

Feeding Behavior of the Western Hoolock Gibbon (*Hoolock hoolock*) in Bangladesh: Response to Temporal Variation of Food Sources

Sufia Akter Neha, Mst. Ummay Habiba Khatun and Md Ashraf Ul Hasan

Department of Zoology, Jagannath University, Dhaka, Bangladesh

Abstract: An understanding of the diet and the factors influencing food choice are important when considering conservation measures for primates. From April 2016 to March 2017, we studied the feeding behavior of the western hoolock gibbon (*Hoolock hoolock*) in response to seasonal variation of food in Satchari National Park (24°7'25.65"N, 91°27'5.43"E), Bangladesh. A group of hoolock gibbons comprising four individuals was studied using scan sampling. The gibbons spent 57.5% of their feeding time eating fruits—figs made up 30.4% and non-fig fruits 27.1%. Other food items included leaves (20.1%), flowers (8.7%), shoots (5.4%), bark (4.7%), and animal prey (3.6%). The gibbons ate whole, small, ripe, juicy fruits such as mature and ripe figs, but were seen to avoid over-ripe fruits. Dietary diversity was higher in the rainy season ($H' = 2.71$) and fruits were generally foremost in the diet at that time. Leaves were an increasing component of the diet during the winter (colder months November to February) and flowers were eaten more during the summer (warmer months March to May). We found a significant correlation between the percentage frequency of feeding on fruits and the percentage of trees in the quadrats bearing them ($r_s = 0.71$, $n = 12$, $p = 0.003$). Fruit availability significantly influenced the gibbons' food choice ($r^2 = 0.726$, $n = 12$, $p = 0.001$). The plant part of the hoolock's diet was diverse—76 plant species in 33 families, with Moraceae being the dominant family (16 species) in providing figs throughout the year.

Keywords: Western hoolock gibbon, seasonal variation, feeding behavior, food availability

Introduction

Primate feeding strategies and the factors that influence their food choice are fundamental for our understanding of the socio-ecological aspects of primate evolution and the habitat requirements necessary for the conservation of threatened primates (Robbins and Hohmann 2006). Food availability depends on the profile of the forest, plant species diversity, and the distribution and seasonality of food resources (see, for example, Feeroz 1998). Seasonal shifts and food availability are known to be the crucial ecological factors affecting feeding behavior as they require a trade-off between energy acquisition and expenditure (Chapman *et al.* 2015). The large majority of primates inhabit tropical rainforest, experiencing, as such, plant phenological cycles that can result in high seasonal fluctuations in the quality and quantity and dispersion of food resources (van Schaik *et al.* 1993; Harrison and Marshall 2011).

The western hoolock gibbon (Hylobatidae; *Hoolock hoolock*) is found in small populations in India, Bangladesh, China and Myanmar, (Ahsan 1984; Tan 1985; Mukherjee 1986; Mootnick *et al.* 1987; Islam *et al.* 2008, 2011). In

Bangladesh, they are restricted to forest in the northeast and south-east of the country. Satchari National Park, in the north-east on the border with India, is one of the crucial protected areas for this species. A number of studies have been carried out on this taxon in Bangladesh, addressing behavior, feeding ecology and habitat preference (Islam and Feeroz 1992; Ahsan 1994; Hasan *et al.* 2005; Muzaffar *et al.* 2007; Hasan and Feeroz 2011; Akers *et al.* 2013), but none in the Satchari National Park, and detailed information on feeding behavior in relation to seasonal change in food availability is still limited. Hence, in the present study we focused on the composition of, and temporal changes in, their diet. Our objectives were to: 1) study their diet and feeding behavior; 2) understand how they budget their time in exploiting different food items; and 3) evaluate the effect of seasonality on feeding behavior.

Methods

Study site

Satchari National Park (24°7'25.65"N, 91°27'5.43"E) is in the Sylhet region of northeastern Bangladesh (Fig. 1). It is a tropical semi-evergreen forest covering an area of 243 ha

