FEEDING ECOLOGY OF THE NORTHERN PLAINS SACRED LANGUR *Semnopithecus entellus* (DUFRESNE) IN JESSORE, BANGLADESH: DIETARY COMPOSITION, SEASONAL AND AGE-SEX DIFFERENCES

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ABSTRACT

Feeding behaviour of the Northern Plains Sacred Langur *Semnopithecus entellus* (Dufresne) was studied from September 2012 to August 2013 in Jessore, Bangladesh. The study was based on direct observation from dawn to dusk and data was collected using focal animal sampling. The results showed that while they were largely folivorous, fruits and other items where actively sought out when available. We identified 54 plant species in the diet (33 trees, 8 shrubs and 13 herbs). Of the time spent feeding, the greatest amount was spent on leaves (57.5%) followed by fruits (20.7%), buds (8.5%), flowers (3.9%) and bark (0.5%). Langurs also consumed provisioned food (8.7%), and non-plant food items including soil, water and fungi (1%). The number of different plant species consumed varied seasonally, being higher in winter (49 spp.) and summer (48 spp.) than in the rainy season (37 spp.). Time spent feeding on natural foods significantly differed between adult males and adult females while no difference between sub-adult males and females was detected. The amount of time allocated to feeding was the highest in the early morning and the lowest at mid-day, regardless of season. Time spent feeding did not significantly fluctuate seasonally.

Keywords: age-class and sex, feeding behaviour, folivorous, Northern Plains Sacred Langur

INTRODUCTION

Primates select what they eat from what is available in their environment at any given time, in order to maximize their daily intake of required energy and nutrients to thrive and survive (e.g. Freeland & Janzen, 1974; Leighton, 1993; Barton & Whiten, 1994; Stevenson, 2003; Jildmann et al., 2008; Jaman et al., 2010; Tsuji et al., 2013). The study of food and feeding behaviour is therefore vital for understanding the basic biology of a species, its ecological adaptation and vulnerability to extinction. It is important to understand whether primates living in marginal habitats can find appropriate resources to survive. Looking at fluctuations in food availability may not always be directly measurable, but by comparing the number of food items ingested across seasons and between groups helps to understand to what extent they are successful. Such information provides baseline data for the management and conservation of a species (Minhas et al., 2010).

Primates are sometimes categorized according to their main diet in spite of seasonal variation in their annual diet (Hill, 1997). In general, the proportion of different food items (leaves, fruit, buds, insects etc.)

in the diet has been found to correlate well with the number of different foods available (Symington, 1987; Strier, 1991; Peres, 1994; Dela, 2007; Nijman, 2012; Tsuji et al., 2013). Macaques and langurs that live in seasonal habitats tend to either concentrate on specific food items available year round or maintain a diet that varies according to season, when different food items are available (e.g. Hill, 1997; Tsuji et al., 2013). It is rare to see extreme dietary specialization among such species, and most utilize a wide range of food resources as they become available (Hill, 1997). For example, largely folivorous Humboldt's Woolly Monkey *Lagothrix lagotricha* (Humboldt) living in seasonal environments feed on fruit when available (Di Fiore, 2004). Similarly, the diet of Purple-faced Langur *Semnopithecus vetulus* (Erxleben) in Sri Lanka varies due to seasonal food availability, and they feed on a wider range of fruits and vegetable crops than previously thought, when available (Dela, 2007; Nijman, 2012).

Food consumption also differs according to age-sex class and depends on such factors as body size, energetic or nutritional requirements, and physical strength. These differences in feeding behaviour have been studied in many wild primate species including Northern Pig-tailed Macaque *Macaca leonina* (Blyth), Sunda Pig-tailed Macaque *Macaca nemestrina* (Linnaeus), and Japanese Macaque *Macaca fuscata* (Blyth) where variation in time and substrate use during feeding has also been found (e.g. Feeroz, 2000; Agetsuma, 2001; Kamilar & Pokempner, 2008; Jaman & Huffman, 2011).

In natural settings, primates tend to have greater access to non-monopolizable food resources and exhibit feeding strategies based more on individual food requirements. In contrast, studies on provisioned Japanese macaques have found that high ranking adults acquire most of their energy from easily accessible provisioned food, whereas low ranking immatures acquire more of their energy from natural plants (Soumah & Yokota, 1991; Jaman & Huffman, 2011), spending more time feeding on plant foods than adults do (Hanya, 2003; Jaman & Huffman, 2011).

The Northern Plains Sacred Langur *Semnopithecus entellus* (Dufresne) is the most widely distributed of the six species currently recognized in the Hanuman Langur group, i.e. Chamba Sacred Langur *S. ajax* (Pocock), *S. entellus*, Terai Sacred Langur *S. hector* (Pocock), Malabar Sacred Langur *S. hypoleucos* Blyth, Tufted Sacred Langur *S. priam* Blyth, Central Himalayan Sacred Langur *S. schistaeus* Hodgson, in the Indian subcontinent (Roos et al., 2014). *S. entellus* inhabits an area spanning over 1900 km across India from east to west between major rivers, the Tapti River (Gujarat State), the Narmada and Krishna Rivers, all the way north to the Himalayan foothills (Mittermeier et al., 2013; Roos et al., 2014; Ashalakshimi et al., 2015).

Only a few studies have been conducted on *S. entellus* in Bangladesh. This population is reported to have possibly originated from a single pair introduced by Hindu pilgrims on the bank of the River Jalangi in early times and now is concentrated in only a few districts, particularly in Jessore, in extremely human dominated landscapes (Brandon-Jones, 2004; Mitra & Molur, 2008). Ahsan & Khan (2006) reported that *S. entellus* in Keshabpur consumed food from over 60 natural and cultivated plants, of which 48 species were identified. Data collected on their feeding ecology included plant parts consumed, but no indication was made of seasonal or age-sex differences. Another study by Khatun et al. (2013) looked at human-langur conflicts in Keshabpur, focusing mainly on the local people's perceptions of crop damage caused by the species. They found 27 different crop species cultivated in these villages, among which the langurs mostly damaged fruits, during the fruiting and harvesting season.

