Int J Primatol (2015) 36:999–1013
DOI 10.1007/s10764-015-9869-6

Fruit Trait Preference in Rhesus Macaques (*Macaca mulatta*) and its Implications for Seed Dispersal

Asmita Sengupta[1] · **Sindhu Radhakrishna**[1]

Received: 11 June 2015 / Accepted: 1 August 2015 / Published online: 15 October 2015

Abstract Primates constitute 25–40 % of the frugivore biomass of tropical forests. Primate fruit preference, as a determinant of seed dispersal, can therefore have a significant impact on these ecosystems. Although the traits of fruits included in primate diets have been described, fruit trait preference has been less studied with respect to fruit availability. We examined fruit trait preference and its implications for seed dispersal in the rhesus macaque (*Macaca mulatta*), a dietarily flexible species and important seed disperser, at the Buxa Tiger Reserve, India. Over a year, we monitored the phenology of selected trees in the study area, observed the feeding behavior of rhesus macaques using scans and focal animal sampling, and documented morphological traits of the fruits/seeds consumed. Using generalized linear modeling, we found that the kind of edible tissue was the chief determinant of fruit consumption, with *M. mulatta* feeding primarily on fruits with juicy-soft pulp and acting as seed predators for those with no discernible pulp. Overall, the preferred traits were external covers that could be easily pierced by a fingernail, medium to large seeds, true stone-like seeds, and juicy-soft edible tissue, thereby implying that fruit taxa with these traits had a higher probability of being dispersed. Macaques were more selective during the high fruit availability period than the low fruit availability period, preferentially feeding on soft-skinned fruits with juicy-soft pulp. We suggest that further studies be conducted across habitats and time to understand the consistency of interactions between primates and fruits with specific traits to

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Electronic supplementary material The online version of this article (doi:10.1007/s10764-015-9869-6) contains supplementary material, which is available to authorized users.

✉ Asmita Sengupta
asmita.sengupta@gmail.com

[1] School of Natural and Engineering Sciences, National Institute of Advanced Studies, Indian Institute of Science Campus, Bangalore 560 012, India

determine the degree of selective pressure (if any) that is exerted by primates on fruit traits.

Keywords Frugivore · Fruit Availability Index · India · Preference Index · Rhesus macaque

Introduction

A frugivore may disperse seeds of numerous plant species and seeds of a fruit-bearing plant species (fruit taxon henceforth) may be dispersed by an assemblage of frugivores. As a result, interactions between frugivores and fruit taxa are rarely tight mutualisms (Lord *et al.* 2002). Nonetheless, frugivores may exert selective pressure on fruit traits (Lord *et al.* 2002) and the latter are generally construed to be adaptations for effective seed dispersal (Horvitz *et al.* 2002). Primates act as seed dispersers for a broad range of plant species (Chapman and Russo 2007; Lambert and Chapman 2005; Lambert and Garber 1998). Because they account for as much as 25–40 % of the frugivore biomass of tropical forests (Eisenberg and Thorington 1973), primate fruit preference can have a significant impact on tropical forest dynamics through seed dispersal (Kunz and Linsenmair 2010; Lambert and Garber 1998).

The typical fruit consumed by primates is yellow or orange with a rind-like skin, sweet juicy pulp, and one or few well-protected seeds (McConkey *et al.* 2002). However, traits of fruits consumed by primates have been widely examined and descriptions of the typical primate fruit differ between studies. In South America, for example, the typical primate fruit is large, yellow, brown, or green with a woody exterior (Janson 1983) whereas in Africa, primates feed on medium-sized, dehiscent, bright red, yellow, or orange fruits with arillate seeds or drupes (Gautier-Hion *et al.* 1985). There are three reasons for such variation. First, studies consider different sets of fruit traits (Lord *et al.* 2002; Stevenson and Link, 2010). Second, different species of primates may feed on fruits with varying morphological attributes because of constraints imposed by their gape size, digestive anatomy, and differential ability to handle fruits (Ungar 1995). Third, primate fruit consumption may be a function of habitat features such as plant community composition, patch characteristics, and seasonal availability of fruits (Chapman and Russo 2007; McConkey *et al.* 2002).