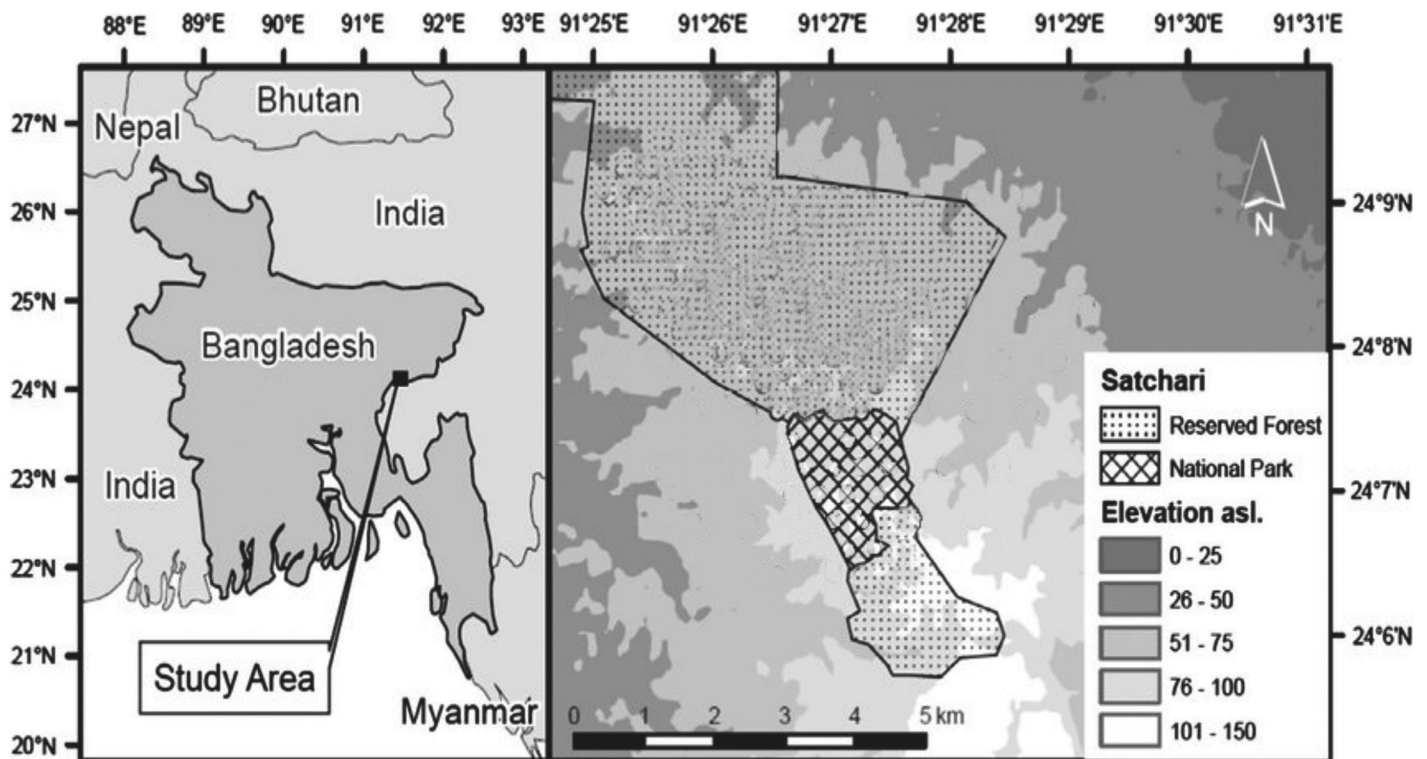


Figure 1. Field site and its location in the north-eastern region of Bangladesh. (Source: Uddin *et al.* 2013).

in a partial transition zone between the Indian sub-continent and the Indo-Chinese ecological region, also comprising the Raghunandan Hills Reserve Forest, within the Satchari range (Sharma 2006). The park is surrounded by tea estates, lemon orchards, oil palm and rubber plantations, and agricultural fields (Hasan *et al.* 2018a). The soils are typically brown, acidic and sandy loam to silty clay. The forest is permeated by small sandy-bedded streams that dry out at the end of the rainy season. The vegetation is evergreen to semi-evergreen, with the majority of the smaller understory trees evergreen and the large dominant trees deciduous (Hasan *et al.* 2018b).

The climate is usually warm and humid in summer (March to May), wet and rainy from June to October, and cool during the winter (November to February), which impacts seasonality in leaf and fruit production (Hasan *et al.* 2018c). Weather parameters (rainfall, temperature, and relative humidity) were obtained from the Bangladesh Meteorological Department. During the study period, the Satchari forest had a mean daily temperature of 27.4°C, mean annual rainfall of 224 mm and monthly average humidity of 75% respectively. The highest temperature recorded was 32°C in April 2016, and the lowest was 14°C in January 2017. The highest rainfall was recorded in May 2016 (647 mm), and there was no rain from December 2016 to March 2017. The highest humidity was recorded in July 2016 (89%) and lowest in March 2017 (47%).

Behavioral data

A group of four hoolock gibbons—an adult male, an adult female, a sub-adult male and a juvenile—was studied in Satchari National Park, from April 2016 to March 2017. The gibbons were followed for 4–5 days each month, totaling 54 days; 336 hours (range = 6–8 hours/day) resulting in 2,192 feeding records. Data on different feeding activities were collected by scan sampling for 5 minutes with 5-minute intervals between the scans (Altmann 1974). The activities performed by the visible members of the study group were reported in each scan. When we encountered the group, we first followed the adult male and then noted the activities of the other group members. We recorded only activities that lasted for >2 min in each scan. Feeding was recorded when an individual was searching for food, manipulating food, masticating and swallowing. We recorded food species, plant types and food parts eaten (leaves, fruits, flowers, bark, shoots).

Phenological data

Phenological data were obtained to determine the seasonal productivity of food plants during the study period. Ten sample plots (each of 50×50 m) were laid over the home range of gibbon. All trees measuring ≥30 cm Diameter at Breast Height (DBH) were identified and marked (Marshall and

Table 1. Food parts eaten among the age sex-classes of hoolock gibbon.

	Adult male n = 574		Adult female n = 568		Sub-adult male n = 571		Juvenile n = 479		Total n = 2192		Kruskal- Wallis
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	p
Feeding	34.57	7.50	33.60	5.12	34.81	6.12	35.87	5.74	34.59	0.65	0.3097
Leaves	18.14	4.34	21.03	3.21	19.04	3.75	22.04	5.54	20.06	1.78	0.3133
Flowers	10.34	3.72	8.80	2.77	10.67	3.98	4.85	2.10	8.66	2.67	0.1114
Fruits	57.38	6.28	55.15	5.48	55.86	6.01	61.92	12.4	57.58	3.04	0.2417

Leighton 2006). The local name of each tree was recorded by the field assistants and verified later by plant taxonomists and the available literature (Mukul *et al.* 2007; Arefin *et al.* 2011; Pasha and Uddin 2013). In cases of doubt plant specimens were collected, photographed and sent to the Bangladesh National Herbarium for verification. The phenological phase (new leaves, flowers and fruits) was recorded every month with the help of binoculars (Bushnell 10×42). The productivity in a given tree canopy was estimated as a score from 1–4: 1 = 1–25%; 2 = 26–50%, 3 = 51–75%, and 4 = 76–100%. When there was no productivity the score was Zero (0 = absent).