As witnessed in many part of the developing world, the rapid increase in human settlements and expansion of agricultural lands in Bangladesh is contributing to a steady decrease in biodiversity, putting the survival of many species at risk (Mukul, 2007; Khatun et. al., 2013). Understanding a species' feeding ecology is an essential component of assessing its ability to survive and is important for management and conservation plans, whether in undisturbed habitats or in highly human-dominated landscapes (e.g. Minhas et al., 2010). A study about the feeding behaviour of *S. entellus* in Bangladesh is necessary for the creation of a more informed local conservation strategy in the country.

The aim of this study was to investigate and provide information on the seasonal variation in plant food choices and species used by *S. entellus.* This baseline information will provide needed insights for future conservation efforts of the species in Bangladesh.

METHODS

Study sites

This study was conducted in Keshabpur (22°54′29.71″N, 89°13′9.18″E) and Manirampur (23°1′0″N, 89°14′0″E) sub-districts of Jessore district

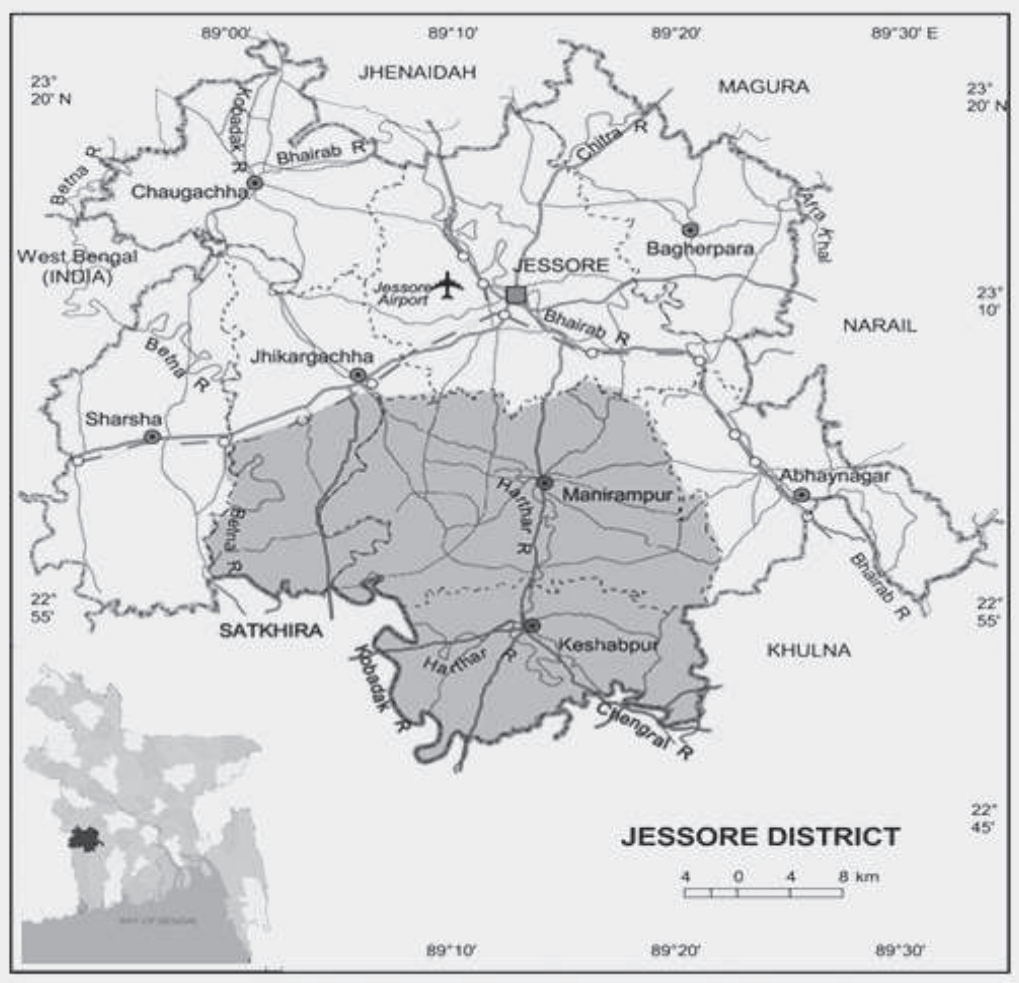

Fig. 1. Jessore District.

located in southwest Bangladesh (Fig. 1). Together, both sub-districts cover an area of 703 km², with a human population density of 953 individuals/km² (Bangladesh Bureau of Statistics, 2011). Annual temperatures in the two areas range between 11.2°C (minimum) around January, and 37.1°C (maximum) around June. Annual rainfall from September 2012 to August 2013 was 1,537 mm.

The topography of Keshabpur and Manirampur is primarily open plains. At the time this study was conducted, there was no existing conservation legislation for the protection of biodiversity in either sub-district. Vegetation in the area is dominated by economically important human crops and plantations. There are fragmented patches of natural vegetation like herbs and shrubs, found mostly in fallow lands.

Study subjects

There were eight groups of *S. entellus* living in Keshabpur and Manirampur when this study was conducted. Each group had a definable home range. Group size varied from 11 to 29 individuals (Table 1). All individuals in each group were made recognizable by marking them with a non-toxic dye; this was done by spraying with a syringe, from a concealed position. A combination of two colours was used consistently according to age-sex class, based on group consensus adopted during our preliminary field observations prior to this study. These colour markings were redone after an individual was estimated to have moved into the next age category.

Age-sex categories used in this study were determined according to age estimates as follows: adult male (>5 years old), adult female (>2.9 years old), sub-adult male (2-5 years old), sub-adult female (2-2.9 years old), juvenile (9 months-2 years old) and infant (<8 months old) (Gron, 2008). Adults are capable of

Table 1. Age-sex composition of Northern Plains Sacred Langur groups in the two study sites.

