FEEDING ECOLOGY OF THE ASIAN ELEPHANT *ELEPHAS MAXIMUS* LINNAEUS IN THE NILGIRI BIOSPHERE RESERVE, SOUTHERN INDIA

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We studied the activity patterns and feeding ecology of Asian Elephants *Elephas maximus* in deciduous and dry thorn forests of the Nilgiri Biosphere Reserve, southern India. Over 20,000 instantaneous scan samplings on elephants revealed that 60% of the daylight hours were devoted to feeding. Feeding patterns were strongly bimodal, with peaks in the morning and evening. Elephants spent less time feeding during the dry season than in the wet season, both in dry deciduous and dry thorn forests. Feeding decreased with increasing ambient temperature and its influence is more pronounced during the dry season in all the habitats. The time spent on feeding was less in dry thorn (53%) than in dry deciduous forests (68%), attributed to higher ambient temperatures coupled with poor shade availability and higher human disturbances in dry thorn forest. The diet of elephants constituted more species of browse (59) than grass (29), but grass formed the bulk of the annual diet (84.6%) than browse (15.4%). Elephants fed on more diverse food plants during the dry than the two wet seasons, and in the dry thorn than dry deciduous forests, which is discussed in the light of availability of grass biomass. The proportion of browsing was significantly more during the dry season in dry thorn forest, coinciding with poor availability of grass. These observations indicate that grass forms the principal diet of elephants in this area.

Key words: Asian elephant, *Elephas maximus*, activity, feeding, seasonal variation, temperature, browse, grass biomass

INTRODUCTION

Both living species of proboscideans, the Asian Elephant *Elephas maximus* and African Elephant *Loxodonta africana*, are well adapted to living in diverse habitats by exploiting a wide spectrum of plant species. Their physiological adaptations, like the large prehensile trunk, dentition and digestive system, which help to collect and process vast quantities of diverse plant food required to compensate for an extremely poor digestive ability and the nutritional demands of the elephant's large body mass, are undoubtedly critical to the survival of the species (Sukumar 2003). However, such physiological adaptations alone are unlikely to be sufficient, especially in tropical ecosystems, which show large spatio-temporal variance in climate, and food quality and quantity. Additional behavioural adaptations may also be necessary for both the species to efficiently exploit the highly changing heterogeneous tropical environments.

The Nilgiri Biosphere Reserve (NBR) in southern India, along with its adjoining contiguous areas in the Western and Eastern Ghats, supports the largest elephant population in Asia (Daniel *et al*. 1995). The Reserve encompasses a wide range of habitats ranging from semi-evergreen to tropical dry thorn forests and shows distinct seasonality – dry versus wet – making it an ideal system to study the effects of the spatial and environmental factors on the activity and feeding behaviour of the Asian Elephant. This paper documents the seasonal influences of ambient temperature and the availability of grass on the activity pattern and feeding behaviour of elephants in the tropical deciduous and dry thorn forests of NBR. Though the study was carried out over a decade back (1992-95), the findings are still important as there exist no detailed published data on the feeding ecology of elephants from optimal habitats (like Mudumalai, Bandipur, Nagarahole and Wayanad) of NBR, which support the major population of elephants in southern India. Additionally, it would provide baseline data to know the impact of the recent changes taking place on the vegetation physiognomy of elephant habitats due to proliferation of exotic weeds like *Lantana camara* and *Eupatorium odoratum* and the reported decline of preferred food plant species (Sivaganesan and Sathyanarayana 1995), and their impact on elephant feeding.

STUDY AREA

Nilgiri Biosphere Reserve (12° 15'-10° 45' N; 76° 0-77° 15' E), spread over an area of 5,520 sq. km is situated at the junction of three southern states — Tamil Nadu, Karnataka and Kerala. It has an undulating terrain with an average elevation of 1,000 m above msl. Rivers such as Nugu, Moyar and Bhavani, and most of their tributaries, are perennial and drain the area. The Reserve has a diverse climate due to its varied reliefs and topography. The temperature ranges from 7°C in December to 37°C in April, and receives rainfall both from the Southwest (May to August) and Northeast (September to December) monsoons. The mean annual rainfall varies from 600 (in the eastern side) to 2,000 mm (in the western side). The dry season is from January to April. Corresponding to the gradient in rainfall, the vegetation varies from southern tropical dry thorn forest in the east to moist deciduous forest in the west with dry deciduous forest in between the two forest types (Champion and Seth 1968). NBR along with its adjoining natural habitats has remarkable faunal diversity and is well-known for supporting the largest population of Asian elephants with an estimated population of 5,750 individuals (Project Elephant 2007). Overgrazing by domestic cattle and firewood collection are serious problems in the eastern fringes of NBR (Baskaran *et al*. 2004).