Data analysis

Percentage time spent feeding on different food items was estimated using the formula $Tf = (nf \times 100)/N$, where Tf = time spent on particular food item as a percentage of total feeding time, nf = number of scan records on a specific food item, and N = total number of scan records. We examined the differences in the monthly proportions of time allocated to feeding on different dietary items by the study group using Kruskal-Wallis one way ANOVA. The F test (analysis of variance) was applied to compare feeding on different food items across the months. Spearman rank correlation was used to test the relationship between monthly feeding percentages on different food items and their availability in the phenological quadrats. Mann-Whitney U test was also

performed to see the differences between monthly feeding on figs, non-figs, ripe and unripe fruits. We excluded the records for feeding on bark, shoots and animal prey because observations each month were too infrequent. Stepwise regression was applied to assess the influence of food availability on the feeding activity of the gibbons. R statistical software [3.6.1, R Core Team 2019] and Statistical Package for Social Sciences (SPSS 19) were used for analysis, considering a p value ≤ 0.05 to be significant.

Results

Overall feeding behavior

As a group the hoolock gibbon spent 57.5% its feeding time feeding on fruits, 20.1% on leaves, 8.7% on flowers, 5.4% on shoots, 4.7% on bark and 3.6% on animal prey. Feeding on fruits was predominant during the early morning, while in the afternoon, they fed on a wide variety of foods, including leaves, flowers, bark, and shoots. In the evening, they would frequently eat fruits while moving towards their sleeping sites. Time spent feeding on each food item differed among the four groups members, each of a different age-sex class, but the differences were not significant: fruits during the study period ($H = 10.34$, $df = 2$, $p = 0.24$); leaves ($H = 9.43$, $df = 2$, $p = 0.31$); flowers ($H = 6.77$, $df = 2$, $p = 0.11$) (Table 1).

Table 2. Percentage in dietary diversity and temporal changes in food choices of hoolock gibbon during the study period.

	Summer				Total	Rainy season				Total	Winter				Total
	Leaves	Fruits		Flowers		Leaves	Fruits		Flowers		Leaves	Fruits		Flowers	
		Non-fig	Figs		Non-fig		Figs	Non-fig		Figs					
Morning	19.5	26.3	30.8	12.1	88.7	14.9	33.2	31.4	6.8	86.3	24.4	24.1	30.6	9.7	88.8
Observations	42	60	67	28	197	37	72	69	18	196	55	52	63	23	193
Food species	3	5	9	4	21	5	10	7	3	25	3	4	7	3	17
Afternoon	21.9	24.2	28.1	9.8	84.0	18.3	32.0	29.5	7.9	87.7	21.8	22.8	31.7	8.0	84.3
Observations	47	53	62	26	188	43	68	65	22	198	46	49	68	19	182
Food species	2	4	6	3	15	4	7	6	2	19	4	8	6	2	20
Evening	18.3	27.8	32.5	7.7	86.3	16.8	28.6	25.7	8.2	79.3	25.5	25.2	33.8	8.1	92.6
Observations	36	62	68	19	185	38	64	58	24	184	56	54	70	19	199
Food species	3	7	8	2	20	2	8	5	3	18	2	5	4	1	12

Table 3. All the food items attributed to plant species that were eaten by hoolock gibbon.

Family	Species name	Life form	Time (%)	Food items
Acanthaceae	<i>Thunbergia grandifolia</i> **	Vine	2.1	Lf, Fl, Sh
Anacardiaceae	<i>Holigarna longifolia</i>	Tree	0.4	Fr
	<i>Spondias pinnata</i> **	Tree	2.8	Lf, Fr
Annonaceae*	<i>Melodorum rubiginosum</i>	Liana	1.3	Lf, Fl
	<i>Desmos chinensis</i>	Liana	0.8	Lf, Fl
	<i>Artabotrys hexapetalus</i>	Vine	1.4	Lf, Fl, Fr
	<i>Polyalthia longifolia</i> **	Tree	1.9	Fr, Br
Apocynaceae	<i>Alstonia scholaris</i>	Tree	1.5	Lf, Br, Sh
Arecaceae	<i>Caryota urens</i> **	Tree	3.1	Fr
Asteraceae	<i>Mikania scandens</i>	Vine	0.8	Lf, Fl
Bombaceae	<i>Bombax ceiba</i>	Tree	0.7	Fl
Burseraceae	<i>Protium serratum</i>	Tree	0.3	Fr
Combretaceae*	<i>Terminalia catappa</i> **	Tree	2.4	Fr, Br
	<i>Terminalia bellirica</i>	Tree	1.1	Fr
Convolvulaceae	<i>Argyreia nervosa</i>	Vine	0.6	Lf
	<i>Merremia umbellata</i>	Vine	0.8	Lf
Dilleniaceae*	<i>Dillenia pentagyna</i> **	Tree	1.8	Fr
	<i>Tetracera sarmentosa</i>	Liana	0.6	Lf, Fr, Fl
	<i>Dillenia scabrella</i>	Tree	1.1	Fl, Fr
Dioscoreaceae	<i>Dioscorea belophylla</i>	Vine	0.9	Lf
	<i>Dioscorea esculenta</i>	Vine	1.0	Lf
Elaeocarpaceae*	<i>Elaeocarpus floribundus</i>	Tree	0.2	Fr
	<i>Elaeocarpus robusta</i>	Tree	0.4	Fr
Euphorbiaceae*	<i>Aporusa dioica</i>	Tree	0.5	Lf, Fr
	<i>Mallotus albus</i>	Tree	0.6	Lf, Sh
	<i>Sapium baccatum</i>	Tree	1.0	Lf, Fr, Br
Fabaceae*	<i>Acacia pennata</i>	Liana	0.9	Lf
	<i>Albizia chinensis</i>	Tree	0.8	Lf
	<i>Cassia siamea</i>	Tree	0.5	Lf, Fl
	<i>Erthrina variegata</i>	Tree	0.4	Fl
	<i>Abrus precatorius</i>	Vine	0.7	Lf
	<i>Dalbergia tamarindfolia</i>	Liana	0.6	Fl
	<i>Mucuna monosperma</i>	Vine	0.5	Lf