Groups	Age-sex class						
	AdM	AdF	SaM	SaF	Juv	Inf	Total
Keshabpur							
K-G 1	2	4	3	6	3	2	20
K-G 2	3	5	4	7	4	3	26
K-G 3	2	4	5	7	2	2	22
K-G 4	4	6	4	8	3	4	29
K-G 5	1	3	3	6	3	-	16
K-G 6	7	-	4	-	-	-	11
Manirampur							
M-G 1	4	5	3	6	2	3	23
M-G 2	2	4	4	6	0	2	18

AdM=Adult male, AdF=Adult female, SaM= Sub-adult male, SaF= Sub-adult female, Juv=Juvenile, and Inf=Infant

reproduction (i.e. hormone production, descended testicles in males, sexual activity, menstrual signs in females and mating behaviour), whereas sub-adults are still not able to reproduce, although they might already display mating behaviours during the breeding period (Lynch et al., 2002).

Observations and sampling protocol

We collected data from September 2012 to August 2013 using 10-minute continuous focal animal sampling (Altmann, 1974; Martin & Bateson, 2007). Data used for our analyses were collected, with a more-or-less equal amount of data from each age-sex class (for adult males 429 focal observations, adult females 478, sub-adult males 436 and sub-adult females 475), of every group at the two study sites by two well-trained field researchers over three consecutive days each month. Each day we collected about 50 focal samples, totaling 1,818 focal samples in 303 hours for the entire study. The study period was divided into three seasons: rainy (July-October), winter (November-February) and summer (March-June). In all months across all seasons, we sampled all focal subjects equally across the four time blocks in a day: early morning (06:00-09:00), late morning (09:00-12:00), mid-day (12:00-15:00) and afternoon (15:00-18:00).

We recorded each behaviour displayed, assigning a time and location. When focal subjects fed, the plant species and plant parts ingested were recorded. Unidentified plant species were collected and labelled for later identification in the laboratory. Plant parts ingested were classified as leaf, fruit/seed, bud, flower, bark, nut or bread (provisioned). Provisioned food was provided at four selected sites once a day, year round, by the local staff of the Forest Department as a conservation measure to prevent the langurs from going hungry, thus helping to reduce human-langur conflict related to crop raiding. For this purpose, the study groups were followed and the type and number of food items taken into the mouth were recorded. During focal observations, if the animal ran away or was out of sight within the last minute we noted down the last behaviour observed, otherwise we discarded the focal sample. On the day prior to the commencement of data collection, the trees on which the focal group roosted overnight were noted. This strategy facilitated our starting observations the next day before the group left its sleeping trees in the early morning.

Data analysis

Equal amounts of observation time were collected (around 75 hours in each category) from the sub-adult and adult age-sex classes, which were equally distributed across time periods of the day, months and seasons. All analyses were done using nonparametric statistics. We examined seasonal variation of plant food consumption and the number of plant species utilized as food items. We used the Friedman test to examine seasonal variation of the number of plant species utilized for different plant parts across seasons. We performed a Wilcoxon Signed Ranks test

to find the differences in the number of plant species utilized for each food item between any two seasons. We employed the Chi-square test to examine variation in the number of plant species in different months and different time periods. We present exact *P* values for each analysis in the results and set the level of statistical significance at α=0.05. All data were analyzed using MS-Excel and SPSS (version 17).

RESULTS

Diet and feeding behaviour

The langurs spent 60.2% (N=1,094) of the total observation time feeding. They consumed different plant parts from 54 plant species (from 33 trees, 8 shrubs and 13 herbs; see Table 2). Among them, nine species were cultivated seasonal crops (constituting 10.2% of total diet). Their folivorous diet came mainly from five plant species, according to frequency and time spent feeding (Table 2). Thirty-seven plant species were consumed in the rainy season, 49 in the winter and 48 in the summer. Langurs fed both on the natural foods available in their home ranges and on provisioned foods and cultivated crops.

Of the total time spent feeding on identified plant parts, langurs spent more than half of their feeding time eating leaves (57.5%, n=629), followed by fruits/seeds (20.7%, n=226) (usually unripe, but occasionally ripe) and buds (8.5%, n=94) (Fig. 2). Less time was spent feeding on flowers (3.9%, n=43) and bark (0.5%, n=6). Provisioned food (8.7%, n=96) consisted of nuts, bananas and bread. Occasionally, they also fed on soil, water and fungi in different seasons. We also observed some group members licking the surface of walls, but not during focal observations. They consumed termites (*Zootermosis* spp.) and body lice eggs (*Pediculus* spp.), which were picked off their own body or from other individuals during grooming. We also observed langurs ingesting insect larvae from stacks of logs at a sawmill.

Monthly and seasonal variation of dietary composition

Semnopithecus entellus consumed the greatest number of plant species in March (n=38) and the least in September (n=25). They spent more or less similar amounts of time feeding on leaves throughout the year and there was no significant variation in the number of

Table 2. Plant food species and the average time spent feeding by food items.

No.	Family	Scientific name	Local name	Vegetation Type	Average feeding time/day (min)	%	Leaf	Fruit	Bud	Flower	Bark
1	Acanthaceae	*Justicia adhatoda* L.	Bashok	Shrub	0.51	0.3	0.3				
2	Anacardiaceae	*Mangifera indica* L.	Aam	Tree	14.19	8.8	3.1	1.8	2.2	1.7	
3		*Spondias dulcis* Parkinson	Misty amra	Tree	7.98	4.2	3.4	0.3	0.4		0.1
4	Annonnaceae	*Annona squamosa* L.	Ata	Tree	0.31	0.2	0.1	0.1			
5	Apocynaceae	*Carissa carandas* L.	Koromca	Shrub	5.59	3.1	2.5	0.6			
6		*Catharanthus roseus* (L.) G.Don	Noyontara	Herb	0.15	0.1	0.1				
7	Arecaceae	*Phoenix dactylifera* L.	Khejur	Tree	0.05	0.03		0.03			
8	Asteraceae	*Mikania scandens* (L.) Willd.	Taralota	Herb	1.44	1.3	1.3				

