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continued on the back inside cover

Cover: Tamil Lacewing *Cethosia nietneri* with colour pencils and watercolours for the background; detailing with fine liners by Elakshi Mahika Molur.

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COMMUNICATION

Diet and nutrient balance of wild Asian Elephants *Elephas maximus* in Nepal

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Abstract: We estimated the nutritional content of major wild (n = 22) and agricultural crop plants (n = 3) consumed by Asian Elephants *Elephas maximus* in Nepal during the wet and dry seasons, respectively. We then used nutritional geometry to explore the macronutrient balance of these plant species, as well as the overall diet of elephants in both the dry and wet seasons. Furthermore, we compared the diet of the Nepal elephants with the previously published diet of Indian population of elephants. We found that despite intraspecific and seasonal variation, the overall diet of elephants was relatively stable in protein (P) intake relative to non-protein macronutrients (fat + carbohydrate; non-protein (NP)), and neutral detergent fibre (NDF) between the wet (16% crude protein (CP): 26.7 % NP: 57.3% NDF; and, 10.4% CP: 13.7% NP: 75.7% NDF) in dry season, which suggests protein intake prioritization in support of previous work on captive elephants. Furthermore, the diet of Indian population of elephants (wet season: 16.0%P: 22.5%NP: 61.4%NDF and dry season: 11.1%P: 18.0 %NP: 70.7 %NDF) showed a similar pattern to the Nepal elephants, suggesting active regulation of macronutrient and NDF intake across populations despite differences in food consumed as part of their diets. Importantly, NDF intake in addition to non-protein macronutrients is likely necessary for elephants to stabilize their protein intake balance; thus, it is important to consider a multidimensional nutritional perspective in elephant conservation planning. The study has concluded that in a well-managed seasonal habitat, elephants can regulate their preferred macronutrient and NDF intake from available natural food plants without resorting to agricultural crop depredation.

Keywords: Crop, depredation, Elephantidae, macronutrient balance, Mammalia, NDF, nutritional geometry, right angled mixture triangle.

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Author contributions: RKK—conceptualized the project, Written the ms, data analysis. SC—analysed, reviewed.

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INTRODUCTION

The diet and nutritional demands of wildlife are crucial aspects to consider when formulating conservation and management strategies. Foraging, however, is a complex process, involving the inter play of physiological and behavioural factors with an animal's multidimensional nutritional environment (Raubenheimer et al. 2009; Simpson & Raubenheimer 2012). The Asian Elephant *Elephas maximus* is a species of conservation concern often involved in food-related human-elephant interactions (Desai 1991) through crop depredation (Santiapillai & Jackson 1990; Nyhus & Sumianto 2000). Recently, studies of captive Asian Elephants suggest that they regulate their intake of multiple nutrients, with protein (P) intake more tightly regulated relative to non-protein macronutrients (fat + carbohydrate; NP) and fibre (NDF; (Koirala 2018). This type of nutrient regulation, however, has not been explored in wild elephant populations.

In this paper, we estimated the proximate nutritional content of plants consumed by migratory and resident elephants during the wet and dry seasons in the far eastern region and central region of Chitwan National Park (CNP) and Parsa National Park (PNP) of Nepal. The consumed plants were identified through feeding sign survey and micro-histological analysis of dung, and also based on a previous study (Koirala et al. 2016). We used nutritional geometry (i.e., right-angled mixture triangle (RMT); Raubenheimer 2011) to explore the proportions of macronutrients and fibre in the seasonal food plants and diets of elephants, including both natural and agriculture crop plants, to evaluate evidence for nutrient intake regulation similar to previous studies. Furthermore, we used published literature on the diet of wild elephants in India (Das et al. 2014) to evaluate if they showed similar dietary patterns to the Nepal elephants, which might suggest active regulation of macronutrient and NDF intake across populations despite consuming different diets.