	<i>Entada phaseoloides</i>	Liana	1.1	Lf
Guttiferae*	<i>Garcinia cowa**</i>	Tree	2.1	Fr, Lf
	<i>Garcinia xanthochymus</i>	Tree	1.2	Fr
Lauraceae	<i>Litsea glutinosa</i>	Tree	0.4	Fr
	<i>Litsea monopetala</i>	Tree	0.3	Lf
Leeaceae	<i>Leea guineensis</i>	Tree	0.2	Fl
	<i>Leea sambucina</i>	Tree	0.4	Fr
Malvaceae	<i>Hibiscus surattensis</i>	Tree	0.6	Lf, Fl
Meliaceae*	<i>Toona ciliata**</i>	Tree	2.1	Lf,
	<i>Chukrasia tabularis</i>	Tree	1.3	Lf, Fr, Sh
	<i>Amoora wallichii</i>	Tree	0.8	Fr
Moraceae*	<i>Ficus variegata**</i>	Tree	4.4	Fr
	<i>Ficus hispida</i>	Tree	1.1	Fr
	<i>Artocarpus chaplasha</i>	Tree	1.4	Fr, Br
	<i>Artocarpus lacucha**</i>	Tree	3.4	Fr
	<i>Ficus benjamina**</i>	Strangler	2.6	Lf, Fr
	<i>Ficus racemosa</i>	Strangler	1.4	Fr, Br
	<i>Ficus bengalensis</i>	Strangler	1.0	Fr
	<i>Ficus retusa</i>	Tree	1.1	Fr, Br
	<i>Ficus religiosa</i>	Strangler	1.4	Fr
	<i>Ficus gibbosa**</i>	Tree	8.2	Lf, Fr
	<i>Ficus auriculata</i>	Tree	1.4	Fr, Br
	<i>Ficus gemiculata</i>	Strangler	1.3	Fr
	<i>Ficus pumila</i>	Vine	0.8	Fr
	<i>Ficus lamponga**</i>	Tree	2.6	Fr
	<i>Ficus obtusifolia</i>	Strangler	0.7	Fr
	<i>Ficus nervosa**</i>	Tree	2.4	Fr
Myrsinaceae	<i>Maesa ramentacea**</i>	Tree	1.7	Fr
Myrtaceae*	<i>Syzygium cumini</i>	Tree	0.9	Fr
	<i>Syzygium fruticosum</i>	Tree	0.2	Fr
	<i>Syzygium nervosum**</i>	Tree	1.7	Fr, Br
Orchidaceae	<i>Acampe praemorsa</i>	Epiphyte	1.1	Lf, Fl
	<i>Aerides odorata</i>	Epiphyte	1.2	Fl
	<i>Cymbidium aloifolium</i>	Epiphyte	1.0	Lf, Fl
Rhizophoraceae	<i>Carallia brachiata**</i>	Tree	2.1	Lf, Fr

Rubiaceae	<i>Anthocephalus chinensis</i>	Tree	0.3	Lf, Fr
Rutaceae	<i>Zanthoxylum rhetsa</i>	Tree	1.2	Lf, Sh
Sapindaceae	<i>Sapindus mukorossi</i>	Tree	1.4	Fr
Sapotaceae	<i>Mimusops elengi</i>	Tree	0.9	Fr
Teliaceae	<i>Microcos paniculata</i> **	Tree	2.2	Fr
Ternstromiaceae	<i>Schima wallichii</i>	Tree	0.7	Lf, Br
Verbenaceae	<i>Vitex peduncularis</i> **	Tree	1.6	Fr, Br
Vitaceae	<i>Cayratia japonica</i> **	Liana	1.6	Lf

Lf = Leaf, Fl = Flower, Fr = Fruit, Br = Bark, Sh = Shoot; ** = top twenty food species used by hoolock gibbon;

* = top ten plant families in relation to the total number of plants in the study area.

The gibbons' fruit diet was dominated by figs 30.4% (Table 2). They preferred mature and ripe fig fruits (syconia) and avoided those that were over-ripe. They ate the mature yellowish-green fruits of *Ficus lamponga* and *Ficus gibbosa* and the ripe yellowish brown *Ficus variegata* but the pinkish red over-ripe fruits were avoided. *Ficus gibbosa* was the species most favored, followed by *Ficus variegata* (Table 3). Monthly differences between feeding on figs and non-figs were significant (Mann-Whitney U test: $Z = -2.41$, $n_1 = 521$, $n_2 = 468$, $p = 0.0151$) over the study period. Other than figs, gibbons took whole, small, ripe and juicy fruits (48.3%), followed by fruit pulp 21.4%, arils 15.2%, peel 7.9%, seeds 5.9% and 1.3% stalks. *Carallia brachiata* (1.35×1.41 cm) provides an example of a small, ripe fruit with a juicy pulp and very thin rubbery coating that they would swallow whole. For medium-sized fruits, the gibbons would eat the fruit pulp but leave the seed (for example, *Holigarna longifolia*, size 2.67×1.49 cm, with a heavy coating). In the case of quite large fruits with thick rubbery coating, the gibbons would peel off the epicarp and then eat the endocarp or aril with the seed (for example, *Artocarpus chaplasha*, size 9.25×12.45 cm). Fruit feeding in terms of ripe and unripe fruits differed significantly (Mann-Whitney U test: $Z = -5.72$, $n_1 = 296$, $n_2 = 146$, $p = 0.0214$). Evidently ideal fruits sought by gibbons were yellow, large, with a juicy-soft pulp, thin skin and available in large crops.