Preferred taxa (or traits) form a subset of all the fruit taxa (or traits) consumed and such preference is determined by taking into account consumption of fruit taxa (or traits) with respect to their availability (Russo *et al.* 2005; Stevenson and Link 2010). Primate fruit trait preference with respect to fruit availability has been documented for frugivorous species such as *Ateles belzebuth*, *Lagothrix lagotricha*, *Pongo pygmaeus* and *Hylobates muelleri* × *agilis* (Dew 2005; Leighton 1993; McConkey *et al.* 2002; Stevenson 2004; Stevenson and Link 2010). Fruit trait preference has also been assessed for *Alouatta guariba* and *Brachyteles arachnoides,* both of which are primarily folivorous, yet may include considerable proportions of fruits in their diet depending on habitat conditions (Martins 2008; Talebi *et al.* 2005).

Little is known of fruit trait preference in dietarily flexible species that are often characterized by omnivory. A good example of such a species, the rhesus macaque

(*Macaca mulatta*), has a wide distribution spanning eastern Afghanistan, northeastern China and Indochina, Southeast Asia, and the Indian subcontinent (Seth *et al.* 2001; Southwick *et al.* 1996). The species inhabits a variety of habitats and feeds on a range of food materials such as fruits, flowers, leaves, seeds, invertebrates, and human foods (Fooden 2000; IUCN 2014). In a recent study at the Buxa Tiger Reserve, India, we found a group of rhesus macaques to be highly frugivorous, with fruits constituting as much as 79 % of their diet (Sengupta *et al.* 2014). Although the seeds of two species were dropped and those of six species destroyed, rhesus macaques spat out and swallowed 53.1 % and 20.4 % of the species included in the diet (*N* = 49 species). For four species, seeds were both swallowed and spat out. The macaques thus acted as potential seed dispersers for 41 of the 49 species they consumed (Sengupta *et al.* 2014). Following up on the results of this study, we examined fruit trait preference in the rhesus macaques. We specifically addressed the following questions: 1) What fruit taxa (and traits) are consumed by rhesus macaques and which taxa (and traits) are preferred? 2) What is the relative influence of different fruit traits on a) consumption of fruit species, b) preference for fruit species, and c) seed dispersal or seed predation?

We hypothesized that

1) *Rhesus macaques would be able to handle fruits and seeds of all sizes.* Rhesus macaques have been observed to spit out seeds >4 mm in diameter after processing the fruits in their cheek pouches and they have also been reported to carry the fruits of *Mangifera* spp. and *Artocapus* spp. in their hands for long distances (Lucas and Corlett 1998). We therefore predicted that rhesus macaques would be able to handle large seeds as well as small ones.

2) *Owing to their dexterity, rhesus macaques would be able to handle fruit taxa with high degree of external fruit protection.* In Hong Kong, rhesus macaques appear to be the only dispersers of *Garcinia oblongifolia* and *Melodinus suavolens*, both of which are protected by thick resinous epicarps that can be removed only by using both hands and teeth (Corlett 2004). Hence we predicted that rhesus macaques would preferentially feed on husked fruits or those with orange-like rinds as they would be able to remove the epicarps of such fruit taxa.

3) *Fruit taxa dispersed by rhesus macaques would have different morphological characteristics from those whose seeds are destroyed by the species.* Primates may feed on the pulp of fruits, or the seeds, and thereby act as seed dispersers or seed predators respectively. Generally, fruits consumed by primates for the pulp differ morphologically from those consumed for their seeds (Hemingway 1996; Kinzey and Norconk 1993; Ungar 1995). Based on these studies, we predicted that fruits consumed for their pulp by rhesus macaques would have juicy edible tissue whereas species whose seeds are destroyed by the macaques would have dry or fibrous edible tissue or no discernible pulp.

4) *Rhesus macaques would be more selective during high fruit availability periods*. Rhesus macaques are highly flexible in their diet and we expected that during periods of food scarcity, or low fruit availability, they would feed on whichever fruit taxa are available. However, during periods of high fruit availability, we expected to see *Macaca mulatta* exercise greater preference in fruit choice, i.e., fruits fed on during this period would be distinguished by a more specific suite of characteristics than those consumed during low fruit availability.