METHODS

Grass biomass

The abundance of grass, in terms of biomass, was estimated twice in a season for three seasons from stratified transects of one to two kilometres in dry deciduous (7 transects of total length of 10 km) and dry thorn forest (6 transects of total length of 10 km). The grass biomass could not be assessed in moist deciduous forest due to inadequate manpower. At 200 m intervals along these transects, two 1 sq. m quadrats were placed at a 5 m distance on either side of the transect. All the grass species were clipped at the ground level from each quadrat and weighed to estimate the grass biomass (wet weight). The biomass estimates using dry weight is more appropriate than wet weight method, due to varied water content in plant samples in different season. However, given the manpower and infrastructure facilities, dry weight method could not be used. Mean grass biomass for grazed and un-grazed (by domestic cattle) areas for each habitat was also estimated, as there were remarkable differences in grazing pressure across habitats. All transect were restricted to areas where direct observations on feeding of elephants was carried out.

Activity and feeding behaviour

Observations were made on elephant clans and bulls using instantaneous scan sampling method (Altmann 1974). Using radio-collared elephant clans and bull, a minimum of two clans and a bull were observed for a period of 2 days/month. Non-collared elephant clans and bulls were also observed, especially during months when radio-collared elephants were not recorded within a habitat. Daylight hours from 06:00 to 18:00 hrs were divided into 12 one-hour blocks for sampling and an attempt was made to sample each one-hour block at least once a month. Scan sampling was made at 15-minute intervals (four scans per hour) presuming that this interval would rule out over-sampling of any particular behaviour. Observations were made on foot (ground) or from a tree, depending on the topography, wind direction and visibility. Care was taken to ensure that the target animal or target group did not detect the observer's presence. During the sampling, animals were systematically scanned and information such as age, sex and activity (feeding, resting, moving and others) were recorded. If the animal was feeding, data on plant species eaten was also recorded. Additionally, the ambient temperature was recorded at every 30-minute intervals using digital thermometer at the observation site.

Data analyses

The frequency of activities and plant species eaten was estimated season-wise for each habitat. The data blocks in the morning (0600-0800 hrs) and evening (1600-1800 hrs) were less compared to other sample blocks primarily due to delay in radio-locating the animals because of weather conditions (mist, rain, etc.) and the remoteness of certain areas. Since the activity of elephants changes according to daylight hours (McKay 1973), any bias in observation at particular hours of the day would result in over- or under-estimation of a particular activity. To standardize such bias, the percentages of various activities/hour was derived from observed hourly-pooled data, and from this percentage, the mean time spent on various activities (weighted average) was calculated for the season. Data on activity pattern and grass, and browse ratio collected from the radio-collared tuskless bull, a habitual crop raider, were not included into the analysis, as its activities and feeding habits were skewed due to crop raiding behaviour. However, its data on food species eaten were included into the analysis mainly to capture the wide spectrum of food species eaten by elephants in this area. All the data were analyzed using non-parametric statistical tests and analyses were done using 'Statistical Package for Social Studies' (Norusis 1990). Kruskal-Wallis' one-way ANOVA and the Man-Whitney U tests were used to test the differences in activity pattern. Chi-square analysis was used to test the differences in the selected browsing and grazing plant species. The relationship between ambient temperature and activities (feeding and resting) was tested using Spearman Rank Correlation.

RESULTS

Overall time activity pattern

Overall, during daylight hours, elephants showed two peaks in feeding, one in the morning (06:00-09:00 hrs) and another in the evening (15:00-17:00 hrs) (Fig. 1a). Time spent on resting was more around midday than in mornings and evenings. Elephants frequently engaged in other activities such as mud-bath, sand-bath, salt-licking and play during 14:00-16:00 hrs. As the temperature increased from morning with a peak between 12:00 and 13:00 hrs, resting became more common. However, comparisons of feeding and resting with ambient temperature, with pooled data over habitats and seasons, showed no significant correlation. Overall, the activity budget revealed that elephants spent 60% of the daylight hours (06:00-18:00 hrs) on feeding and 20% on resting. Time spent on moving was 14% and 6% on other activities

Seasonal difference in time activity in different habitats

Dry deciduous forest: During the dry season, elephants showed a bimodal feeding activity with a peak each at 07:00 hrs and 18:00 hrs in dry deciduous forests (Fig. 1b). Elephants mainly rested during midday between 11:00 and 14:00 hrs. Feeding decreased significantly with increasing ambient temperature (r_s = - 0.7671, *df* = 12, *P* = 0.01), while resting increased positively (r_s = 0.8581, *df* = 12, *P* = 0.01). Movement was mostly restricted to the mornings and evenings. Unlike the dry season, elephants spent a minimum of 50% of time on feeding in all the hours of day during the first wet season, and resting being considerably less (Fig. 1c). Feeding and resting showed no significant correlation with temperature during the first wet season, as the ambient temperature during this season was relatively lower than the dry season. During the second wet season, the pattern of elephant activities observed was similar to the first wet season (Fig. 1d), but resting positively increased with temperature (r_s = 0.5874, *df* =12, *P* = 0.04), as ambient temperature increased gradually in this season unlike the first wet season.

Activity budget data show that in dry deciduous forest, elephants spent a major part (68%) of the annual daylight hours feeding (Table 1). However, time spent on feeding and resting varied among the three seasons. During the dry season, elephants fed for significantly less time than the first (M-W U = 14475, *P* = 0.01) and the second (M-W U = 14503, *P* = 0.01) wet seasons. Time spent on resting was significantly more during the dry season than the first (M-W U = 15402, *P* = 0.01) and second (M-W U=14864.5, *P* = 0.01) wet seasons.

