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Influence of Fruit Availability on Fruit Consumption in a Generalist Primate, the Rhesus Macaque *Macaca mulatta*

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Abstract Fluctuations in resource availability occur in all ecosystems. To survive, species must alter their foraging strategies according to the quantity, quality, and distribution of available food. The rhesus macaque (*Macaca mulatta*), a commensal primate, is considered a generalist omnivore and very few studies have addressed how its feeding strategies change with respect to resource availability. We examined dietary diversity and frugivory levels in a group of rhesus macaques at the Buxa Tiger Reserve in northern India across one year. Using behavioural observations of diet and phenological monitoring, we found that although rhesus macaques fed on 107 food items including leaves, flowers, fruits, seeds, and insects, fruits made up *ca*. 74% of their diet. Fruit consumption correlated positively with fruit availability, but fruit preference appeared to play an important role; 16% of all the fruit species they fed on accounted for >50% of all fruit feeding observations. We suggest that afforestation programs involving preferred fruit species at the agricultural land–forest interface would prevent forest groups of rhesus macaques from gravitating toward human habitations and reduce conflict over anthropogenic resources. We further propose that the movement of certain primates in the direction of human habitations may be contingent on resource availability and food preference rather than an inherent propensity to gravitate to anthropogenic areas.

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Introduction

The quantity and quality of food available across habitats is one of the principal drivers of primate distribution and abundance (Bracebridge *et al.* 2012; Brugiere *et al.* 2002; O'Driscoll-Worman and Chapman 2006). The feeding ecology of primates is thus central to an understanding of primate population dynamics and socio-ecology (Marshall *et al.* 2009; Robbins and Hohmann 2006). Resource availability varies in natural ecosystems and the existence of distinct dry and wet seasons regulates the availability of plant parts such as immature leaves, flowers, fruits, and seeds, thereby inducing periods of food abundance as well as those of scarcity (Brugiere *et al.* 2002; Janson and Chapman 1999; van Schaik *et al.* 1993). Depending on varying resource availability, species change their foraging strategies to survive (Felton *et al.* 2008; van Schaik *et al.* 1993). In times of resource scarcity, primates may increase foraging effort and home range sizes to locate specific food items such as fruits (Krishnadas *et al.* 2011; Mourthé 2014; Wallace 2005). Alternatively, they may depend on "fallback foods," i.e., foods of comparatively low quality that are available all the year round but are fed on only in times of food scarcity (Marshall *et al.* 2009).

Researchers have studied dietary modifications in response to resource fluctuations in primate frugivores such as spider monkeys (*Ateles*: Terborgh 1983; Wallace 2005), folivores such as colobus monkeys (*Colobus*: Bocian 1997; Oates 1977), and seed eaters such as uakaris (*Cacajao*: Bowler and Bodmer 2011). Frugivores are generally known to fall back on figs as well as leaves, flowers, unripe fruits, and seeds in times of fruit scarcity (Terborgh 1983; Wallace 2005). Folivores feed on fruits and seeds when the availability of young leaves is low (Bocian 1997; Oates 1977) and some seed-eating primates shift to fruit pulp, leaves, insects, and flowers when seeds are scarce (Boubli 1999; Cunningham and Janson 2006).

Several studies have investigated the feeding ecology of various omnivorous primates such as baboons (*Papio*) and macaques (*Macaca*) (Altmann 1998; Codron *et al.* 2006; Hill and Dunbar 2002; Kunz and Linsenmair 2008; Swedell *et al.* 2008; Tang *et al.* 2016; Zhou *et al.* 2014). Little, however, is known about food preference in omnivorous primates, which are known to include a wide range of foods in their diets such as fruits, seeds, flowers, leaves, buds, shoots, twigs, stems, roots, bark, pith, and resin of a large number of plant species, as well as fungi, various invertebrates, fish, bird eggs, and honey combs (Fooden 2000). Preferred foods form a subset of all the food items consumed and such preference is determined by taking into account consumption of foods with respect to their availability (*sensu* Russo *et al.* 2005; Stevenson and Link 2010).