MATERIALS AND METHODS

The CNP (952.632 km^2) and PNP (637.37 km^2) are two of Nepal's protected areas, and are situated in the south-central region of the country (Koirala et al. 2016). On the other hand, Nepal gets migratory elephants from northern Bengal of India (Koirala et al. 2015) in the forests of the eastern district of Jhapa. We collected food plant species of elephants' diets for nutritional analysis based on our previous study on food preference, which identified 57 plant species (12 grasses, five shrubs, two climbers, one herb, and 37 tree species) consumed by elephants (Koirala et al. 2016). However, only the most preferred species (n = 22) and three agriculture crop plants were collected for proximate nutrient analysis (Table 1). Plant and crop samples were collected during the late rainy ("wet") season (August/September 2013) and summer "dry" season (March/April 2014) from elephant habitat, where habitat was determined by the presence of elephant foraging signs and direct observation. The wet season collection period coincided with the beginning of crop raiding time in late monsoon season with a peak in pre-winter, while April/May was the beginning of crop raiding in the dry season. After collection, samples were air-dried and kept in paper bags for transport to the laboratory. The proximate nutritional estimates were analysed in the laboratory of Nepal Agricultural Research Centre and Nepal Environmental and Scientific Services, Kathmandu, Nepal, following standard methods (AOAC 2012) for crude protein (Kjeldahl; CP), ether extract for lipid (Soxhlet extraction; EE), fiber (digestion method; NDF), and ash. Non-structural carbohydrate (NSC) was calculated by difference. To correct for indigestible waxes and lipids in plants consumed, we subtracted 1% from EE to estimate crude fat (CF) following Rothman et al. (2012). Proportional data were transformed using a "logit" transformation to approximate normality before running the stat test.

We used the Right angled mixture triangle (RMT) to investigate the proportion of macronutrients and NDF in the food plants and seasonal diet of elephants. Following Koirala et al. (2016), we plotted NP and NDF on the x- and y-axis of the RMT, respectively, while CP was represented on the implicit axis (z) which varies inversely with distance from the origin (Raubenheimer 2011). Macronutrients and NDF were expressed as a percentage of the sum of each (i.e., non-structural carbohydrate + neutral detergent fibre + lipid + protein) on a dry matter basis. NDF was included in the analysis, because elephants derive energy from fibre through hindgut fermentation (Anguita et al. 2006). We estimated the seasonal mixture space provided by the plant foods by forming minimum convex polygons around food points for each season.

We determined the overall macronutrient balance of seasonal diets by weighing the nutritional estimates for each plant species by the relative utilisation percentage determined as described by Koirala et al. (2016), which is the product of the frequency of occurrence and rank

score of each plant in the micro-histological analysis (Holechek & Gross 1982) and feeding-sign survey respectively (Koirala et al. 2016). We also used RMT analysis to compare the balance of CP, NP, and NDF (Koirala 2018) in the diet of elephants in our study area with existing data on the available diets of wild elephants in India (Das et al. 2014).

Independent sample t- test was performed to see the seasonal difference in the nutrient dry matter/ balance in the plants. Pearson correlation was performed to see the relationship between utilisation and availability of protein and NDF in the diet. All tests were done using Excel and IBM SPSS statistical package version 22.

RESULTS

The nutrient contents of the leaves of plants consumed by elephants didn't vary with species and season (Table 1). The highest estimates for CP (*Lagerstroemia parviflora*; 25.97%), NSC (*Litsea monopetala*; 31.85%), and NDF (*Saccharum bengalensis*; 88.62%) were found in the wet season. The average percent dry matter CP content of food plants was 12% in the wet season and 11 % in the dry season (t_{37} = 0.372, p = 0.712). The average NDF content was 55.9% (wet season) and 66% (dry season) (t_{37} = -1.556, p = 0.128), and average EE content was 1.7 % and 1.2% (t_{37} = 1.427, p = 0.162) in wet and dry seasons, respectively.