Moist deciduous forest: In moist deciduous forest, the activity pattern shown (Fig. 1e) for the first wet season was based on a small number of observations (*n* = 221) collected over a short period of three days in a disturbed area around human settlements, and may therefore not accurately represent a picture for the entire season. Similarly, as the observations made on elephants were limited during dry season (*n* = 35) and nil during second wet season, the time activity pattern of elephants could not be constructed.

Dry thorn forest: The pattern of elephant feeding and resting observed in thorn forest during the dry season was similar to the pattern observed in dry deciduous forest (Fig. 1f-h), but there was a sharp rise in time spent on movement between 11:00 and 12:00 hrs. The peak temperature recorded during midday hours coincided with peak resting time. Resting increased positively with temperature (r_s= 0.7273, *df* =11, *P* = 0.01), while feeding decreased (r_s= - 0.7091, *df* = 11, *P* = 0.01). During the first and second wet seasons, the activities observed among elephants were similar, except for an unusually longer time (>55%) spent in resting in the morning hours (06:00-07:00 hrs) observed during second wet season (November and December), which is similar to that observed in the early dry season (January). No significant correlation was observed between ambient temperature and feeding, and resting during first and second wet seasons.

Data on activity budget showed that annually, elephants in thorn forest devoted significantly less time for feeding and more time for resting compared to dry deciduous forest (Table 1). On a seasonal basis, elephants in thorn forest also spent significantly less time on feeding (M-W U = 3838, *P* = 0.03) and more on resting during the dry season than the first wet season (M-W U = 2936, *P* = 0.01). The time spent on various activities did not vary much between the dry and

Table 1: Time spent (%) in various activities by elephants in the different habitats in Nilgiri Biosphere Reserve

Habitat and Activity	Season			Annual
	Dry	First wet	Second wet	
Dry deciduous	(*n* = 4603)	(*n* = 3310)	(*n* = 3203)	(*n* = 11116)
Feeding	59.55	72.25	72.16	67.99
Moving	11.54	11.06	12.06	11.55
Resting	24.49	12.02	10.57	15.69
Others	4.42	4.66	5.2	4.76
Moist deciduous	(*n* = 35)	(*n* = 221)	(*n* = 0)	(*n* = 256)
Feeding	22.2	60.0	-	41.10
Moving	33.12	26.37	-	29.74
Resting	31.21	9.23	-	20.22
Others	13.46	4.4	-	8.93
Dry thorn	(*n* = 2715)	(*n* = 819)	(*n* = 5562)	(*n* = 9096)
Feeding	47.08	57.63	52.35	52.35
Moving	17.21	12.14	15.46	14.94
Resting	29.55	13.77	24.26	22.33
Others	6.16	16.45	7.92	10.18

