., dry	80.0	24.6	0.15	1.05	0.04
	bark	July, I wet	176.6	57.2	0.16	2.12	0.20
	bark	Dec., II wet	75.4	26.5	0.13	1.19	0.19
Grewia tiliaefolia	bark	Feb., dry	74.4	22.6	0.20	0.99	0.06
	bark	Dec., II wet	98.7	27.6	0.17	1.28	0.07
Zizyphus xylopyrus	leaves	Feb., dry	51.1	17.7	0.11	0.83	0.09
	bark	Feb., dry	102.4	37.4	0.12	1.37	0.20
Acacia pennata	bark	Feb., dry	68.2	21.8	0.17	0.83	0.07
Acacia torta	bark	Mar., dry	66.4	19.0	0.15	0.88	0.02
Acacia suma	bark	Jan., dry	58.3	17.9	0.18	0.74	0.04
	bark	Aug., I wet	63.2	?	0.18	0.76	0.28
Acacia leucophloea	bark	Mar., dry	79.5	23.5	0.14	0.99	0.03
Bambusa arundinacea	leaves	May, I wet	96.0	2.9	0.27	1.14	0.48
Dendrocalamus strictus	leaves	Dec., II wet	64.5	2.5	0.13	0.79	0.11
		Wild grasses					
Themeda cymbaria	leaves	Nov., II wet	73.7	4.6	0.13	0.80	0.14
	bases	Nov., II wet	52.3	2.3	0.16	0.59	0.08
Cymbopogon flexuousus	leaves	Nov., II wet	81.2	1.9	0.12	0.77	0.34
	bases	Nov., II wet	75.1	0.8	0.28	0.57	0.43
		Cultivated grasses					
Sorghum vulgare	inflorescence stage	July, I wet	42.5	0.8	0.10	0.53	0.06
Zea mays	entire cob	July, I wet	60.2	0.9	0.25	0.75	0.10
Eleusine coracana	vegetative stage	Sept., II wet	105.1	7.6	0.57	1.06	0.18
	inflorescence stage	Oct., II wet	73.7	10.8	0.94	1.00	0.25
	grain stage	Nov., II wet	47.9	7.4	0.24	0.66	0.09
Oryza sativa	inflorescence and grain stage	Nov., II wet	160.1	2.6	0.36	1.26	0.21