The proportion of P: NP: NDF in plants was variable between seasons (Figure 1). For example, the protein balance of most frequently consumed plants *Spatholobus parviflorus* and *Mallotus philippensis* was higher during the wet season. In both seasons, however, most of the dominant plant species consumed were similar, for example, *Spatholobus parviflorus*, *Mallotus philippensis* (Koirala et al. 2016). In the case of agricultural crops, in the wet season paddy was 12.34 % P: 18.31% NP: 69.35% NDF, and in the dry season 9.55% P: 15.42% NP: 75.03% NDF (Figure 1).

The estimated seasonal diets of elephants was (Figure 2): 16 % CP: 26.7 % NP: 57.3% NDF in wet season; and, 10.4% CP: 13.7% NP: 75.7 NDF in dry season.

DISCUSSION

The utilisation pattern of food plants showed that browse forms the major diet of elephants in the dry season in both PWR and CNP. While the wet season diet was slightly dominated by grass in PWR and browse in CNP (Koirala et al. 2016). The nutritional content (Table 1) of plant species was stable between seasons.

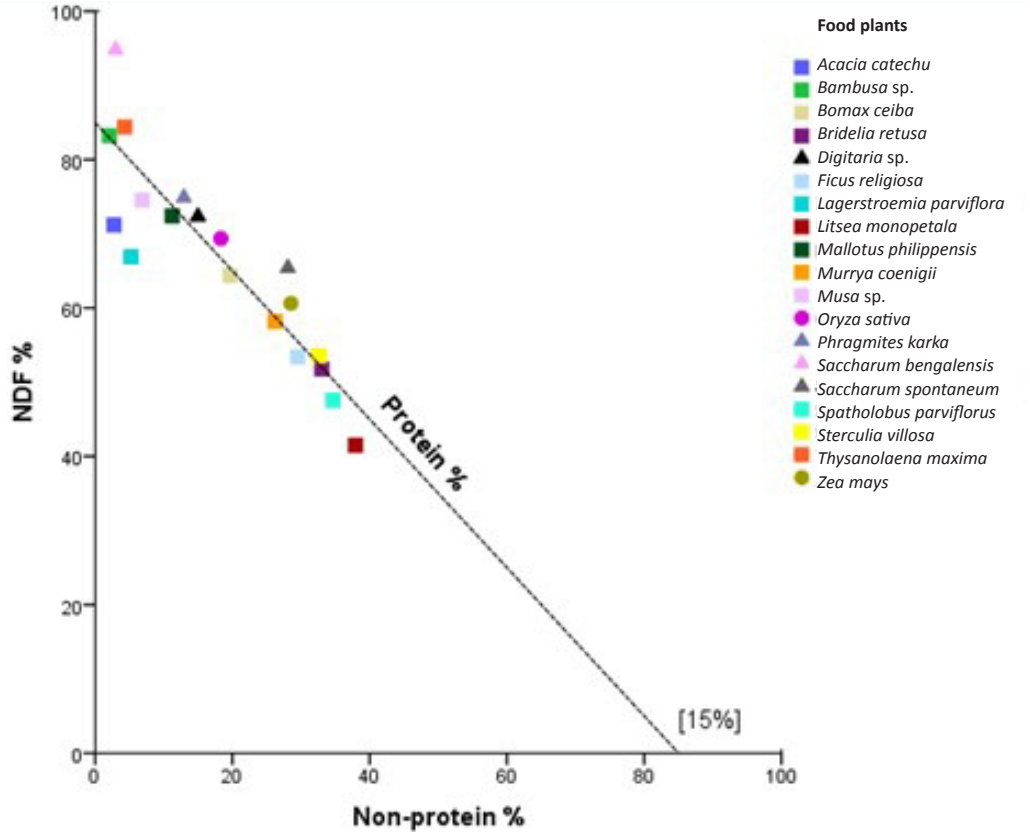
The combined dry season diet was greater in NDF than the wet season diet. The combined wet season diet was greater in protein and non-protein than the dry season diet. However, both summer and winter diets were somewhat similar in nutrient balance. NDF balance was the highest difference of 12% (±2.09 SE) while non-protein showed a difference of 11.6% (±2.04 SE) and protein at the least difference of 6% (±1.05 SE).