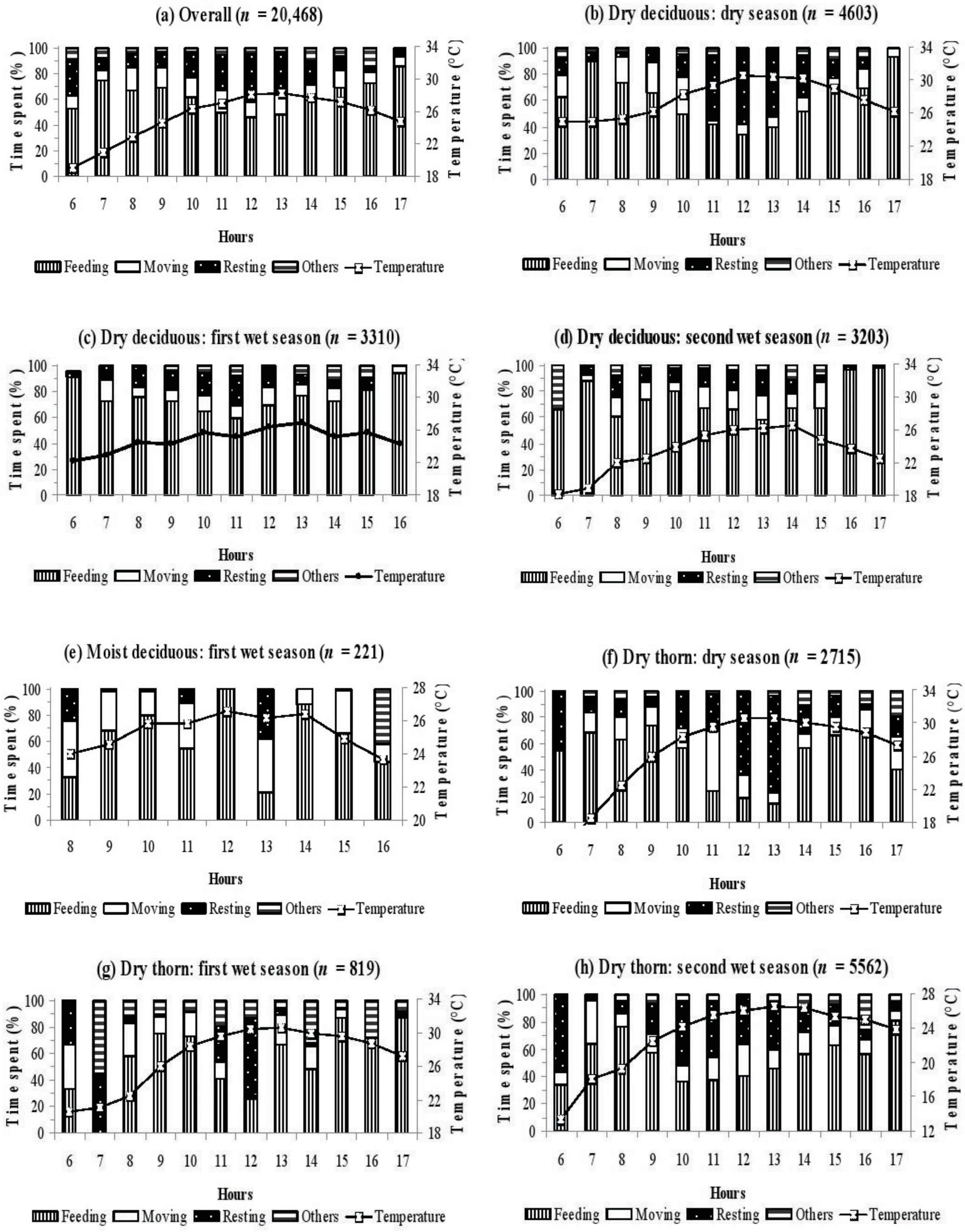

Fig. 1: Diurnal activity pattern of elephants season-wise in different habitats of Nilgiri Biosphere Reserve

second wet seasons, but there were significant variations in resting (M-W U = 4581, *P* = 0.01) and moving (M-W U = 5500, *P* = 0.01) between the wet seasons.

Grass biomass

In dry deciduous forest, mean grass biomass varied significantly across the three seasons (K-W-χ^2 = 32.1122, *P* = 0.0001) (Table 2). The biomass was significantly higher during the second wet season (921 gm/m²) as compared to the dry (573.9 gm/m², M-W U = 1838.5, *P* = 0.0001) and the first wet (618.1 gm/m², M-W U = 3033, *P* = 0.0014) seasons, and in the first wet season as compared to the dry season (M-W U=2039.5, P = 0.0002). Similarly, in thorn forest, grass biomass varied significantly across the three seasons (K-W-χ^2 = 102.46, *P* = 0.0001), and was significantly higher during the second wet season (524.1 gm/m²) than the dry (156.9 gm/m², M-W U = 781.5, *P* = 0.0001) and the first wet (405 gm/m², M-W U = 2263.5, *P* = 0.003) seasons. The grass biomass in the first wet season was also significantly more than in the dry season (M-W U=1088, P = 0.0001). Sampling was not carried out in moist deciduous forest due to manpower constraints as mentioned under methods. The observed variation in biomass between dry and wet seasons could marginally be due to variation in water content in grass samples.

The areas under cattle grazing had significantly lower grass biomass in the dry deciduous forest during the dry season (un-grazed = 725 gm/m² and grazed =188 gm/m², M-W U = 220, *P* = 0.0002) and in second wet season (ungrazed = 1019 gm/m² and grazed = 520 gm/m², M-W U = 388.5, *P* = 0.0016). However, the influence of grazing was statistically insignificant in dry deciduous during the first wet season (un-grazed = 677gm/m² and grazed = 600 gm/m², M-W U = 511, *P* = 0.10), and in all the seasons in dry thorn forest (dry season ungrazed = 190 gm/m² and grazed = 152 gm/m², M-W U = 318.5, *P* = 0.23; first wet: ungrazed = 420 gm/m² and grazed = 390 gm/m², M-W U = 426.5, *P* = 0.34; second wet season ungrazed = 528 gm/m² and grazed = 480 gm/m², M-W U = 238.5, *P* = 0.69).

Browse and grass ratio in the diet

Out of 10,743 feeding observations (*viz.*, 7,003 in dry deciduous, 153 in moist deciduous and 3,587 in dry thorn forest), grazing and browsing constituted 84.6% and 15.4%, respectively. Grass dominated the diet of elephants during all the seasons in dry deciduous and dry thorn forests, indicating the importance of grass in the diet of elephants in this region. Browsing was more during the dry season in dry deciduous (15.1%) and dry thorn (47.1%) forests than during the wet seasons (Table 2). The percentage of grazing and browsing varied significantly across seasons in dry deciduous (χ^2 = 148.64, *df* = 2, *P* = 0.00001) and dry thorn forests (χ^2 = 554.24, *df* = 2, *P* = 0.00001). Elephants fed significantly more on grass and less on browse in dry deciduous than in dry thorn forest in all the seasons (dry season - χ^2 = 459.43, *df* = 1, *P* = 0.00001; first wet season - χ^2 = 6.37, *df* = 1, *P* = 0.01 and second wet season - χ^2 = 65.71, *df* = 1, *P* = 0.00001), indicating the importance of grass in dry deciduous forest.