No.	Family	Scientific name	Local name	Vegetation Type	Average feeding time/day (min)	%	Leaf	Fruit	Bud	Flower	Bark
9	Brassicaceae	*Brassica oleracea** L.	Badhakopi	Herb	0.1	0.04	0.04				
10	Caricaceae	*Carica papaya** L.	Papaya	Tree	6.62	4.1	2.9	1.2	0.1		
11	Combretaceae	*Terminalia arjuna* (Roxb. ex DC.) Wight & Arn.	Arjun	Tree	1.17	0.8	0.5		0.1		0.2
12	Cucurbitaceae	*Coccinia cordifolia* (L.) Cogn.	Talakocu	Herb	2.38	1.6	1.6				
13	Fabaceae	*Acacia nilotica* (L.) Delile	Babla	Tree	11.03	5.9	5.5		0.3		
14		*Albizia saman* (Jacq.) Merr.	Koroi	Tree	6.77	4.6	2.9	0.6	1.1		
15		*Bauhinia variegata* L.	Kanchon	Tree	1.99	1.4	1.4				
16		*Dalbergia sissoo* DC.	Sisoo	Tree	8.67	5.2	4.7		0.5		
17		*Delonix regia* (Hook.) Raf.	Krisnocura	Tree	0.75	0.5	0.5				
18		*Lablab purpureus** (L.) Sweet	Sheem	Herb	3.22	1.4	0.5	0.4		0.5	
19		*Lathyrus sativus** L.	Khasary	Herb	0.71	0.4	0.3	0.1			
20		*Lens calinaris** Medik.	Mosur	Herb	0.08	0.06		0.06			
21		*Leucaena leucocephala* (Lam.) de Wit	Epil-epil	Tree	1.85	1.2	0.5	0.7			
22		*Tamarindus indica* L.	Tatul	Tree	8.97	6	5.3	0.4	0.3		
23	Lamiaceae	*Ocimum tenuiflorum* L.	Tulsi	Herb	0.78	0.5	0.5				
24	Malvaceae	*Corchorus capsularis** L.	Pat	Shrub	2.95	2	2				
25	Meliaceae	*Melia azadirachta* L.	Neem	Tree	0.47	0.3	0.3				
26		*Swietenia mahagoni* (L.) Jacq.	Mahogony	Tree	0.3	0.2	0.2				
27		*Syzygium cumini* (L.) Skeels	Jaam	Tree	5.05	3.3	1	1.4	0.4	0.4	0.1
28		*Syzygium paniculatum* Gaertn.	Bon jam	Shrub	1.47	0.9		0.9			

No.	Family	Scientific name	Local name	Vegetation Type	Average feeding time/day (min)	%	Leaf	Fruit	Bud	Flower	Bark
29	Moraceae	*Artocarpus heterophyllus* Lam.	Kanthal	Tree	0.11	0.1	0.1				
30		*Artocarpus lakoocha* Ruxb.	Deuwa	Tree	0.49	0.3	0.2				0.1
31		*Ficus benghalensis* L.	Bot	Tree	0.79	0.5	0.3		0.2		
32		*Ficus carica* L.	Dumur	Tree	2.61	1.8		1.8			
33		*Ficus congesta* Roxb.	Jag dumur	Tree	1.11	0.6		0.6			
34	Moringaceae	*Moringa oleifera* Lam.	Sojina	Tree	6.35	3.7	3.7				
35	Musaceae	*Musa sapientum* L.	Kola	Herb	4.67	3.3		3.3			
36	Myrtaceae	*Eugenia javanica* L.	Jamrul	Tree	2.32	1.6		0.9	0.7		
37		*Psidium guajava* L.	Payara	Tree	4.12	2.4	1.5	0.7	0.2		
38	Oleaceae	*Nyctanthes arbor-tristis* L.	Seuli	Tree	0.22	0.1				0.1	
39	Oxalidaceae	*Averrhoa carambola* L.	Kamranga	Tree	2.54	1.7	1.1	0.4	0.2		
40	Phyllanthaceae	*Phyllanthus acidus* (L.) Skeels	Royel boroi	Tree	1.05	0.6	0.6				
41		*Phyllanthus emblica* L.	Amloki	Tree	1.35	1.6	1.6				
42		*Phyllanthus reticulatus* Poir.	Khud	Shrub	0.3	0.2	0.2				
43	Poaceae	*Cynodon dactylon* (L.) Pers.	Durba	Herb	3.66	2.1	2.1				
44		*Cynodon incompletus* Nees	Ghass	Herb	1.75	1.2	1.2				
45	Rhamnaceae	*Ziziphus mauritiana* Lam.	Boroi	Tree	4.14	2.6	0.9	0.8	0.1	0.8	
46	Rubiaceae	*Ixora chinensis* Lam.	Rongon	Shrub	0.28	0.2	0.2				
47	Rutaceae	*Aegle marmelos* (L.) Corrêa	Bael	Tree	0.75	0.4	0.3		0.1		
48		*Citrus aurantiifolia* (Christm.) Swingle	Labu	Shrub	1.35	0.9	0.7	0.2			
49		*Limonia acidissima* Groff	Kodbael	Tree	0.4	0.3	0.3				
50	Sapindaceae	*Litchi chinensis* Sonn.	Litchi	Tree	1.61	0.9	0.3	0.2	0.2	0.2	

No.	Family	Scientific name	Local name	Vegetation Type	Average feeding time/day (min)	%	Leaf	Fruit	Bud	Flower	Bark
51	Sapotaceae	*Manilkara zapota* (L.) P.Royen	Sofeda	Tree	2.73	1.7	0.4	1.3			
52	Solanaceae	*Lycopersicon esculentum** Mill.	Tomato	Herb	0.56	0.4		0.4			
53		*Solanum melongena** L.	Bagun	Shrub	1.82	1.2	0.2	1			
54		*Solanum tuberosum** L.	Aalu	Herb	1.01	0.6	0.3	0.3			
		Provisioned food									
		Banana			6.69	4.3					
		Bread			2.31	1.6					
		Nut			7.94	3.3					
		Non plant food									
		Soil, water and fungi			1.41	1					
Total					162	100					