During the wet season, the protein content of food plants like *Acacia catechu, Litsea monopetala,* and *Lagerstroemia parviflora* was high to compensate for the deficiency of protein from *Saccharum bengalensis, Saccharum spontaneum*, and *Phragmites karka*, suggesting that these foods were complementary to each other (Figure 1A).

Similarly, in dry season, the protein balance of diet of highly utilised browse and agricultural crops like paddy and wheat were similar. Although there was less protein in *Spatholobus parviflorus,* a highly preferred plant in the dry season, so elephants may be using plants species like *Phragmatus karka, Acacia catechu, Litsea monopetala*, and *Ficus semicordata* to slightly increase protein content to balance the deficit of protein from *Spatholobus parviflorus, Cymbopogon* sp., *Saccharum spontaneum*, and *Saccharum bengalensis* (Figure 1B).

Moreover, there was no significant relationship between utilisation and availability of protein (r=-0.146, p=0.418 and NDF (r = -0.188, r = 0.293) in the weighed diet. The preference of plants is different irrespective of their presence and frequencies in the diet. The utilisation of these plants varies with season and localities (Koirala et al. 2016*)*. Subsequently, the combined macronutrient balance of dry and wet season food plants was almost similar. The balance of different macronutrients showed no significant seasonal difference (t_{30} = 1.030, p = 0.311) protein; (t_{30} 0.760, p = 0.453) and non-protein t_{30}=-2.039, p= 0.050 NDF. This gives an indication that although elephants utilised many types of food plants with different nutritional content, the animals compose their diet to achieve a preferred macronutrient intake target (Raubenheimer 2011; Coogan 2014).

At the time of this study in both of these study periods, crops act as a complementary food source to replace low protein grasses. The lower protein in grasses like *Cymbopogon* sp., *Saccharum spontaneum*, *S. bengalensis,* and *Digitaria* spp. in in the dry season and higher accessibility and protein content in crops may lead to crop raiding. This is consistent with the assertion that the nutritional composition of crops could