Plants were the main dietary sources of hoolock gibbon. Seventy-six plant species belonging to 33 families were included in the gibbon group's diet. Moraceae was the family

most favored, with 16 species, and 35.2% of their feeding time spent eating Moraceae fruits (Table 3). The top 20 species contributed 53.4% of their annual diet (Table 3). Selectivity was observed in relation to their food preference and plant species consumption. The gibbons used 27 (36%) plant species for their fruits, 12 (16%) for leaves, 5 (6%) for flowers, and the remaining 32 (42%) species were eaten for two or more food items (Table 3). Feeding selectivity on the top 20 food species was different each month. The differences were found to be significant (One-way ANOVA: $F = 4.02$, $df = 11$, $p = 0.02$). Dietary diversity was $H' = 2.48$. It was higher in the rainy season ($H' = 2.71$) than in the winter ($H' = 2.29$) and summer ($H' = 2.45$) months.

Food resources and their temporal availability

In all, 412 plants (mean dbh = 62.37, range = 16–139.2 cm, SD ±32.43), including trees, stranglers and lianas, were recorded in the ten 2.5-ha vegetation quadrats. Trees were dominant comprising 67.1% of the total plants recorded. Overall density was 133 plants/ha. The top 10 families accounted for 68.9% of the plants. Moraceae was the most dominant family contributing 18.4% of the total plants, accounting for 27.4% of the total basal area (1,717,018 cm²). Average species diversity was 30 species/ha. The top 10 species accounted for 29.1% of the total plants, of which *Artocarpus chaplasha* was the most common (6.8 trees/ha) in the quadrats.

Leaf cover was below 40% in the winter (November to February). Flowers were invariably scarce compared to

Table 4. Stepwise regression analysis with monthly feeding activity (mean for all four individuals) as a dependent variable and availability of leaves, flowers and fruits as independent variables.

On monthly feeding activity	Coefficient	SE	Df	p
Null intercept	11.13	3.98	11	
Leaf availability	0.388			0.223
Flower availability	0.075			0.318
Fruit availability	0.726	0.148	1	0.001

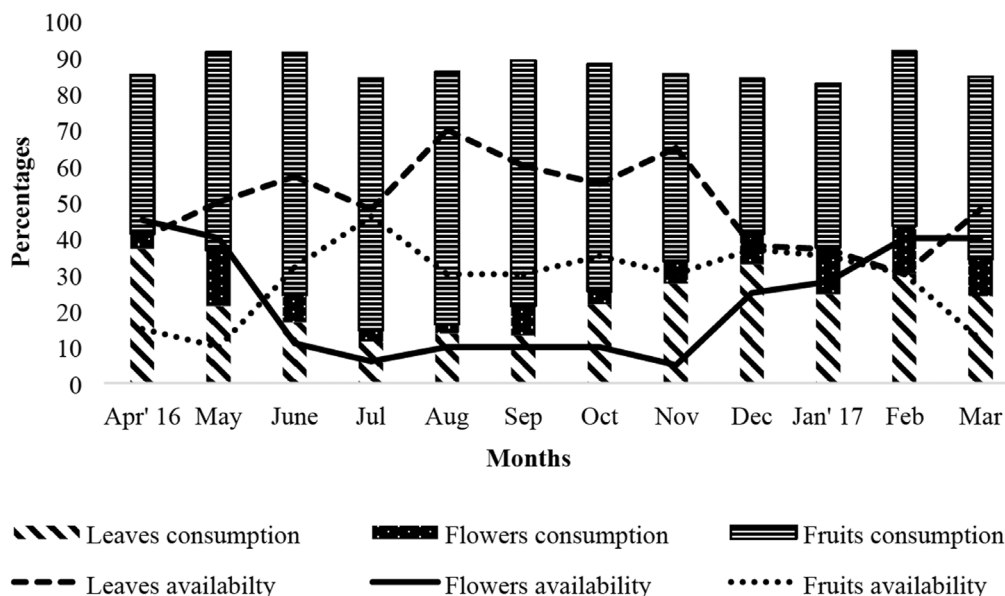


Figure 2. Monthly dietary percentage on food items and plant productivity in the study area.

the leaves, but more or less flowers were found in different plants all year round in patchy areas of the forest. The number of plants flowering peaked in April (40%, summer season) and was lowest in November (5%, early winter). Fruits were available in moderate quantities during the entire study period, but fruit production was particularly high in July (46%, early rainy season) and lowest in March (10%, beginning the summer) (Fig. 2).

Diet in response to seasonal variation

Food choice varied in response to seasonal shifts of food availability in the gibbons' home range. Fruit feeding was highest during the rainy season (60.1%) when fruits were relatively abundant, and somewhat reduced in early winter (56.0%) through to late summer. Overall, leaf consumption was low year-round, but higher in winter (23.9%) compared to the other seasons (Table 2). In winter (November to February), the gibbons ate flowers, floral buds and nectar from epiphytes, for example, *Acampe praemorsa*, and vines, for example, *Thunbergia grandifolia*, palms (*Caryota urens*) and syconia from immature figs. During the rainy season, they usually preferred to feed on ripe fruits and mature figs, although palm fruits were available. Shoots, bark and animal prey were consumed largely at the end of winter. The gibbons ate some flowers throughout the year but showed a gradual increase in flower-eating in summer (9.8%) when the flowers were more available (Table 2).