Species composition in the diet

Overall, 83 plant species eaten by elephants were recorded from 11,186 feeding scans. Feeding scan observations (*n* = 443) made on the habitual crop raiding bull were also included in this analysis to know the diversity of food plants eaten by elephants. Of the 83 plant species, 59 were browse species (trees, shrubs, herbs and bamboo), and the rest (24) were grass species (Appendix 1). Among the 24 grass species, six constituted more than 75% of the total diet (*Themeda cymbaria* 39.5%, *Heteropogon contortus* 13.4%, *Themeda triandra* 10.9%, *Bothriochloa* sp. 7.3%, *Aristida adscensionis* 2.4% and *Cymbopogon flexuosus* 2.3%). Among the 59 browse species, *Acacia intsia*, bamboo spp. and *Kydia calycina* were the most important, and contributed 5.4, 4.4 and 1.8%, respectively to the total diet.

Table 2: Grass biomass (gm/sq. m) and grass: browse ratio in the diet of elephants in dry deciduous and dry thorn forests of Nilgiri Biosphere Reserve (grass biomass not assessed in moist deciduous forest due to inadequate manpower)

Season	Dry deciduous		Moist deciduous	Dry thorn	
	Grass biomass/m² (*n* = 254)	Grass: browse ratio (*n* = 7003)	Grass: browse ratio (*n* = 153)	Grass biomass/m² (*n* = 251)	Grass: browse ratio (*n* = 3587)
Dry	573.9	85: 15	78: 22	156.9	53: 47
First Wet	618.1	92: 8	31: 69	405.0	89: 11
Second Wet	921.0	95: 5	-	524.1	88: 12
Annual	720.2	91: 9	54: 46	352.0	74: 26

In dry deciduous forest, 36 species of food plants were recorded from 7,003 feeding observations (Appendix 1). The number of grass species eaten (13) was less than browse species (23). The tall grass *T. cymbaria* alone contributed 62.8% of the diet and *T. triandra* 17.1%, other grass species formed <5%. Bamboo (4.4%) and *K. calycina* (2.9%) were the two major browse species (Table 3). Seasonal use of these food plants varied considerably, but the tall grass *T. cymbaria* was always the principal diet during all the seasons (Table 3). The proportion of the top four species (*T. cymbaria*, *T. triandra*, bamboo and *C. flexuosus*) and the rest of the browse and grass species (pooled separately as other browse and other grass spp.) utilised varied significantly among seasons ($\chi^2 = 1118.87$, df =10, $P = 0.01$).

Table 3: Major food species eaten (%) by elephants in different habitats in Nilgiri Biosphere Reserve

Food species	Season			Annual
	Dry	First wet	Second wet	
Dry deciduous	(*n* = 2510)	(*n* = 2236)	(*n* = 2257)	(*n* = 7003)
Bamboo spp.	6.9	3.1	3.1	4.4
Cymbopogon flexuosus	-	2.4	8.0	3.4
Themeda cymbaria	71.4	70.9	45.2	62.8
Themeda triandra	12.2	14.8	24.8	17.1
Other browse spp.	8.2	4.9	1.9	5.1
Other grass spp.	1.3	3.8	17.0	7.2
Moist deciduous	(*n* = 9)	(*n* = 289)	(*n* = 71)	(*n* = 369)
Bamboo spp.	-	34.9	25.4	32.20
Curcuma spp.	-	6.9	45.1	14.30
Helicteres isora	-	4.2	-	9.75
Cyrtococcum patens	-	12.8	-	11.60
C. flexuosus	-	4.8	7.0	5.14
T. cymbaria	-	8.0	1.4	6.50
Other browse spp.	22.2	17.3	21.1	11.55
Other grass spp.	77.8	11.1	-	8.96
Dry thorn	(*n* = 1430)	(*n* = 497)	(*n* = 1887)	(*n* = 3814)
Acacia intsia	27.3	10.1	8.8	15.9
Bothriochloa sp.	4.9	72.8	20.2	21.3
Heteropogon contortus	30.1	11.5	48.8	36.9
Other browse spp.	24.2	1.4	5.6	12.0
Other grass spp.	13.4	4.2	16.6	13.9

In moist deciduous forest, 22 species of food plants were recorded from 369 feeding observations. The diet of elephants was dominated by browse species both in terms of number of species (15) and bulk (67.8%) (Appendix 1). Bamboo (32.2%), *Curcuma* sp. (14.3%), *Helicteres isora* (9.75%) and *Dioscorea* sp. (2.16%) were the major browse plants of elephants in this habitat (Table 3). Short grass, *Cyrtococcum patens*, contributed a major part (11.6%) followed by *T. cymbaria* (6.5) and *C. flexuosus* (5.14%). Other grass and browse species contributed very little to the total diet. Seasonal use of these food plants varied significantly between the first and the second wet seasons ($\chi^2 = 83.57$, $df = 7$, $P = 0.01$).