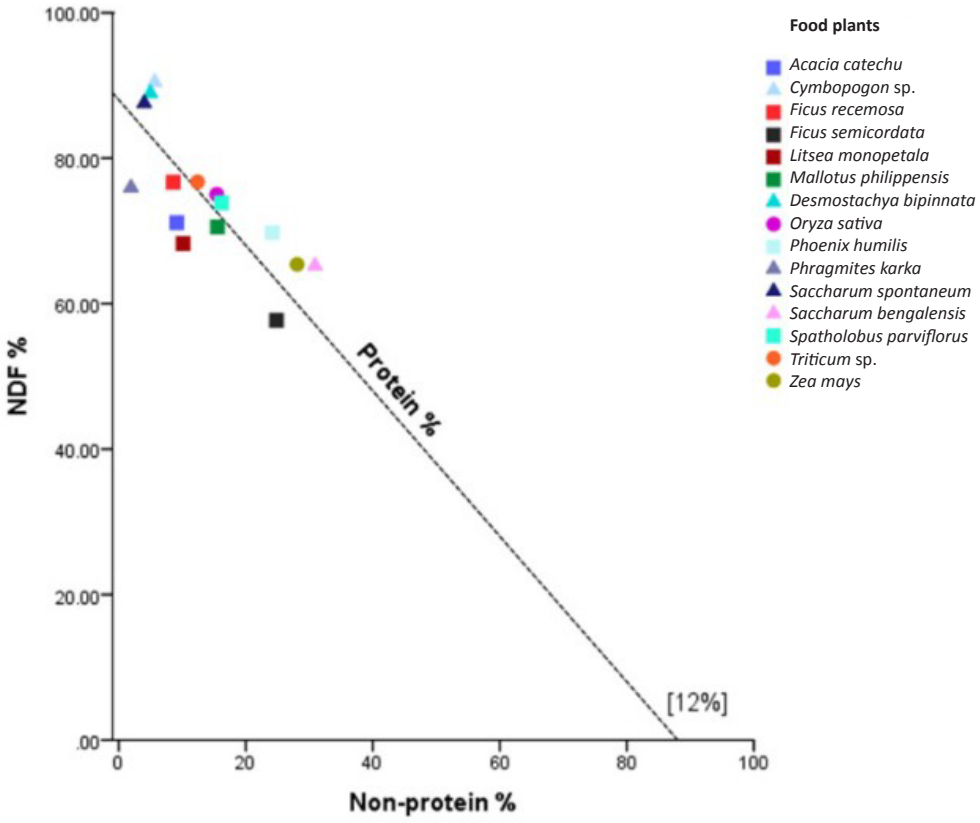


Figure 1. RMT showing the balance of crude protein, non–protein macronutrients (NSC+ crude fat), and NDF in plants consumed by elephants in both the seasons: A—wet season | B—dry season. Browse species are shown as squares, grasses as triangles, and agriculture crops as circles.

Table 1. Nutritional composition (percent dry matter) of major plants consumed by Asian elephants, including crude protein (CP), ether extract (EE), ash, neutral detergent fibre (NDF), acid detergent lignin (ADL), and non-structural carbohydrates (NSC).

Plant species	CP	(EE)	Ash	NDF	ADF	ADL	NSC
Wet season							
Lagerstroemia parviflora	25.97	1.20	5.82	62.32	52.14	24.32	4.69
Ficus religiosa	13.99	1.40	16.90	43.86	35.79	12.98	23.85
Thysanolaena maxima	10.20	0.87	8.67	76.35	57.30	12.90	3.91
Musa sp.	15.89	6.25	12.62	63.65	59.89	11.58	1.59
Saccharum bengalensis	2.07	0.80	5.73	88.62	62.22	32.58	2.77
Saccharum spontaneum	5.76	0.80	11.00	57.67	49.15	39.30	24.76
Sterculia villosa	12.80	1.00	6.40	49.60	46.50	19.50	31.20
Bomax ceiba	14.04	0.86	11.10	56.57	41.36	19.09	18.29
Acacia catechu	24.15	1.30	6.35	65.94	43.65	12.40	2.26
Digitaria ciliaris	10.80	0.86	14.04	61.55	43.13	9.07	12.75
Paspalum scrobiculatum L	5.00	3.00	7.18	7.77	2.50	2.05	4.71
Murrya coenigii	13.70	0.90	6.60	54.32	41.22	14.25	24.48
Bridelia retusa	13.75	1.20	8.36	46.95	41.04	16.74	29.74