The rhesus macaque (*Macaca mulatta*) has the widest geographic distribution among nonhuman primates (primates henceforth) and can adapt to a range of habitats including temperate coniferous forests, moist and dry deciduous forests, bamboo thickets, mixed forests, mangroves, scrub vegetation, rainforests, and areas in and around human settlements (IUCN 2016; Srivastava and Mohnot 2001). The rhesus macaque also forages on crops in many parts of their geographic range (Radhakrishna and Sinha 2011). The feeding ecology of rhesus macaques has been studied mostly in commensal populations (Goldstein and Richard 1989; Lindburg 1977); in contrast, the number of studies addressing the diet of completely wild rhesus macaques is much smaller. Largely described as a generalist omnivore (Clymer 2006; Johnson 2000; Zhou *et al.* 2014), rhesus macaque diet may vary strongly across different habitats (Tang *et al.* 2016). For example, in the temperate forests of northwestern Pakistan, and in the limestone forests of China, rhesus macaques are mostly folivorous, whereas in tropical forests, they are generally frugivorous (Goldstein and Richard 1989; Lindburg 1977; Tang *et al.* 2016). Studies of rhesus macaque feeding ecology also report extremely variable levels of frugivory: from 6.2% in China (Zhou *et al.* 2009) to 70% in Uttar Pradesh, India (Lindburg 1977).

Our previous studies at the Buxa Tiger Reserve, West Bengal, India, revealed that a group of rhesus macaques in the Checko Block of the Reserve were completely dependent on natural resources and that an unusually high percentage of their diet (79%) was accounted for by fruits and seeds (Sengupta *et al.* 2014). These findings led us to investigate how rhesus macaques adapt to changing fruit availability at the study site. More specifically, we addressed the following questions: 1) How does fruit consumption in rhesus macaques vary with changing fruit availability? 2) How does dietary fruit diversity vary with respect to fruit availability? We predicted that the percentage of fruit included in the diet of the rhesus macaques as well as the dietary fruit diversity would increase with increasing fruit availability, given the dietary flexibility of the species.

Methods

Study Area

We carried out the study at the Buxa Tiger Reserve (BTR, 26°30′–23°50′N, 89°25′–89°55′E) located at the foothills of the Eastern Himalayas (see Sengupta *et al.* 2014 for map) from July 2012 to June 2013. Located in the Alipurduar district, West Bengal, India, BTR is adjacent to the Phibsoo Wildlife Sanctuary in Bhutan, Manas National Park, and Jaldapara Wildlife Sanctuary to its north, east, and west. BTR has a core and a buffer zone spanning 385 and 376 km^2 respectively (Sukumar *et al.* 2003). The northern tracts are hilly; the elevation ranges from 60 to 1750 m, and the mean annual rainfall is 4100 mm with temperatures ranging between 12 and 32 °C. A larger portion of the reserve lies within the plains (Sukumar *et al.* 2003). Tropical moist deciduous forest is the main forest type alongside regions of evergreen, semievergreen, scrub and riverine forests, grasslands, and plantations (Sivakumar *et al.* 2006). We collected rainfall data between July 2012 and June 2013, from the Rajabhat Tea Estate located in the vicinity of the Reserve. The wet season (rainfall >100 mm, following Bracebridge *et al.* 2012) lasted from April to October while November to March constituted the dry season (rainfall <100 mm). Rainfall peaked in July 2012 (1245 mm) while there was no rainfall between November 2012 and January 2013. The mean monthly rainfall during the wet season was 622.9 mm (SD ± 350.3 mm) while that during the dry season was 5.2 mm (SD ± 6.5 mm).

We followed and observed a group of rhesus macaques in the Checko Block within the buffer zone of BTR. The group comprised 41 individuals (9 adult males, 11 adult females, 9 juvenile males, 10 juvenile females, and 2 infants; age classes assigned in accordance with National Research Council 1981) and was nonprovisioned and solely dependent on natural resources. The group had a home range of 45 ha (range: 25.5–70 ha, based on monthly means over the year; $N = 12$ months). This site was a mosaic of natural forest and mixed-species plantation and the dominant species were *Terminalia chebula*, *Terminalia belerica*, *Terminalia crenulata*, *Terminalia myriocarpa*, *Tectona grandis*, *Shorea robusta*, *Lagerstroemia speciosa*, *Gmelina arborea*, *Syzygium cumini*, and *Michelia champaca*.