* cultivated/ seasonal crops

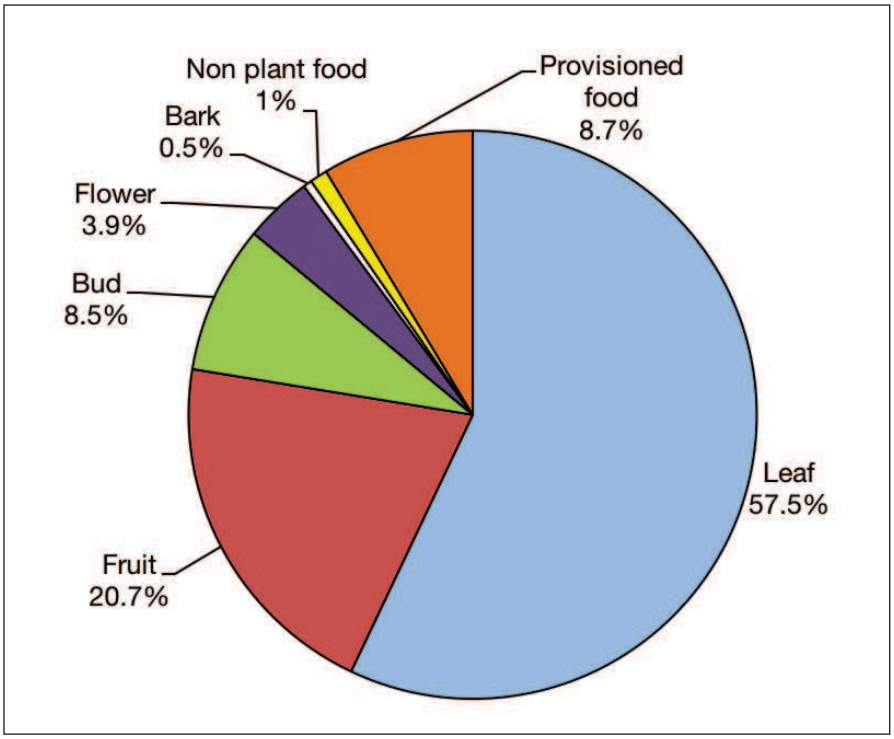

Fig. 2. Time spent feeding on different food items (N=1,094).

plant species whose leaves were fed on each month (χ^2=7.68, df=11, p>0.05, n=629). The consumption of fruit, bud and flower peaked in June, October and February, respectively. Statistically-significant variation in the number of plant species whose fruits and buds were eaten each month was found (fruit: χ^2 =20.13, df=11, p<0.05; and bud: χ^2 =20.8, df=11, p<0.05; Fig. 3).

In contrast, we found that the number of plant species utilized for leaf food items differed significantly across three seasons, while the consumption of other plant parts did not (leaf: χ^2=8.16, df=2, p=0.017; bud: χ^2=2.92, df=2, p>0.05; fruit: χ^2=4.09, df=2, p>0.05; and flower: χ^2=3.5, df=2, p>0.05; Fig. 4). While langurs are known to be folivorous, they also opportunistically fed on other food items when available. Pair-wise comparison showed that the study animals consumed buds from more species in winter than summer or the rainy season (p<0.05 for each comparison), more fruit species in summer than other seasons (p values were the same for each comparison; p=0.018), more leaf species in winter than other seasons (p values were the same for each comparison; p<0.01), and more flower items in winter than other seasons (p values were the same for each comparison; p<0.05; Fig. 4).

The percentage of consumption of natural food by the langurs dominated over cultivated food across the entire study period. Percentage of cultivated food in the diet during the winter season was 5.7% (n=62), followed by other seasons (5.0%, n=55) in summer and 1.8% (n=20) in the rainy season).

Age-sex class differences in time spent feeding on natural foods

A different number of plant species were consumed by adults (n=53 plant species) and sub-adults (n=48 plant species). Time spent feeding on natural foods by adults differed notably between males and females, while sub-adults did not show any significant difference according to sex (Fig. 5). These findings suggest that sex did not affect the feeding time of sub-adults, while adult females spent more time than adult males feeding on natural foods. Adults spent approximately 13.6% (n=149) of their feeding time in the upper canopy layers, whereas sub-adults spent almost double (23.6%, n=258) that amount of time there. Conversely, adults and sub-adults spent 24.2% (n=265) and 17.09% (n=187) of the time feeding on the ground, respectively.

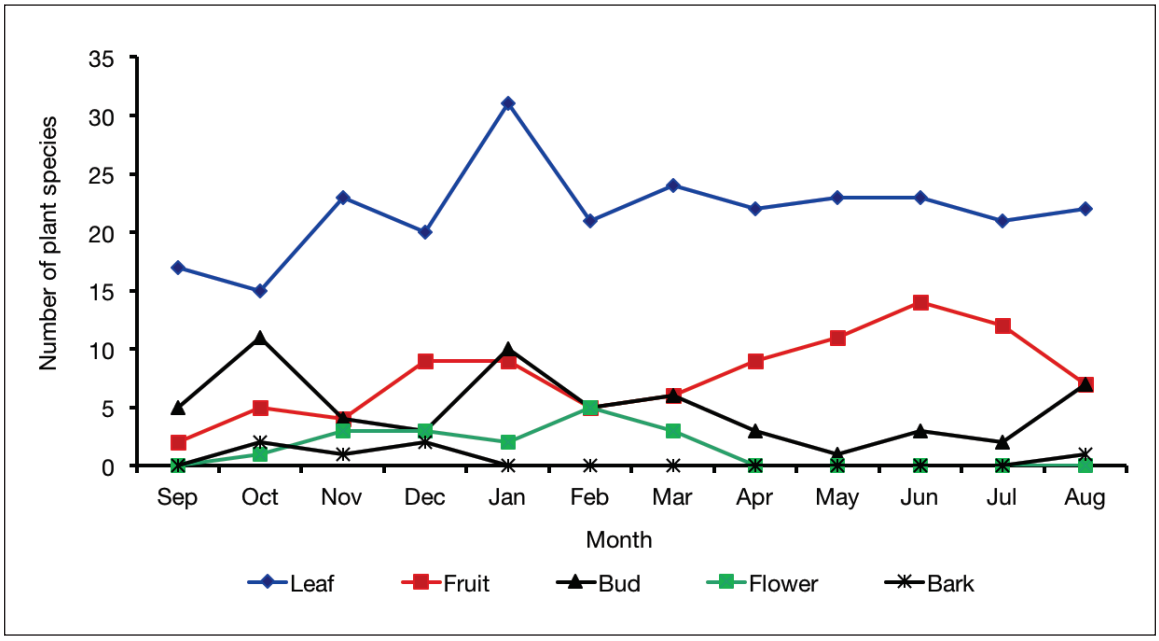

Fig. 3. Monthly variation in the number of plant parts and species ingested (N=1,094).