Mallotus philippensis	14.35	2.30	11.25	63.54	53.98	25.62	8.56
Spatholobus parviflorus	14.69	2.85	11.70	41.99	35.02	11.18	28.77
Phragmites karka	6.60	0.60	10.36	80.99	64.97	40.88	1.45
Saccharum spontaneum	6.10	0.65	6.32	82.45	66.02	13.20	4.48
Bambusa sp.	12.50	2.00	13.80	70.91	51.85	17.52	0.79
Litsea manopetala	17.44	3.22	10.22	37.27	28.22	13.12	31.85
Saccharum bengalensis	3.56	1.87	7.31	60.84	1.31	6.62	27.42
Desmostachya bipinnata	12.17	1.78	9.59	55.95	43.86	17.75	14.42
Paddy	11.25	0.60	8.20	63.25	52.35	24.30	16.70
Maize	9.69	0.90	10.00	54.00	42.00	34.00	25.41
Dry season							
Spatholobus parviflorus (bark)	6.50	0.34	15.03	54.73	48.19	21.43	23.40
Saccharum spontaneum	7.56	1.25	9.92	77.97	54.13	11.95	3.30
Saccharum bengalensis	7.94	1.0	8.88	77.46	50.47	7.1	4.72
Acacia catechu	18.50	1.40	5.30	66.65	59.89	11.58	8.15
Cymbopogon sp.	3.55	0.50	8.36	82.45	81.48	12.92	5.14
Spatholobus parviflorus	8.70	0.34	12.03	64.73	47.11	21.46	14.20
Mallotus philippensis	12.35	3.78	10.40	62.50	51.78	22.72	10.97
Ficus semicordata	15.56	0.73	10.99	51.35	47.16	19.90	21.37
Ficus racemosa	12.61	1.20	13.53	65.54	49.97	29.08	7.12
Phoenix humilis	6.00	1.50	0.96	64.23	53.12	19.20	27.31
Phragmites karka	20.56	1.31	6.98	70.68	34.79	7.48	0.47
Litsea monopetala	20	2.56	6.56	63.10	49.34	27.85	8.82
Paddy	8.53	0.7	10	67	*	*	13.77
Maize	5.76	0.80	11.00	57.67	49.15	39.30	24.76
Wheat	9.75	0.6	9.5	69	*	*	11.15
Unidentified	10.66	1.26	9.39	65.73	51.89	17.81	12.95