Fruit Availability

We assessed fruit availability along seven transects in the home range of the study group. Three of the transects were oriented in the north–south direction (one of them 1 km long, the remaining 500 m each) and four were oriented in the east–west direction (each 500 m in length). The width of each transect was 20 m, and together the seven transects covered 18% of the home range area. We tagged all trees with diameter at breast height (DBH) ≥10 cm and lianas present on trees along the transects. We conducted measurements on 2439 trees (of which 134 were lianas) belonging to 107 species (of which nine were lianas). We calculated the basal area of a tree (B) with the following formula:

$$B = (0.5 * \mathrm{DBH})^2 * \pi$$

Once a month across the year, we visually estimated the percentage of crown area covered by fruit of all the trees marked in the transect, and on that basis, we ranked trees on a 5-point scale where a score of 0 implied no fruit and 1, 2, 3, and 4 implied 1–25%, 26–50%, 51–75%, and ≥ 76% of the crown area covered by fruit respectively (Albert *et al.* 2013). We calculated indices to quantify overall fruit availability (FAI) and dietary fruit availability (DFAI; Table I).

Dietary Observations

We followed the macaques for 10 days every month from their waking sites to the sleeping trees and collected data from 06:00 to 18:00 h. We used scan sampling at intervals of 30 min (Altmann 1974; Giraldo *et al.* 2007; Robinson 1986) and in each sample, we scanned the group for 15 min and noted the following activities: moving, resting, social interactions, and feeding. We included all male and female adult and juvenile individuals in scans. When we observed a macaque feeding (defined as the actual manipulation or intake of food items, as per Menon and Poirier 1996), we noted the *food species* as well as the *food class* (fruit, seed, leaf, flower of plant species, insects) fed on. We defined a *food item* as *food species* × *food class*, calculated time spent feeding on each food item from scan data as a proportion of all feeding observations and summarized this as monthly percentages (Bracebridge *et al.* 2012). When we observed the macaques feeding on fruits, we used focal sampling for up to 30 min or until the macaques stopped feeding on fruits on randomly chosen adult individuals to understand which parts of the fruit they fed on (whole fruit, only pulp,

Table I Indices used in this study of the influence of fruit availability on fruit consumption in rhesus macaques in Buxa Tiger Reserve, India

Name of index	Abbreviation	Metric	What it measures	Mean (±SD); $N = 12$ months	Range
Fruit Availability Index (Albert *et al*. 2013; Chapman *et al*. 1992)	FAI	$FAI = \sum_{i=1}^{n} D_i B_i P_{im}$ D_i = mean density of species i in the home range B_i = mean basal area of trees of species i (cm^2) P_{im} = mean phenology score of fruit in species i in month m, n = number of species in the phenology transects	Overall fruit availability in the phenology transects	470,001 (±443,939)	99,765–1,266,063
Dietary Fruit Availability Index	DFAI	Same as above but only considering species included in the diet	Fruit availability of species included in the diet	238,959 (±256,398)	28,898–629,858
Dietary Diversity Index	h'	$h' = -\sum_{i=1}^{S} p_i \ln p_i$ s = number of food classes in the diet of the macaques p_i = proportion of total number of food classes represented by class i in a particular month	Diversity of food classes included in the diet	0.84 (±0.25)	0.48–1.15
Dietary Evenness Index	e'	$e' = \frac{h'}{\ln(s)}$	How evenly the feeding observations are distributed over the different food classes	0.55 (±0.12)	0.37–0.71
Dietary Fruit Diversity Index	Fruit h'	Same as that for h'; s = number of fruit species in the diet of the macaques p_i = proportion of total number of fruit species represented by fruit species i in a particular month	Diversity of fruit species included in the diet	2.07 (±0.19)	1.72–2.44
Dietary Fruit Evenness Index	Fruit e'	$\text{Fruit}\, e' = \frac{\text{Fruit}\, h'}{\ln(s)}$ s = number of fruit species in the diet of the macaques	How evenly the fruit feeding observations are distributed over the different fruit species	0.85 (±0.12)	0.67–0.99
Effective Number of Species	ENS	$\text{ENS} = \exp\left(\text{Fruit}\, h'\right)$	For a given Fruit h', ENS is the number of fruit species that, when included in the diet equally, would generate the same value of Fruit h'	8.08 (±1.44)	6–11

only seed). We also studied the remnants of fruits/seeds beneath the feeding trees to confirm the exact part consumed and collected fresh fecal samples to check the number and status (intact/crunched) of seeds within. When macaques crunched seeds or consumed unripe fruits, we considered those plant species to be specifically targeted for seeds; we considered the remaining species to be targeted for fruit pulp.