The extent to which the gibbons fed on different food items was variable, but the monthly variation in fruit feeding was marked ($F = 39.14$, $df = 2$, $p = 0.004$). There was a significant correlation between the percentage frequency of feeding on fruits and the percentage of trees in the quadrats bearing fruits ($r_s = 0.71$, $n = 12$, $p = 0.003$). Stepwise

regression analysis revealed a significant positive correlation between feeding and fruit availability ($r^2 = 0.726$, $n = 12$, $p = 0.001$; Table 4).

Discussion

The hoolock gibbon group we studied was comparatively less frugivorous (57% of the time spent feeding) and more folivorous than has been found in earlier studies in Bangladesh—fruits 89% (Islam and Feeroz 1992); fruits 71% (Ahsan 1994); fruits 90% (Hasan *et al.* 2005); fruits 89% (Feeroz 2011). Their fruit feeding was closer to that found, for example, by Gupta (1994) 59% in Tripura, India; Tilson (1979) 67% in Assam, India; Borah *et al.* (2018) 51% in Assam, India; and by Kim *et al.* (2010) 63% for *Hylobates moloch*, Java, Indonesia. The possibility is that tree felling has reduced the number of fruit trees in Satchari, but there is no doubt that the diet will depend on the species composition and phenological regimes of the various forests where gibbons occur.

Fig trees are an important source of food for primates in the tropical world (Reynolds and Reynolds 1965; Hladik 1968; Ripley 1970; Terborgh 1983; Kinnaird and O'Brien 2005). They are aseasonal in their fruiting, and hence play a crucial role year-round for the gibbons. The proportion of time the Satchari gibbon group spent feeding on figs was similar to the findings of previous hoolock gibbon studies in Bangladesh: 38% (Islam and Feeroz 1992); 32.6% (Ahsan 1994); 42% (Hasan *et al.* 2005); and 40.3% (Feeroz 2011).

Islam and Feeroz (1992) found that gibbons collected food from 40 plant species, and Hasan *et al.* (2005) reported 30 species at Lawachara National Park, Bangladesh. Zhou and Deng (2018) reported 133 plant species in Bawangling

National Nature Reserve, China; and Borah *et al.* (2018) reported 54 species in Northeast India. The inconsistency in the number of plant species as sources is to be expected as a result of the differing periods of study and the prevailing availability, the taste and choice preferences of the gibbons, and plant phenological cycles (Raemaekers 1977).

Primate species choose their food based on their availability in the home range (Lee and Hauser 1998). The gibbons in this study took more fruits during periods of high fruit availability (rainy season) and turned to leaves and other items during periods of low fruiting, compatible with the patterns observed elsewhere (Chivers 1974; Bricknell 1999; Ahsan 2001; McConkey *et al.* 2002, 2003; Feeroz 2011; Bach *et al.* 2017; Clink *et al.* 2017). Flowers, shoots, bark and animal prey were consumed to a large extent at the end of winter when other food items and even water were in short supply.

Ficus gibbosa was the most favored food species, ranked as 1st, providing both leaves and fruits throughout the year. The common red stem fig (*Ficus variegata*), dewa (*Artocarpus lacucha*), the palm (*Caryota urens*) and hog plum (*Spondias pinnata*) were ranked as the 2nd, 3rd, 4th and 5th most utilized species, respectively. The manifestation of five preferred food plants and 14 heavily used aseasonal fig species in their diet supports the idea that gibbons are mostly dependent on these plants round the year, while diversifying their diets when seasonal fruits were available during the rainy season.

Overall, our results suggest that gibbons are selectively frugivorous when the fruits are available and tend to diversify their diet during lean periods. Although time spent feeding on fruits was predominant throughout the year, non-fruit items were found to be supplements in the winter when fruits were scarce. A good understanding of the floristic composition of actual and potential gibbon habitat provides the wherewithal for understanding demographic patterns and the key features that need to be protected for the maintenance of gibbon populations, most especially in fragmented forests, and besides to estimate the suitability of forests for reintroduction programs. In this regard, we recommend long-term data collection for further research investigating the hoolock gibbons' feeding selectivity and the effect of logging and forest degradation on their food resources.

Acknowledgments

We thank the Department of Zoology, Jagannath University, Dhaka, for giving us the opportunity to conduct this research. The Bangladesh Forest Department kindly granted the research permits. We are most grateful to our field assistants for their invaluable support during data collection. The authors thank Dr Anthony B. Rylands for his valuable comments on this paper. The study was supported by a National Science and Technology Fellowship, an Explorer Club Youth Activity Fund grant, and Idea Wild.