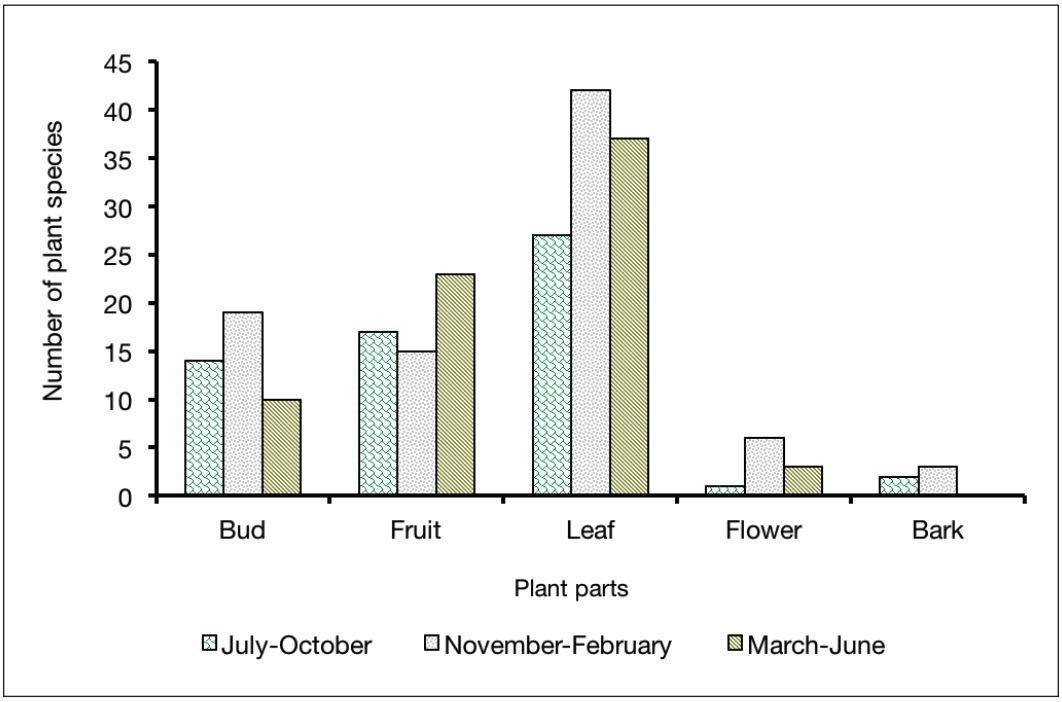

Fig. 4. Seasonal variation of plant species and plant parts consumed (N=1,094).

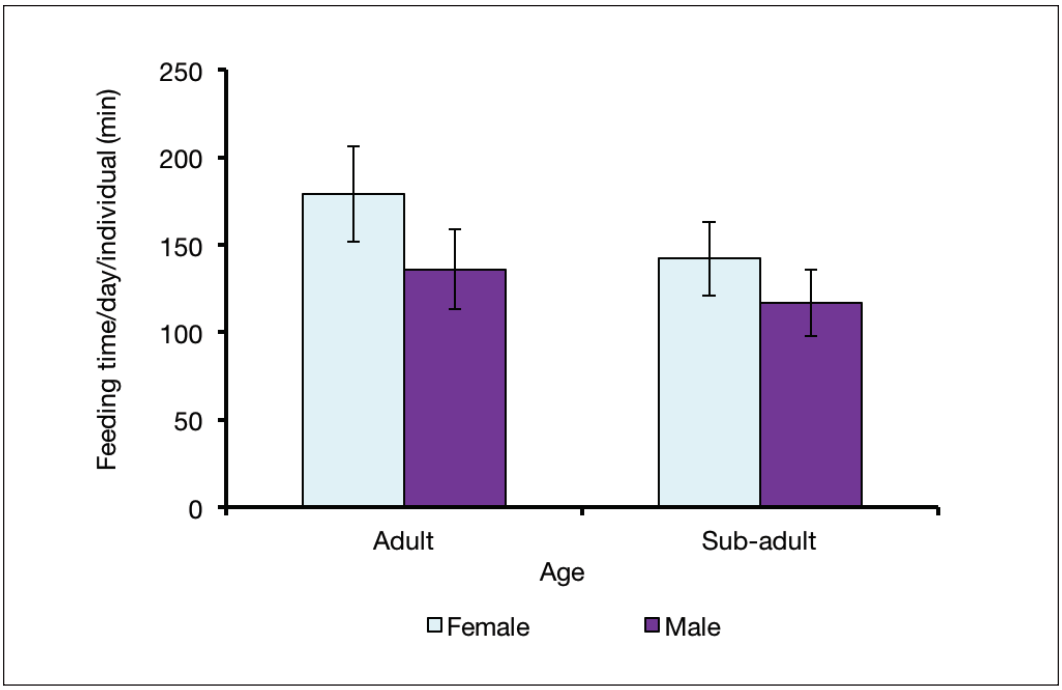

Fig. 5. Age-sex differences in time spent feeding on natural foods (N=1,094).