We calculated dietary diversity (h') and evenness indices (e') (Table I). We additionally calculated diversity of fruit in the rhesus macaque diet (dietary fruit diversity index, Fruit h') taking into account number of fruit species consumed as well as their evenness index (Fruit e'). From Fruit h', we also calculated the Effective Number of Species (ENS; Table I).

Statistical Analyses

We used Spearman's rank correlation coefficients (Zar 2010) to understand the relationships between FAI and 1) the percentage of diet constituted by each of the food classes, 2) h', and 3) e' ($a = 0.05$). We used the same statistical measure to assess the relationship between DFAI and 1) Fruit h', (ii) Fruit e', and 3) ENS. We conducted all the analyses using R version 3.2.0 (R Core Team 2015).

Results

Fruit Availability and Dietary Fruit Availability Indices

The mean FAI was 470,001 (± SD 443,939, $N = 12$ months) and ranged from 99,765 in April to 1,266,063 in June (Tables I and II). The DFAI ranged between 28,898 (December) to 629,858 (June; mean = 238,959 ± SD 256,398, $N = 12$ months, Tables I and II).

Dietary Observations

We collected 2865 scans (amounting to 716.25 observation hours) and 600 focal animal protocols (amounting to 300 observation hours) of macaque feeding behavior. We collected data on 26 (mean ± SD 4) individuals (range: 20–39 individuals) in each scan, which included adult males (mean = 6 ± SD 2, range: 5–9), adult females (mean = 8 ± SD 3, range: 6–11), juvenile males (mean = 6 ± SD 2, range: 4–9), and juvenile females (mean = 6 ± SD 3, range: 5–10). Individuals spent 58% of their active time feeding. Macaques fed on 107 food items, including leaves, flowers, fruits, and seeds of 77 species, insects, and fungi (since fungi accounted for just 0.1% of the diet, we excluded it from the rest of the analysis; Fig. 1 and Electronic Supplementary Material [ESM] Table SI). They consumed fruits, leaves, flowers, and seeds of 72% of the species present in the phenology transects ($N = 107$ tree species in the phenology transects). Fruits comprised 73.6% of the diet with leaves, flowers, seeds, and insects accounting for 12.5, 5.8, 5.7, and 2.4% of the diet respectively ($N = 1667$ dietary scans).

The dietary diversity index (h') ranged between 0.48 in June and 1.15 in November (mean = 0.84 ± SD 0.25, $N = 12$ months; Tables I and II) and negatively correlated with Fruit Availability Index (FAI; $r = -0.94$, $P < 0.001$; Fig. 2, Table III). The dietary

Table II Fruit Availability Index (FAI) and Dietary Fruit Availability Index (DFAI) at Buxa Tiger Reserve; Dietary Diversity Index (*h*′), Dietary Evenness Index (*e*′), Dietary Fruit Diversity Index (Fruit *h*′), Dietary Fruit Evenness Index (Fruit *e*′) of rhesus macaques; Actual Number of Species consumed (ANS) and Effective Number of Species (ENS) consumed by rhesus macaques in Buxa Tiger Reserve, India, between July 2012 and June 2013

Month	FAI	DFAI	*h*′	*e*′	Fruit *h*′	Fruit *e*′	ANS	ENS
July	1,007,661	589,791	0.53	0.38	2.21	0.73	21	9
August	824,089	510,194	0.52	0.37	1.95	0.67	18	7
September	379,016	276,554	0.80	0.58	1.72	0.72	11	6
October	142,847	50,841	1.11	0.69	2.16	0.98	9	9
November	101,315	32,115	1.15	0.71	2.12	0.96	9	8
December	129,193	28,898	0.95	0.59	2.18	0.91	11	9
January	207,293	45,169	1.03	0.64	2.07	0.86	11	8
February	194,551	44,900	1.02	0.63	1.98	0.90	9	7
March	191,479	46,809	0.96	0.59	1.78	0.99	6	6
April	99,765	52,419	0.96	0.59	2.04	0.98	8	8
May	1,096,742	559,963	0.60	0.43	2.15	0.73	19	9
June	1,266,063	629,858	0.48	0.44	2.44	0.76	25	11