Literature Cited

- Ahsan, M. F. 1984. Study of Primates in Bangladesh: Determination of Population Status and Distribution of Non-human Primates in Bangladesh with Emphasis on Rhesus monkey. MPhil thesis, Department of Zoology, University of Dhaka, Dhaka.
- Ahsan, M. F. 1994. Behavioural Ecology of the Hoolock Gibbon in Bangladesh. PhD thesis, University of Cambridge, Cambridge, UK.
- Ahsan, M. F. 2001. Socio-ecology of the hoolock gibbon (*Hylobates hoolock*) in two forests of Bangladesh. In *The Apes: Challenges for the 21st Century: Conference Proceedings, May 10–13, 2000*, Brookfield Zoo (compiler), pp.286–299. Brookfield Zoo, Brookfield, IL.
- Akers, A. A., M. A. Islam and V. Nijman. 2013. Habitat characterization of western hoolock gibbons *Hoolock hoolock* by examining home range microhabitat use. *Primates* 54: 341–348.
- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49: 227–267.
- Arefin, K. M., M. M. Rahman, M. Z. Uddin and M. A. Hasan. 2011. Angiosperm flora of Satchari National Park, Habiganj, Bangladesh. *Bangladesh J. Plant Taxon.* 18: 117–140.
- Bach, T. H., J. Chen, M. D. Hoang, K. C. Beng and V. T. Nguyen. 2017. Feeding behaviour and activity budget of the southern yellow-cheeked crested gibbons (*Nomascus gabriellae*) in a lowland tropical forest. *Am. J. Primatol.* 79: 1–14.
- Borah, M., A. Devi and A. Kumar. 2018. Diet and feeding ecology of the western hoolock gibbon (*Hoolock hoolock*) in a tropical forest fragment of Northeast India. *Primates* 59: 32–44.
- Bricknell, S. 1999. Hybridisation and Behavioral Variation: A Socio-Ecological Study of Hybrid Gibbons (*Hylobates agilis* × *H. muelleri*) in Central Kalimantan, Indonesia. PhD thesis, Australian National University, Canberra.
- Chapman, C. A., V. A. M. Schoof, T. R. Bonnell, J. F. Gogarten and S. Calme. 2015. Competing pressures on populations: long term dynamics of food availability, food quality, disease, stress and animal abundance. *Phil. Trans. R. Soc. B.* 370: 20140112. doi.org/10.1098/rstb.2014.0112.
- Clink, D. J., C. Dillis, K. L. Feilen, L. Beaudrot and A. J. Marshall. 2017. Dietary diversity, feeding selectivity, and responses to fruit scarcity of two sympatric Bornean primates (*Hylobates albibarbis* and *Presbytis rubicunda rubida*). *PLoS ONE* 12(3): e0173369. doi:10.1371/journal.pone.0173369.
- Chivers, D. J. 1974. The siamang in Malaya: a field study of a primate in tropical rain forest. *Contrib. Primatol.* 4: 1–335.
- Feeroz, M. M. 1998. Ecology and Behaviour of Pig-tailed Macaque (*Macaca nemestrina*) in Bangladesh. PhD thesis, University of Cambridge, Cambridge, UK.

- Feeroz, M. M. 2011. Resource partitioning among the sympatric primate species of West Bhanugach Forest Reserve of Bangladesh. In: *Proceedings of the International Conference on Biodiversity – Present State, Problems and Prospects of its Conservation, University of Chittagong, Chittagong, Bangladesh, 8–10 January, 2011*, E. Røskaft and D. J. Chivers (eds.), pp.33–43. Norwegian University of Science and Technology (NTNU) Trondheim, Norway.
- Gupta, A. K. 1994. Status and conservation of non-human primates in Tripura, India. In: *Current Primatology: Ecology and Evolution*, B. Thierry, J. R. Anderson, J. J. Roeder and N. Herrenschmidt (eds.), pp.101–111. University of Louis Pasteur, Strasbourg, France.
- Harrison, M. E. and A. J. Marshall. 2011. Strategies for the use of fallback foods in apes. *Int. J. Primatol.* 32: 531–565.
- Hasan, M. A. U., S. A. Neha and M. H. Mineuddin. 2018a. New locality records of the crab-eating mongoose *Urva urva* in Satchari National Park, Sylhet, Bangladesh. *Small Carniv. Conserv.* 56: 26–30.
- Hasan, M. A. U., S. A. Neha, M. A. Baki and M. Q. Babu. 2018b. An inventory of butterfly species in relation to food sources and climatic factors influencing their diversity and richness in a semi-evergreen forest of Bangladesh. *Arthropods* 7(3): 53–68.
- Hasan, M. A. U., M. U. H. Khatun and S. A. Neha. 2018c. Group size, composition and conservation challenges of capped langur (*Trachypithecus pileatus*) in Satchari National Park, Bangladesh. *Jagannath Univ. J. Life Earth Sci.* 4(2): 135–153.
- Hasan, M. K., M. M. Feeroz, M. A. Islam, M. M. Kabir, S. Begum, M. A. Aziz and G. C. Sarker. 2005. Food and feeding behavior of hoolock gibbon (*Bunopithecus Hoolock hoolock*) in a semi-evergreen forest of Bangladesh. *Bangladesh J. Life Sci.* 17(1): 43–49.
- Hasan, M. K. and M. M. Feeroz. 2011. Space sharing by Hoolock Gibbons (*Hoolock hoolock*) in Lawachara National Park, Bangladesh. In: *Proceedings of the International Conference on Biodiversity – Present State, Problems and Prospects of its Conservation, University of Chittagong, Chittagong, Bangladesh, 8–10 January, 2011*, E. Røskaft and D. J. Chivers (eds.), pp.44–48. Norwegian University of Science and Technology (NTNU), Trondheim, Norway.
- Hladik, C. M. 1968. Recherché des caractéristiques histo-chimiques et cytologiques de la muqueuse intestinale des primates et des corrélations avec le régime alimentaire. *Mém. Mus. Natl. Hist. Nat.* 52: 1–69.
- Islam, M. A. and M. M. Feeroz. 1992. *Ecology and Behavior of Hoolock Gibbons of Bangladesh*. MARC (Multidisciplinary Action Research Centre), Dhaka, Bangladesh.
- Islam, M. A., M. M. Feeroz, S. B. Muzaffar, M. Kabir, S. Begum, K. Hasan, S. Mahmud and S. Chakma. 2008. Population status and conservation of hoolock gibbons in Bangladesh. *J. Bombay Nat. Hist. Soc.* 105: 19–23.
- Islam, M. A., S. B. Muzaffar, M. M. Feeroz, M. M. Kabir, S. Begum, G. W. Chowdhury, M. A. Aziz, S. Chakma and I. Jahan. 2011. Hoolock gibbon conservation in Bangladesh. *Gibbon J.* 6: 13–17.
- Kim, S., S. Lappan and J. C. Choe. 2010. Diet and ranging behavior of the endangered Javan gibbon (*Hylobates moloch*) in a submontane tropical rainforest. *Am. J. Primatol.* 73: 270–280.
- Kinnaird, M. F. and T. O'Brien. 2005. Fast foods of the forest: the influence of figs on primates and hornbills across Wallace's Line. In: *Tropical Fruits and Frugivores: The Search for Strong Interactors*, J. L. Dew and J. P. Boubli (eds.), pp.155–184. Springer, The Netherlands.
- Lee, P. C. and M. D. Hauser. 1998. Long-term consequences of changes in territory quality of feeding and reproductive strategy of vervet monkey. *J. Anim. Ecol.* 67: 347–358.
- Marshall, A. J. and M. Leighton. 2006. How does food availability limit the population density of white-bearded gibbons? In: *Feeding Ecology of the Apes and Other Primates*, G. Hohmann, M. M. Robbins and C. Boesch (eds.), pp.311–333. Cambridge University Press, Cambridge, UK.
- McConkey, K. R., F. Aldy, A. Ario and D. J. Chivers. 2002. Selection of fruit by gibbons (*Hylobates muelleri* × *agilis*) in the rain forests of central Borneo. *Int. J. Primatol.* 23: 123–145.
- McConkey, K. R., F. Aldy, A. Ario and D. J. Chivers. 2003. Influence of forest seasonality on gibbon food choice in the rain forests of Barito Ulu, Central Kalimantan. *Int. J. Primatol.* 24(1): 19–32.
- Mootnick, A. R., E. H. Haimoff and K. Nyunt-Lwin. 1987. Conservation and captive management of hoolock gibbons in the Social Republic of the Union of Burma. *AAZPA Annual Conference Proceedings, Portland, Oregon*. American Association of Zoological Parks and Aquariums (AAZPA), Wheeling, WV.
- Mukherjee, R. P. 1986. Ecology of the hoolock gibbon, *Hylobates hoolock*, in Tripura, India. In: *Primate Conservation*, J. G. Else and P. C. Lee (eds.), pp.115–123. Cambridge University Press, Cambridge, UK.
- Mukul, S. A., M. B. Uddin and M. R. Tito. 2007. Medicinal plant diversity and local healthcare among the people living in and around a conservation area of northern Bangladesh. *Int. J. For. Usuf. Mngt.* 8(2): 50–63.
- Muzaffar, S. B., M. A. Islam, M. M. Feeroz, M. Kabir, S. Begum, M. S. Mahmud, S. Chakma and M. K. Hasan. 2007. Habitat characteristics of the endangered hoolock gibbons of Bangladesh: the role of plant species richness. *Biotropica* 39: 539–545.
- Pasha, K. M. and S. B. Uddin. 2013. *Dictionary of Plant Names of Bangladesh (Vascular Plants)*. Janokalyan Prokashani, Chittagong, Bangladesh.
- Raemaekers, J. J. 1977. Gibbons and Trees: Ecology of the Siamang and Lar Gibbons. PhD thesis, University of Cambridge, Cambridge, UK.