* Indicates analysis was not done.

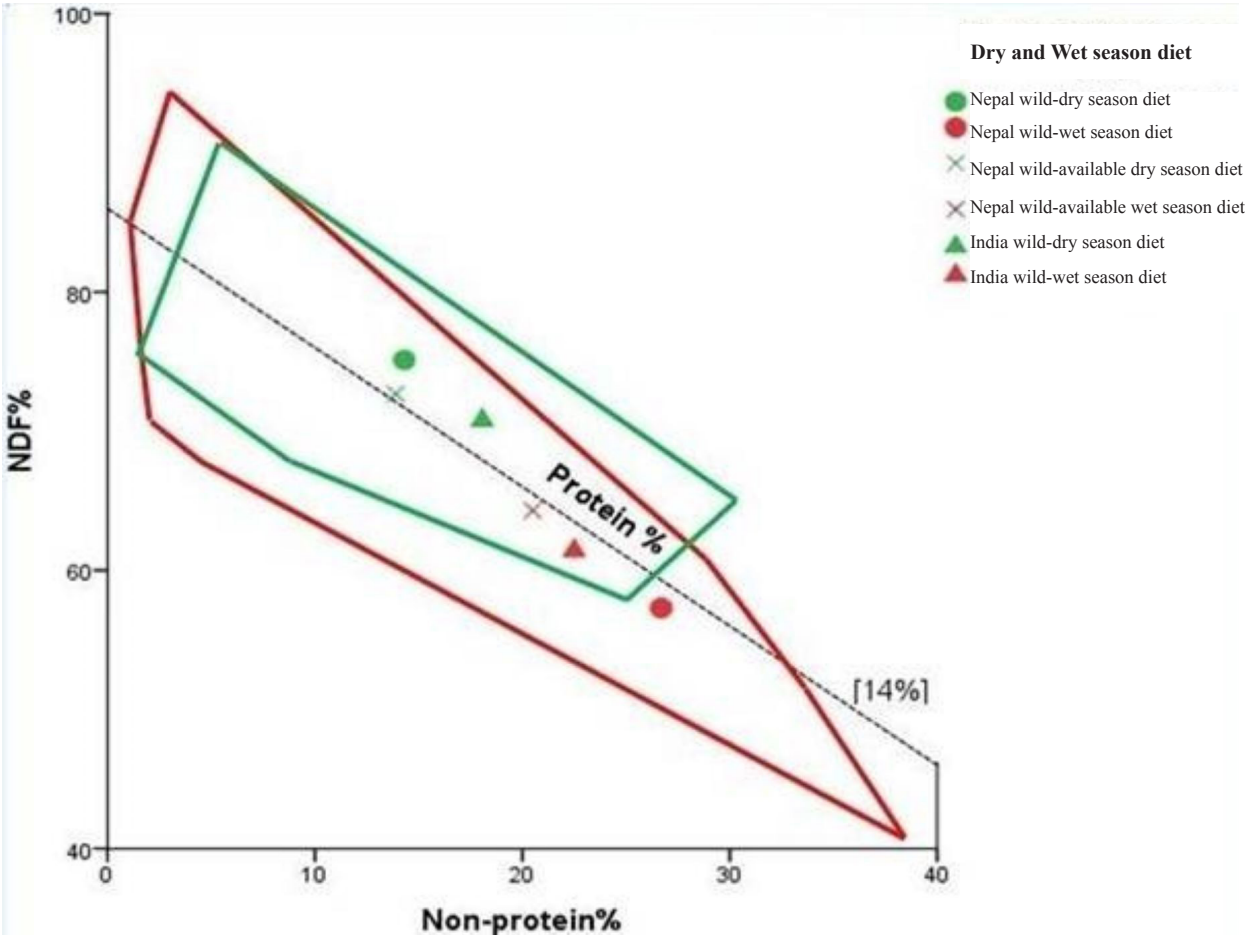


Figure 2. An enlarged view estimated diet composition of combined food in Right-angled mixture triangles (RMT; Raubenheimer 2011). Solid green circle (Dry season), and solid red circle, (wet season) diet weighed by utilisation percentage (Koirala et al. 2016). The crops and the leaves of all plants combined weighed by the seasonal availability in the environment (solid cross symbols), wet season (Red symbol), and dry season (Green symbol). The red and green solid triangles represent the wet and dry season diet of Asian Elephants (India population) respectively. Crude protein is represented on the implicit axis which varies inversely with distance from the origin. For reference, the dashed grey line indicates 14% protein content. The estimated seasonal nutrient space provided by food plants is shown by green polygon dry season and red polygon wet season around the food points.

be related to the crop raiding behaviour of elephants (Sukumar & Gadgil 1988; Sukumar 1989, 1991, 2006).

Our previous study has found that there was a negative relationship between utilisation and availability. As such there could be a reasonable selection of foods. The present study attempted to validate our hypothesis that the elephants are selectively feeding with a null hypothesis of feeding proportional to availability through the pattern of use seen in some of the highly preferred food plants like *Mallotus philippensis*, *Bambusa* sp., *Bombax ceiba*, *Spatholobus perviflorus*, and *Thysanolaena maxima*. The difference shown in the availability and utilisation in dry and wet season diet showed that there is selective mode of feeding. The availability of plant foods and their utilisation determines the preference. The preference based on availability and usage may be primary information in relation to conservation of probable food plants in the habitat. However for the long term population sustainability of elephants, utilisation information based on nutritional content of plants is vital for the conservation and management of habitat for elephants. Further, the geometric analysis of food plants has revealed that besides the relationship between utilisation and macro nutrient content, the balance of nutrients of different diets plays a vital role in food selection. The ratio focused selection was located by this study as the diagonal clustering of expected dry and wet seasonal diet points, together with similar seasonal diet points of Indian wild elephants. The significant relationship of utilisation and macronutrient balance of highly preferred browse, grasses, and crops at least in these periods of the year

have revealed that crop raiding can be seen as part of protein makeup of elephants due to lower protein in grasses and some browse. In nutrient space, crops have been found to be occupying a place in between browse and grass. Thus, the elephants move away from their natural habitat to seek an alternative source of fodder with a high nutritive value such as crops.

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