evenness index (*e*′) ranged from 0.37 (August) to 0.71 (November) (mean = 0.55 ± SD 0.12, $N = 12$ months) and also had a negative correlation with FAI ($r = -0.90$, $P < 0.001$; Fig. 2, Table III). Fruit consumption ranged from 60.4% (November) to 86.3% (June) across the year (mean = 73.6%, SD = 9.06%, $N = 12$ months; Fig. 1) and increased with increasing FAI ($r = 0.94$, $P < 0.001$; Fig. 3, Table III). While consumption of leaves ($r = -0.36$, $P = 0.30$, Table III) and insects ($r = 0.25$, $P = 0.40$, Table III) did not correlate with FAI, consumption of seeds and flowers negatively correlated with FAI (seeds: $r = -0.77$, $P < 0.001$; flowers: $r = -0.69$; $P < 0.001$, Table III).

The dietary fruit diversity index (Fruit *h*′) ranged between 1.72 (September) and 2.44 (June; mean = 2.07 ± SD 0.19, $N = 12$ months; Tables I and II) and did not significantly

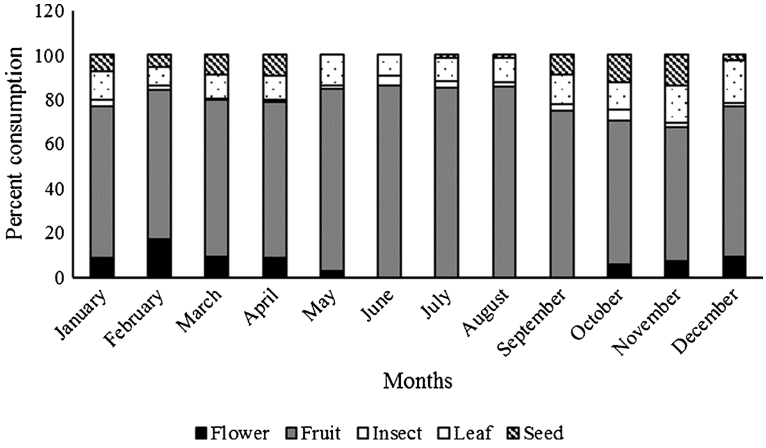

Fig. 1 Diet composition of rhesus macaques in Buxa Tiger Reserve, India, between July 2012 and June 2013.

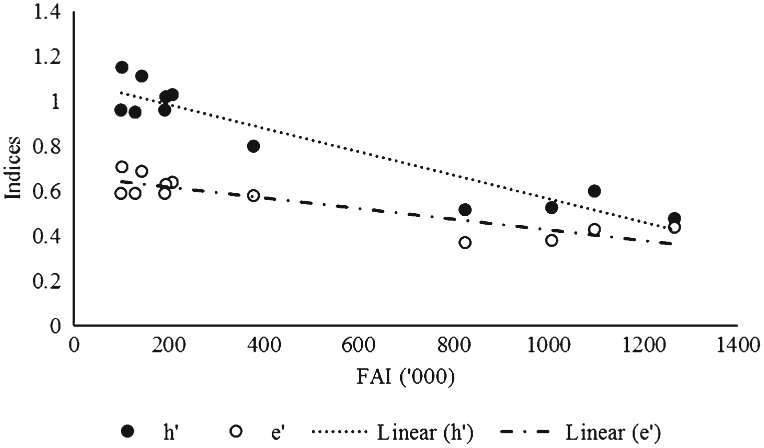

Fig. 2 Dietary diversity and evenness indices of rhesus macaques in Buxa Tiger Reserve, India, between July 2012 and June 2013.

correlate with DFAI ($r = 0.37$, $P = 0.21$, Table III). The Fruit e' ranged between 0.67 (August) and 0.99 (March; mean = 0.85 ± SD 0.12, $N = 12$ months) and had a negative correlation with DFAI ($r = -0.88$, $P < 0.001$; Fig. 4, Table III). Thus, some fruit species were consumed more irrespective of the availability of other species. Although the actual number of fruit species consumed varied from 6 to 25, the ENS consumed each month ranged from 6 (March and September) to 11 (June; Tables I and II). ENS did not significantly correlate with DFAI ($r = 0.41$, $P = 0.11$; Table III). During the entire study period, just seven species—*Artocarpus chaplasha*, *Elaeocarpus varuna*, *Premna bengalensis*, *Beilschmiedia gammaeiana*, *Ziziphus mauritiana*, *Chisocheton paniculatus*, *Anthocephalus chinensis*—accounted for 51.1% of the fruit feeding scans ($N = 1226$ fruit feeding scans; Table IV). Every month, just two to four species accounted for >50% (mean = 57.1%, SD = 3.7%, $N = 12$ months) of time spent on fruit consumption (Table IV).