- Reynolds, V. and F. Reynolds. 1965. Chimpanzees of the Budongo forest. In: *Primate Behavior: Field Studies of Monkeys and Apes*, I. DeVore (eds.), pp.368–424. Holt, Rinehart and Winston, New York,
- Ripley, S. 1970. Leaves and leaf-monkeys: the social organization of foraging in grey langurs, *Presbytis entellus thersites*. In: *Old World Monkeys: Evolution, Systematics and Behavior*, J. R. Napier and P. H. Napier (eds.), pp.481–509. Academic Press, London.
- Robbins, M. M. and G. Hohmann. 2006. Primate feeding ecology: an integrative approach. In: *Feeding Ecology in Apes and Other Primates: Ecological, Physical, and Behavioral Aspects*, G. Hohmann, M. M. Robbins and C. Boesch (eds.), pp.1–13. Cambridge University Press, Cambridge, UK.
- Sharma, R. 2006. Management Plan for Satchari National Park. Nishorgo. Support Project. Report. Forest Department, Government of the People's Republic of Bangladesh.
- Tan, B. 1985. The status of primates in China. *Primate Conserv.* (5): 63–81.
- Terborgh, J. 1983. *Five New World Primates: A Study in Comparative Ecology*. Princeton University Press, Princeton, NJ.
- Tilson, R. L. 1979. On the behavior of the hoolock gibbons (*Hylobates hoolock*) during different seasons in Assam, India. *J. Bombay Nat. Hist. Soc.* 76: 1–16.
- Uddin, M. B., M. J. Steinbauer, A. Jentsch, S. A. Mukul and C. Beierkuhnlein. 2013. Do environmental attributes, disturbances and protection regimes determine the distribution of exotic plant species in Bangladesh forest ecosystem? *For. Ecol. Manag.* 303: 72-80.
- van Schaik, C. P., J. W. Terborgh and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Ann. Rev. Ecol. Evol. Syst.* 24: 353–377.
- Zhou, J. and H. Deng. 2018. Thirteen years observation on diet composition of Hainan gibbon (*Nomascus hainanus*). *North-West J. Zool.* 14(2): 213–219.

Authors' address:

Sufia Akter Neha, Mst. Ummay Habiba Khatun and Md Ashraf Ul Hasan, Department of Zoology, Jagannath University, Dhaka 1100, Bangladesh. *Corresponding author:* Sufia Akter Neha, e-mail: <neha.jnu463@gmail.com>.

Received for publication: 19 April 2020

Revised: 9 May 2020