In dry thorn forest, 56 species of food plants were recorded from 3,814 feeding observations (Appendix 1). Elephants fed on more number of browse species (41) over grass (15) in this habitat. However, in terms of bulk, browse constituted only 27.9% of the overall diet, while grass species contributed 72.1% (Table 3). Among the grass species, *H. contortus* (36.9%) and *Bothriochloa* sp. (21.3%) were important. Elephants ate the thorny shrub *A. intsia* more (15.9%) among the 41 browse species in this habitat. The percent composition of each species in the diet of elephants varied among the seasons ($\chi^2 = 1525.33$, $df = 16$, $P = 0.01$). Elephants ate more diverse food species during the dry season in dry deciduous (19 species) and dry thorn (42 species) forests than during the wet seasons (first wet: 17 and 9 spp. and second wet: 18 and 25 spp. respectively in dry deciduous and dry thorn forests). The number of species eaten was also greater in the dry thorn forest (56 spp.) than in the dry deciduous (36 spp.).

DISCUSSION

Overall, elephants showed bimodal feeding peaks, one in the morning and another in the evening, while at midday almost equal time was devoted for feeding and resting, which is similar to the pattern observed on African elephants (Wyatt and Eltringham 1974; Guy 1976; Kalemera 1987) and Asian elephants (McKay 1973; Vancuylenburg 1977; Easa 1989). Ambient temperature influences feeding activity significantly in dry deciduous and thorn forests more in the dry season than wet seasons. This is reflected in the bimodal feeding pattern and the significant negative correlation obtained between feeding and temperature during the dry season. Ambient temperature influences the body temperature of both the Asian and African elephants (Elder and Rodgers 1975; Weissenbock 2006). The most likely reason for the afternoon inactivity is heat avoidance rather than sleep due to the poor thermoregulatory capacity of the large body mass (low surface-to-volume ratio) and the absence of sufficient sweat glands in their skin (Wyatt and Eltringham 1974; Hiley 1975).

The overall feeding time (60%) estimated in this study is comparable to 65% reported in Asian elephants in Parambikulam (Easa 1989), but low compared to 74% reported in Mudumalai (Sivaganesan and Johnsingh 1995), and Idukki (Vinod and Cheeran 1997) wildlife sanctuaries in India and >75% in Sri Lanka (McKay 1973; Vancuylenberg 1977). The variation in feeding time, in NBR between Sivaganesan and Johnsingh (1995) and the present study is likely due to differences in sampling area (habitat) and time of observation, as elephants spent more time feeding in dry and moist deciduous forests than in dry thorn forest (as recorded in this study). In most secondary forests, direct observation on elephants is difficult especially during midday resting, which mostly take place in dense undergrowth and thick canopied shady areas like riverine and stream beds. Inadequate observations during such midday resting hours and pooling of such data without standardization would result in bias towards feeding activity. Thus, the observed difference in feeding time estimated by Sivaganesan and Johnsingh (1995) and this study could be due to any or a combination of the above-mentioned reasons. The same reasons could also be attributed for the higher feeding time (>75%) estimated by McKay (1973), Vancuylenberg (1977), and Vinod and Cheeran 1997 (Idukki).

Elephants spent significantly less time feeding during the dry season compared to the first and second wet seasons in dry deciduous forest, and the first wet season in dry thorn forest. These may be attributed to higher ambient temperatures and poor shade availability as shown by studies on savannah elephants in Africa (Guy 1976; Barnes 1979) and the Asian Elephant (McKay 1973; Vancuylenberg 1977). Elephants in dry thorn forest spent significantly less time on feeding during the second wet season than the first wet season, even though climatic conditions were ideal in thorn forest during the second wet season with lower ambient temperatures than in the first wet and dry seasons. A possible reason could be the higher availability of grass (the principal food of elephants – discussed further on) during the second wet season than in the other seasons as shown by grass biomass results. With an increase in food abundance, elephants could reduce overall feeding time through higher intake rate as reported elsewhere in African elephants (Guy 1975). Conversely, the lower time spent on feeding in the dry thorn forest, despite less biomass of food in this habitat (than in the dry deciduous forest), could be a result of exposure to higher ambient temperature, coupled with poor shade availability and greater human disturbance. Barnes (1983) states that the time spent on feeding may depend not only on the quality of food, but also upon the cost (e.g., heat stress, disturbance) imposed in its acquisition. Thus, feeding time seems to vary between areas, influenced by factors such as food availability, ambient temperature and human disturbance.

Browse and grass ratio in the diet

Extensive variation in the proportion of grass and browse consumption by elephants in different areas has raised questions as to whether the Asian Elephant is primarily a grazer or browser. Given that Asian elephants inhabit a wide range of habitats from rainforest (a predominantly browse-dominated habitat), to savanna (a predominantly grass dominated habitat), there is bound to be a significant variation in the grass and browse ratio in the elephant diet. Browse dominates the diet of elephants in rainforests of Malaysia (Olivier 1978), northeastern India (Sukumar *et al*. 2003) and in Bihar, central India (Daniel *et al*. 1995), and also in relatively low rainfall degraded areas in the Eastern Ghats of southern India (Sukumar 1990; Rameshkumar 1994; Daniel *et al.* 2006, 2008). On the other hand, grass dominates the diet of elephants in grass-dominated habitats of Sri Lanka (McKay 1973), deciduous forests of Mudumalai Wildlife Sanctuary (Sivaganesan and Johnsingh 1995) and mixed forests (evergreen, semi-evergreen, moist and grasslands) of Idukki Wildlife Sanctuary (Vinod and Cheeran 1997). Similarly, African elephants also showed wide variations in grass and browse consumption (Buss 1961; Field 1971; Beekman and Prins 1989; Kalemera 1989; Viljoen 1989; White *et al.* 1993) according to the habitats they occupy. In this study in NRB, the diet of elephants was found dominated by grass (84.6%), consistent with the observations of Sivaganesan and Johnsingh (1995) for the same area.