Table III Correlation matrix showing relationships between FAI and 1) h', 2) e', percent consumption of 3) fruits, 4) seeds, 5) flowers, 6) leaves, 7) insects, and between DFAI and 1) Fruit h', 2) Fruit e', 3) ENS, for rhesus macaques in Buxa Tiger Reserve, India, between July 2012 and June 2013

Variables	FAI	DFAI
h'	−0.94 ($P < 0.001$)	
e'	−0.9 ($P < 0.001$)	
Fruit consumption (%)	0.94 ($P < 0.001$)	
Seed consumption (%)	−0.77 ($P < 0.001$)	
Flower consumption (%)	−0.69 ($P < 0.001$)	
Leaf consumption (%)	−0.36 ($P = 0.3$)	
Insect consumption (%)	0.25 ($P = 0.4$)	
Fruit h'		0.37 ($P = 0.21$)
Fruit e'		−0.88 ($P < 0.001$)
ENS		0.41 ($P = 0.11$)

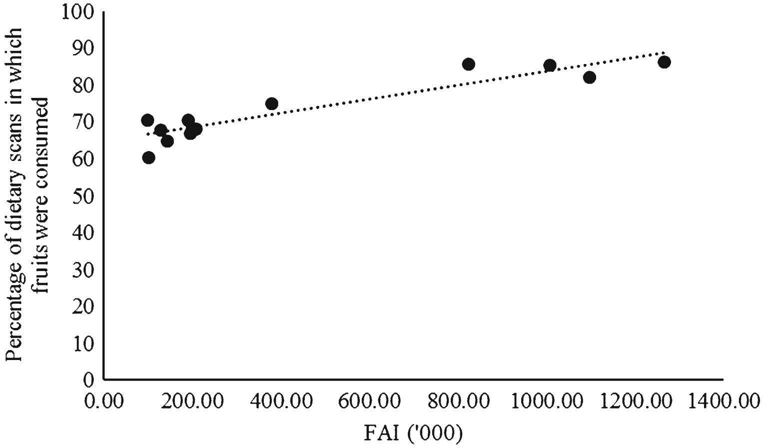

Fig. 3 Relationship between percent of diet of rhesus macaques constituted by fruits and Fruit Availability Index in Buxa Tiger Reserve, India, between July 2012 and June 2013.

Discussion

Rhesus macaques included leaves, flowers, fruits, or seeds of 77 plant species in their diet. However, fruits accounted for almost 74% of their time spent feeding, indicating that this population was primarily frugivorous. This degree of frugivory is comparable to those reported for several other macaque species such as the Tonkean macaque (*Macaca tonkeana*), southern pig-tailed macaque (*M. nemestrina*), Celebes crested macaque (*M. nigra*), Gorontalo macaque (*M. nigrescens*), Siberut macaque (*M. siberu*), northern pig-tailed macaque (*M. leonina*), lion-tailed macaque (*M. silenus*), Formosan rock macaque (*M. cyclopis*), bonnet macaque (*M. radiata*), and the long-tailed macaque (*M. fascicularis*: Richter *et al.* 2013; Tsuji *et al.* 2013). However, many studies have reported low levels of frugivory in rhesus macaques (6.2%: Zhou *et al.* 2009; 8%: Goldstein and Richard 1989; 27.3–28.7%: Tang *et al.*

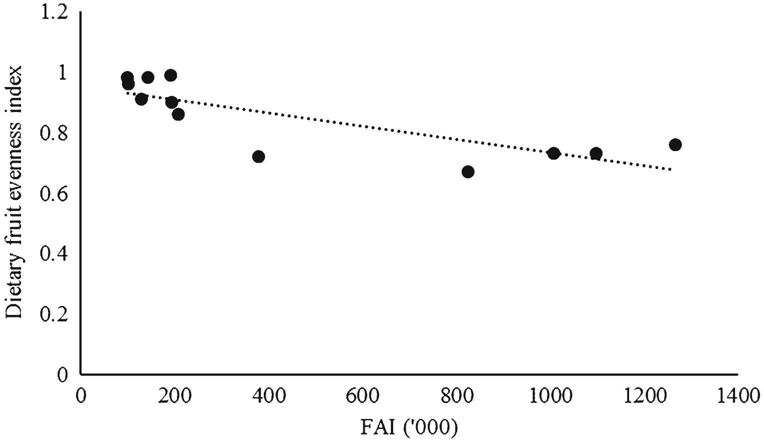

Fig. 4 Relationship between dietary fruit evenness index of rhesus macaques and Dietary Fruit Availability Index in Buxa Tiger Reserve, India, between July 2012 and June 2013.