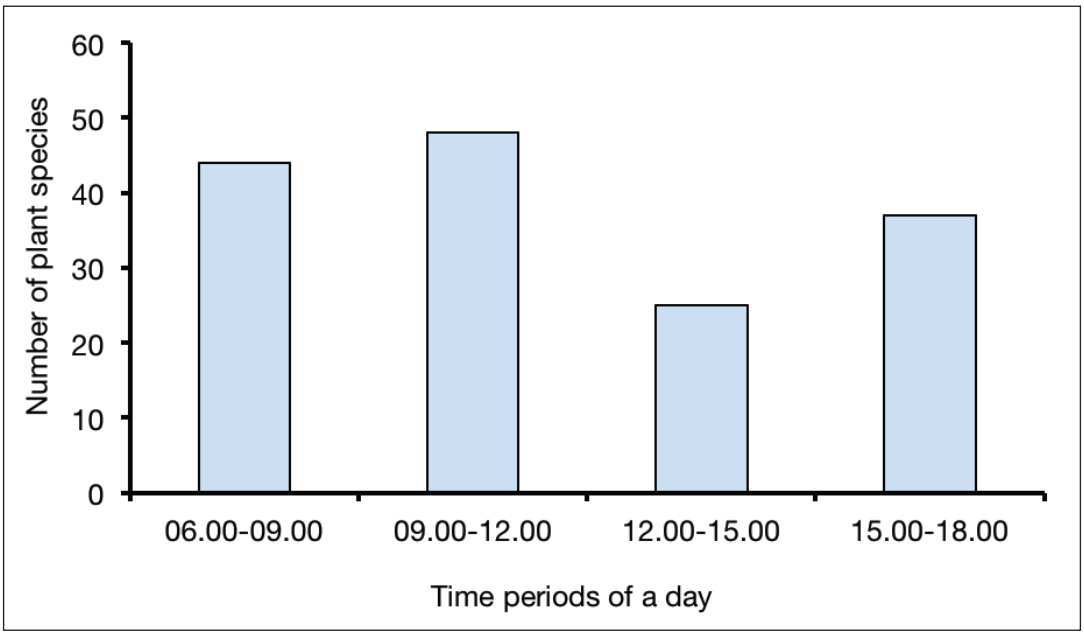

Fig. 6. Number of plant species used in different time blocks.

Variation of food consumption across different time periods of the day

We found that the number of plant species consumed by langurs differed significantly at different time periods of the day (χ^2=7.9, df=3, p<0.05; Fig. 6). They consumed the highest number of different plant species in late morning (n=48) and the lowest at mid-day (n=25). Regardless of season and age-sex class, they allocated the maximum time for feeding in the early morning (c. 50 minutes out of 180, or 28%) and the minimum time at mid-day (c. 30 minutes out of 180, or 20%).

DISCUSSION

Food items and feeding behaviour

Most studies categorize *Semnopithecus* spp. as being highly folivorous, but this is a narrow interpretation of the actual situation. In some habitats they are known to consume many other parts of plant food species when seasonally available, as well as various types of human-provisioned or cultivated crops in areas where they are commensal (Rajpurohit, 2005; this study). Various studies have shown that *Semnopithecus* spp. eat between 49 and 184 different flowering plants in their habitat (see Table 3) and different plant parts are consumed at different study sites (see Table 4). Observations of *S. entellus* in the open scrub forest of Jodhpur, India, revealed that insects may also constitute a regular part of the diet (Srivastava, 1991). The percentage of food items consumed (Table 4) do not total 100% because cultivated crops were excluded from the analysis.

In Sri Lanka, *S. priam* and *S. vetulus* are categorized as folivorous (Amerasinghe et al., 1971). However, more recent studies have also shown that *S. vetulus* consumes a variety of different food items, including fruits when available (Dela, 2007; Nijman, 2012).

Monthly and seasonal variation in food consumption

The dietary diversity of langurs in our study was quite high. Cultivated crop consumption seemed to play a role in influencing the monthly and seasonal variation in food consumption by *S. entellus* at Keshabpur and Manirampur although the total time spent feeding on these items was comparatively low overall. They consumed the highest number of different plant species in March, with access to seasonal food sources obtained by raiding cultivated fields, consuming the leaves and flowers from these crop species during their growing cycles. The lowest number of plant species utilized was in September, a period of lower availability of cultivated crops. As a result, consumption of cultivated crops in the rainy season was almost half of that consumed in other seasons. A similar study done by Minhas et al. (2010) in Pakistan showed that *S. ajax* consumed the greatest number of plant species in August (n=27), during the monsoon, when the number of new-growth plant food species increased to a yearly maximum.

Table 3. Comparison of plant food species diversity among *Semnopithecus* spp.

Species*	Location	No. of plant food species	Reference
Malabar Sacred Langur *Semnopithecus hypoleucos*	Madhya Pradesh, India	54	Majumder et al. (2010)
Chamba Sacred Langur *Semnopithecus ajax***	Machiara National Park, Pakistan	49	Minhas et al. (2010)
Northern Plains Sacred Langur *Semnopithecus entellus*	Jessore, Bangladesh	More than 60	Ahsan & Khan (2006)
Northern Plains Sacred Langur *Semnopithecus entellus*	Kumbhalgarh Wildlife Sanctuary, Rajasthan, India	184	Changani (2004)
Malabar Sacred Langur *Semnopithecus hypoleucos*	Western Ghats of Maharashtra, India	126	Punekar (2002)
Northern Plains Sacred Langur *Semnopithecus entellus*	Western Uttar Pradesh, India	51	Kar-Gupta & Kumar (1994)
Northern Plains Sacred Langur *Semnopithecus entellus*	Keshabpur, Jessore, Bangladesh	91	Khatun (2011)
Northern Plains Sacred Langur *Semnopithecus entellus*	Keshabpur, Jessore, Bangladesh	54	This study

*Taxonomic reference based on Mittermeier et al., 2013; Roos et al., 2014; Ashalakshmi et al., 2015.

**The taxonomic designation of *S. ajax* as a distinct species is still under molecular investigation.

The number of plant species utilized varied considerably across seasons at our study site. Compared to other seasons, in winter, the largest number of plant species were consumed (Fig. 4). Minhas et al. (2010) reported that there were notable differences in the number of plant species in the *S. ajax* diet between summer (n=37) and winter (n=22), due to plant availability and cold weather, respectively. Differences in altitude, hence in environmental attributes such as temperature and humidity, are likely responsible for the differences in diet seasonality between this study site and ours.