Seasonal variations in grazing and browsing by elephants have been related to changes in the chemical composition of food plants (Field 1971; Olivier 1978; Sukumar 1989; Sivaganesan and Johnsingh 1995). Increased browsing during the dry season and grazing during the wet seasons have been related to higher level of crude protein. Since an elephant's daily requirement is 0.3 gm of digestible protein/kg of body weight (McCullagh 1969), a marginal increase in browse consumption would be sufficient to meet this requirement. Excessive protein intake is also undesirable, as nitrogen excretion requires more water, which may be in short supply (Sukumar 1990). Grass contains more carbohydrates (53%) than browse (49%) (Field 1971), and is also more accessible to all the age classes of elephants. Therefore, elephants need not selectively feed on protein-rich browse during the dry season, but a marginal increase in browsing would perhaps be sufficient to compensate for the lower intake of protein from the consumption of low-protein grass during the dry season. This means that when browse and grass are equally available, elephants could predominantly feed on grass with a marginal increase in browse during the dry season to meet the optimum requirements as recorded in dry deciduous forest in this study.

In this study, an almost equal consumption of browse (47%) and grass (53%) by elephants in dry thorn forest during the dry season coincided with the significantly lower grass biomass. For example, from the second wet season to the dry season, the grass biomass dropped from 524 gm/m² to 157 gm/m². Elephants were seen scraping the short grass with their forefoot toenails in this season as grass height was too short (<10 cm) to be grasped by the trunk. Very low consumption of grass by elephants despite high crude protein during the first wet season in 'short grass browse dominated habitat' of Sathyamangalam Forest Division was also attributed to poor grass growth (Sukumar 1989). Therefore, the increase in browse consumption by elephants in dry thorn forest during the dry season could not be taken only as browse preference due to high protein content, but as an alternative to inadequate grass resources. In the dry deciduous forest, the browsing rate doubled during the dry season but its percentage was still much less than that of grass, supporting the earlier hypothesis. Similarly, the reason for the consumption of more diverse food plants during the dry season than in the wet season, and likewise, in the dry thorn than in the dry deciduous forests could be due to lower availability of grass. The larger number of food species consumption by elephants reported from the high rainfall browse dominated habitats of Asia (Olivier 1978; Roy *et al*. 2006; Himmelsbach *et al*. 2006; Chen *et al*. 2006; Campos-Arceiz *et al*. 2008) and Africa (White *et al*. 1993) further suggests the above reasoning that elephants in the absence of sufficient grass availability would go for more diverse food species. This could be the effect of secondary compounds from browse plants as reported (Clauss *et al*. 2003).

Although studies on stable carbon isotope ratios in the bone collagen of Asian elephants state that browse is more important than grass for elephants (Sukumar *et al*. 1987; Sukumar and Ramesh 1992, 1995), browse was not preferred by elephants over grass in the study area. Cerling *et al*. (1999), through isotopic analysis from modern and fossil proboscideans, showed that extinct elephants (those that survived from Pliocene or Miocene up to almost 1 million years ago) were predominantly grazers, and the modern elephants are predominantly browsers, but with grazing dominating the diet of elephants in some regions in Africa and Asia. This study (Cerling *et al*. 1999) for the modern Asian species used the findings from Sukumar and Ramesh (1992, 1995). Although the bone samples for the analysis by Sukumar and Ramesh (1992, 1995) were collected from the dead elephants in the Nilgiri-Eastern Ghats region, details such as where these elephants predominantly ranged and what proportion of the samples came from the elephants that ranged in the grass or browse dominated habitats are unknown. A more detailed stable carbon isotope study with sufficient samples from individuals with known ranging history would shed better light on these aspects of elephant ecology. However, Olivier (1978) argued that the trend in body size and dental features suggest that elephants are highly adapted to grass feeding and thus can cope up with an abrasive, nutritionally poor diet of high fiber and low protein. Because of seasonal variations in grass availability, he believed that they must be able to switch over alternatively to browsing. Such a trend indicates that elephants may be basically grazers, but their ability to survive in rain forests and deserts indicate that they are highly adapted, being also able to exploit browse in the absence or insufficient grass supply. Overall, our findings support Olivier (1978) and show that grass forms the principal diet of elephants in this part of Nilgiri Biosphere Reserve.