Table IV Species accounting for >50% of total fruit consumption (percent of fruit feeding scans) in each month (%) for rhesus macaques in Buxa Tiger Reserve, India, between July 2012 and June 2013

Species	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Anthocephalus chinensis										16.7		
Artocarpus chaplasha						27.5	22.0	27.7				
Baccaurea sapida				11.2								
Beilschmiedia gammeiana	33.0	34.4	17.4									
Casearia spp.										11.1	14.3	
Chisocheton paniculatus			20.4	19.4	30.7	12.5						
Elaeocarpus varuna				11.2	17.5	13.3	17.8	23.5	39.4			
Eurya acuminata			17.4	18.4								
Polyalthia simiarum	16.0	9.7								12.2	10.7	11.7
Premna bengalensis					13.2		17.8		23.1			
Spondias mangifera										15.6	9.5	12.8
Ziziphus mauritiana	11.7	12.9									23.8	27.7
Total monthly contribution	60.7	57.0	55.2	60.2	61.4	53.3	57.6	51.2	62.5	55.6	58.3	52.2

2016). In limestone forests, young leaves seem to be their main food item (Huang *et al.* 2015; Zhou *et al.* 2009, 2011), similar to reports for the species in the temperate forests of Pakistan (Goldstein and Richard 1989). The low levels of frugivory of rhesus macaques in these habitats can also be explained by differing levels of overall fruit availability and seasonal fruit scarcity (Tang *et al.* 2016).

Fruits were the preferred foods of rhesus macaques. In this study, fruits were available throughout the year, but availability was greater in May to September. Supporting our predictions, fruit consumption by rhesus macaques at this study site positively correlated with fruit availability; contrary to our predictions though, Fruit e' negatively correlated with fruit availability. Seed consumption and flower consumption were negatively related to the availability of the preferred food class, i.e., fruit, implying that these may be fallback foods (Marshall *et al.* 2009) for rhesus macaques. However, this hypothesis needs further examination as fallback foods, by definition, are food items available throughout the year but consumed only when preferred food is scarce (Altmann 1998). We did not measure flower and seed availability throughout the year. Hence we cannot confirm that these are indeed fallback foods for rhesus macaques.

An increase in fruit consumption with higher fruit availability has been noted in other species of primates such as the black-faced black spider monkey (*Ateles chamek*: Symington 1987), variegated spider monkey (*A. hybridus*: Link *et al.* 2012), Humboldt's woolly monkey (*Lagothrix lagotricha*: Peres 1994), northern muriqui (*Brachyteles hypoxanthus*: Strier 1991), and the Japanese macaque (*Macaca fuscata*: Hanya 2004). Even during the months of low fruit availability at the study site, fruits accounted for 60.4–70.5% of the diet of rhesus macaques. This may be attributed to the lack of competition from other primate species for the same resource, as has been observed for variegated spider monkeys in Colombia (Link *et al.* 2012). However, the study site is home to a host of arboreal frugivores such as common palm civet (*Paradoxurus hermaphrodites*, which can be both arboreal and terrestrial), Malayan giant squirrel (*Ratufa bicolor*), Oriental pied hornbill (*Anthracoceros albirostris*), Alexandrine parakeet (*Psittacula eupatria*), rufous necked hornbill (*Aceros nipalensis*), great hornbill (*Buceros bicornis*), and red breasted parakeet (*Psittacula alexandri*) (Sekar and Sukumar 2013; N. P. Sharma and S. Roy *pers. comm.*). Further studies that investigate the degree of dietary overlap between rhesus macaques and any of these species would shed more light on the effects of interspecific competition on frugivory in rhesus macaques.