We found that the number of food items from different plant species consumed by *S. entellus* varied significantly across seasons. Consumption of leaves and buds from different species were the highest in winter, most likely due to their greater availability. After dropping off mature leaves, plants flush with new leaves in the winter season. At this time, the immature leaves and buds became their main food items. In addition, there were some cultivated winter crops to consume, allowing them to utilize more plant species than in other seasons. On the contrary, bud consumption in terms of time spent feeding by these langurs, reached its peak in the rainy season. This may be due to the heavy rainfall that stimulated the budding of food plants, increasing their abundance (Minhas et al., 2010).

The results of our study also suggest that *S. entellus* ingested more immature leaves than mature leaves, which is also common in other colobine species, and has been suggested to be due to the high protein-to-fibre ratio of young leaves (e.g. Davies et al., 1988) and also because they can better meet their water requirements from immature leaves in this dry environment (e.g. Jildmalm et al., 2008). In summer, *S. entellus* at our study site utilized a large number of plant species and more time was spent feeding on fruit, suggesting that they are opportunistic in terms of the seasonal variation of food sources. Fruit was not available in winter.

We observed the langurs drinking water only in the summer, the period when immature leaf food items were also absent. Group members also ingested dead wood in the rainy season, though this was not observed during focal animal sampling. It might be that dead wood is softer at this time due to water absorption; in which case it might be an alternative source of water and fibre. Alternatively, consumption of the wood pulp of some species has also been shown to be an important source of minerals like sodium, medicine

Table 4. Comparison of the distribution of (non-cultivated) food items consumed by *Semnopithecus* spp. across study sites.

Species*	Location	Percentage of food items**				Reference
		leaves	fruits	buds	flowers	
Northern Plains Sacred Langur *Semnopithecus entellus*	Jodhpur, India	6	23	-	7	Rajpurohit (2005)
Northern Plains Sacred Langur *Semnopithecus entellus*	Rajaji National Park, Uttara-khand, India	52.6	11-12	-	11-12	Kar-Gupta & Kumar (1994)
Grey langur *Semnopithecus priam*	Arid zone of Sri Lanka	71.9-83.7	7.9-12.5	-	7.9-6.8	Hladik & Hladik (1972)
Northern Plains Sacred Langur *Semnopithecus entellus*	Gir Sanctuary, Gujrat	85.4		-	-	Rahman (1973)
Malabar Sacred Langur *Semnopithecus hypoleucos*	Dharwar	94.6	1.7	-	1.2	Yoshiba (1967)
Northern Plains Sacred Langur *Semnopithecus entellus*	Keshabpur, Jessore, Bang-ladesh	57.5	20.7	8.5	3.9	This study

*Taxonomic reference based on Mittermeier et al., 2013; Ashalakshmi et al., 2015.

**Cultivated crops were omitted, therefore consumption does not total 100%.

and toxins in primates (Oates, 1978; Huffman, 1997; Reynolds et al., 2009). We found budding at its peak during the rainy season, which is most likely why buds constituted a major part of the diet in this season. Bark was eaten for more or less similar amounts of time across all seasons (Fig. 3 & 4).

Age-sex class differences in feeding behaviour on natural foods

We found that adults and sub-adults consumed a slightly different number of plant parts; 53 and 48 respectively, but the difference is not great. Females consumed more plant species than males. We also found that females spent less time feeding on provisioned foods, where provided, than did males. Males tended to gain priority of access to these highly sought-after foods, suggesting that feeding competition resulted in the lower intake by females. To overcome this limited access to provisioned foods, females may have spent more time feeding on natural food items, which is supported by our data (Fig. 5) and previously published work on *M. fuscata* (Soumah & Yokota, 1991; Jaman & Huffman, 2011). Several other factors may also be responsible for their food choices. Due to conception, pregnancy and offspring care, females may require more energy than males (e.g. Nakagawa, 1989).

Variation of foods consumed in different time periods of the day

During this study, the number of plant species and the time spent feeding on them fluctuated across time of day. They utilized the greatest number of plant species in the late morning and the lowest number at mid-day. There should be more feeding on plant species in the early morning, but in our study area, the langurs usually fed more on provisioned foods provided by humans in the early morning, though it sometimes was also provided in the afternoon at selected sites. Due to this, they spent considerably more time feeding on provisioned foods rather than natural foods whenever available. The highest feeding rate recorded for natural plant food items was in the afternoon. Conversely, langurs allocated the smallest amount of time at mid-day to feeding on any food item because they rested more at this time, perhaps due to high temperatures, particularly in summer. In winter, they spent more time feeding during all periods of the day compared with other seasons.

Practical implications of this study

Our observations did not show *S. entellus* consuming a whole fruit on any occasion; rather they ate only part of it and dropped the rest. They were also found to break branches of trees frequently while foraging. From this perspective, they can be assumed to play a positive role in the ecosystem by making the upper canopy nutrients (fresh fruit, leaves etc.) available to organisms on the ground. This commensal relationship has been described for a variety of birds, fish, reptiles, primates and other mammals (e.g. Majolo & Ventura, 2004; Heymann & Hsia, 2015). While not originally native to Bangladesh, they have lived there long enough to be considered a naturalized species and they have become an integral part of the ecology across their current habitat. We argue that this makes them a good indicator of the general health of the ecosystem, and special attention to these langurs is required for proper conservation planning. They are currently facing numerous threats, among which include scarcity of natural foods, habitat fragmentation, and conflict with humans. Although globally listed as Least Concern by the IUCN Red List of Threatened Species (Mitra & Molur, 2008), these langurs have been considered Critically Endangered in Bangladesh (IUCN, 2000).

In this study, we recorded the diversity of their feeding habits in relation to season and by the differences in their individual traits. This information will likely have beneficial implications for the conservation planning of this species in Bangladesh. We also noted that to minimize potential human-langur conflicts, some of the important food sources for this species, such as figs and raintrees could be planted in areas currently not intensively used by humans. *Semnopithecus entellus* not only consumed leaf of raintrees, but also used them for roosting. Besides reducing potential human-langur conflicts over food resources, planting these trees may possibly lead to a reduction in provisioning costs. In addition, the trees could also be harvested selectively.

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