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Appendix 1: Food plants (%) in diet of elephants in different habitats in Nilgiri Biosphere Reserve

S. No.	Plant species	DDF (*n* = 7003)	MDF (*n* = 369)	TF (*n* = 3814)	Overall (*n* = 11186)
	Browse species				
1	*Acacia chundra*			0.55	0.18
2	*Acacia ferruginea*			0.26	0.08
3	*Acacia intsia*	0.02	0.27	15.8	5.44
4	*Acacia leucophloea*			0.57	0.19
5	*Acacia suma*			0.05	0.01
6	*Achyranthes aspera*			0.15	0.05
7	*Aerva lanata*			0.02	0.001
8	*Albizia amara*			1.31	0.44
9	*Albizia lebbeck*		0.27		0.001
10	Bamboo spp.	4.44	32.2	1.75	4.44
11	*Bauhinia racemosa*	0.04		0.6	0.23
12	*Boerhavia diffusa*			0.02	0.001
13	*Capparis sepiaria*			0.02	0.001
14	*Catunaregam torulosa*			0.05	0.01
15	*Commiphora caudata*	0.02		0.02	0.02
16	*Curcuma* spp.		14.3		0.47
17	*Cynotis* sp.			0.05	0.01
18	*Dalbergia latifolia*			0.02	0.001
19	*Dalbergia sissoides*			0.02	0.001
20	*Desmodium triquetrum*	0.01			0.001
21	*Dichrostachys cinerea*			0.07	0.02
22	*Dioscorea* sp.		2.16		0.07
23	*Diospyros montana*			0.05	0.01
24	*Eriolaena quinquelocularis*	0.19		0.26	0.12
25	*Ficus benghalensis*			0.49	0.08
26	*Ficus* sp.	0.1		0.05	0.17
27	*Ficus virens*			0.02	0.01
28	*Furcraea foetida*			0.07	0.02
29	*Givotia rottleriformis*	0.05		0.05	0.08
30	*Gmelina arborea*	0.01			0.001
31	*Grewia glabra*			0.47	0.001
32	*Grewia hirsuta*	0.04		0.05	0.18
33	*Grewia orbiculata*			0.13	0.13
34	*Grewia tiliaefolia*	0.14	0.81		0.13
35	*Hardwickia binata*		1.62		0.05
36	*Helicteres isora*	0.01	9.75		0.33
37	*Ipomoea* sp.		1.08	0.68	0.26
38	*Kydia calycina*	2.87	0.54		1.81
39	*Lagerstroemia lanceolata*	0.02	0.27		0.02
40	*Laggera alata*		0.27		0.001

Appendix 1: Food plants (%) in diet of elephants in different habitats in Nilgiri Biosphere Reserve (*contd.*)

S. No.	Plant species	DDF (*n* = 7003)	MDF (*n* = 369)	TF (*n* = 3814)	Overall (*n* = 11206)
41	*Malvastrum coromandelianum*			0.02	0.001
42	*Mangifera indica*	0.02			0.01
43	*Mimosa pudica*		0.54		0.01
44	*Mimusops* sp.			0.15	0.05
45	*Olea dioica*		0.27		0.001
46	*Phyllanthus emblica*	0.08		0.02	0.06
47	*Pleiospermium alatum*			0.02	0.001
48	*Pongamia glabra*	0.02			0.01
49	*Pterocarpus marsupium*			0.02	0.001
50	*Randia dumetorum*	0.14		0.18	0.15
51	*Solanum* sp.	0.29			0.18
52	*Strychnos potatorum*			0.39	0.01
53	*Syzygium cuminii*	0.02			0.01
54	*Tamarindus indica*			0.78	0.26
55	*Tectona grandis*	0.65	1.89	0.49	0.64
56	*Terminalia tomentosa*	0.01			0.001
57	*Zizyphus mauritiana*			0.78	0.26
58	*Zizyphus oenoplia*			0.02	0.001
59	*Zizyphus xylopyrus*	0.05		0.55	0.22
	Unidentified browse spp.	0.25	1.35	0.55	0.39
	Grass species				
60	*Apluda mutica*	0.31	0.27	2.14	0.93
61	*Aristida adscensionis*			6.92	2.36
62	*Bothriochloa* sp.			21.3	7.27
63	*Chrysopogon* sp.			1.23	0.42
64	*Cymbopogon flexuosus*	3.35	5.14		2.27
65	*Cymbopogon* sp.			0.15	0.05
66	*Cyperus* sp.			0.05	0.01
67	*Cyrtococcum patens*		11.6		0.38
68	*Digitaria* sp.	1.55		0.68	1.2
69	*Eragrostiella bifaria*			0.1	0.03
70	*Eragrostis tenuifolia*	0.89			0.56
71	*Heteropogon contortus*	1.32		36.9	13.4
72	*Imperata cylindrica*		2.71		0.08
73	*Oplismenus compositus*	0.04		0.26	0.11
74	*Oryza granulata*	0.14			0.08
75	*Panicum* sp.			0.07	0.02
76	*Pennisetum hokanackeri*	0.01			0.001
77	*Pennisetum* sp.			0.1	0.03
78	*Phoenix pusilla*	0.01			0.001
79	*Setaria intermedia*	0.07	1.89		0.1
80	*Sporobolus* sp.	0.07		0.31	0.15
81	*Themeda cymbaria*	62.8	6.5		39.5
82	*Themeda triandra*	17.1	0.54	0.68	10.9
83	*Vetiveria lawsonii*			0.05	0.01
	Unidentified grass spp.	2.72	3.52	1.04	2.18

■ ■ ■