Our results underline the importance of food preference in the rhesus macaques, an aspect of feeding ecology that is often ignored in generalist species. An animal might feed on a particular food material not just because it is abundantly available but also because it chooses to do so (McConkey *et al.* 2002). The general notion is that omnivorous primates can be dietarily flexible and can include in their diet a vast range of food items (Milton 1987). In fact, their success as crop foragers has been attributed to the fact that they can potentially feed on any crop at any stage of its maturity (Sillero-Zubiri and Switzer 2001). We found that the dietary evenness index of rhesus macaques had a negative correlation with FAI, suggesting that when overall fruit availability increased, dietary diversity went down and the macaques ate fewer food types and thus became more selective. Also, Fruit *e′* negatively correlated with FAI. This implies that even among the fruit species that were included in the diet, some species were consumed in greater proportions than the others. For example, although the actual number of species included in the diet in June was 25, the ENS amounted to 11. Such dependence on a relatively small number of fruit species has been noted in other primates such as spider monkeys, mangabays (*Lophocebus*), kipunjis (*Rungwecebus*), gibbons (*Hylobates*), and howlers (*Alouatta*: Ahsan 1994; Bracebridge *et al.* 2012; Dew 2005; Julliot 1996; Poulsen *et al.* 2001) and questions the notion of omnivory as it is usually used. Altmann's (1998, 2009) concept of eclectic omnivory, used to describe the Amboseli baboons, rests on three central tenets: dietary preference, dietary flexibility, and dietary diversity. Our study reveals that 1) rhesus macaques consumed as many as 107 food items from 77 sources, 2) fruit consumption in rhesus macaques was driven by fruit availability, and 3) rhesus macaques exhibit preference for certain fruit species. As these findings support dietary diversity, dietary flexibility, and dietary preference in the species, we suggest that rhesus macaques may also be eclectic omnivores.

Across the year, >50% of time spent consuming fruits by rhesus macaques was accounted for by just seven species. All of these species had juicy edible tissue—the main fruit trait that rhesus macaques prefer (Sengupta and Radhakrishna 2015). Three of these species— *Elaeocarpus varuna*, *Beilschmiedia gammeiana*, and *Chisocheton paniculatus*—were characterized by all the fruit and seed traits that are preferred by rhesus macaques, i.e., external covers that can be easily pierced by a fingernail, juicy soft edible tissue, and medium to large true stone-like seeds (Sengupta and Radhakrishna 2015). Thus, the preference for these species may be explained by their traits.

Several generalist primate species such as macaques and baboons have become problem primates because they forage on crops, and a better understanding of how generalist species adapt to resource scarcity in natural ecosystems may help in devising appropriate management options to mitigate human–wildlife conflict over shared resources (Naughton-Treves *et al.* 1998; Riley *et al.* 2013). Richard *et al.* (1989) suggested that some "weed" macaques (including rhesus macaques) have a natural propensity to gravitate toward human habitations and thrive in anthropogenic areas.

However, such dependence on human-generated food resources may also be because cultivated food resources are usually high-calorie, easily digestible, have a spatiotemporally predictable distribution, and are available in greater proportions than natural resources in any given area (Saj *et al.* 1999). Indeed, many studies have reported that crop raiding occurs during periods of low food availability in the forests (Agetsuma 2007; Dove 1993; Siex and Struhsaker 1999). However, in Uganda, foraging on crops by baboons, red-tailed monkeys (*Cercopithecus ascanius*), and chimpanzees (*Pan troglodytes*) was not related to lower food availability as a whole, but to the reduced availability of a particular tree species: *Mimusops bagshawei* (Naughton-Treves *et al.* 1998).

Based on our findings, we propose that rhesus macaques' gravitation toward anthropogenic areas in many situations may be in response to lack of or decline of preferred tree species. We therefore suggest that 1) afforestation programs involving preferred tree species at the forest–agricultural land interface, may prevent infiltration of rhesus macaque groups into human-dominated areas and that 2) it is critical to ensure the natural regeneration and recruitment of these species by not disturbing forests any further. Similar measures have also been suggested to prevent Tonkean macaques from raiding cacao plantations in Indonesia (Riley *et al.* 2013). This mitigation measure has also been reported to be successful in Costa Rica, where buffer plantations of plantain restricted the movement of capuchins toward other cash crops (Baker and Shutt 2005). We further recommend long-term studies of primate diets across years and habitats to improve the understanding of the influence of spatiotemporal variation in food availability on their foraging and ranging behaviors, and consequently, on their interactions with humans.

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