Methods

Study Area

We conducted the study at the Buxa Tiger Reserve (26°30′–26°50′N, 89°25′–89°55′E), a protected forest area situated in the northern part of the State of West Bengal, India (Fig. 1) from July, 2012 to June, 2013. The Reserve is contiguous with the Phibsoo Wildlife Sanctuary in Bhutan in the north, Manas National Park in the east, and Jaldapara Wildlife Sanctuary in the west and together, these forested areas cover an expanse of *ca*. 2197 km^2. Located along the foothills of the Eastern Himalayan Region, the Buxa Tiger Reserve has a core and a buffer zone spanning 385 km^2 and 376 km^2 respectively (Sukumar *et al.* 2003). Whereas the northern tracts are hilly, a larger portion of the reserve lies within the plains. The elevation ranges from 60 to 1750 m; the mean annual rainfall is 4100 mm with temperatures ranging between 12 and 32°C (Sukumar *et al.* 2003). The main forest type is tropical moist deciduous forest interspersed with evergreen, semi-evergreen, scrub, and riverine forests, grasslands, and plantations (Sivakumar *et al.* 2006).

Study Group

We selected a group of rhesus macaques located near the Checko Timber Depot (26°38′N, 89°32′E) within the buffer zone of the Buxa Tiger Reserve for our observations. The study group comprised 9 adult males, 11 adult females, 9 juvenile males, 10 juvenile females, and 2 infants ($N = 41$). The group was solely dependent on natural resources and their home range (mean: 45 ha; range: 25.5–70 ha, $N = 12$ mo; Sengupta *et al.* 2014) included patches of natural forest as well as mixed-species plantations.

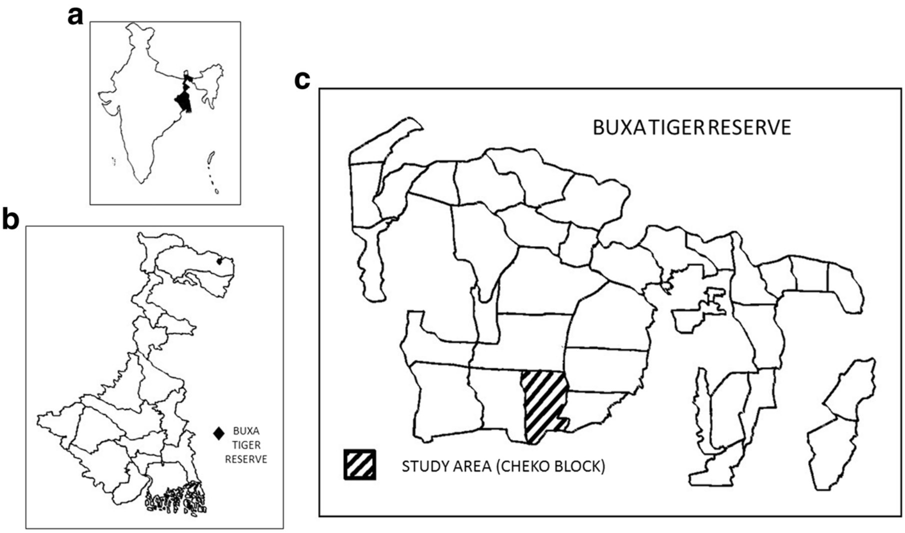

Fig. 1 Location of the study area. **(a)** Location of West Bengal in India. **(b)** Location of Buxa Tiger Reserve in West Bengal. **(c)** Map of Buxa Tiger Reserve.

Dietary Observations

From July, 2012 to June, 2013, we followed the macaques for 10 days every month from their waking sites to their sleeping trees (12 h each day). We recorded dietary activity using scan sampling with 30-min intervals (Giraldo *et al.* 2007; Robinson 1986). In each sample, we scanned the group for 15 min starting from left to right and noted the first item (parts of plant species—fruit, leaf, flower; insects; fungi) consumed by the individuals. When the macaques ate fruits, we used focal sampling for 30 min on randomly chosen individuals to understand which parts of the fruit they fed on (whole fruit, only pulp, only seed) and how the seeds were handled (swallowed alongside fruit and then defecated, spat out, destroyed).We also studied remnants of fruits/seeds beneath the feeding tree to confirm the exact part fed on and opportunistically collected fresh fecal material to record the number and status (intact/crunched) of seeds in the feces.

Fruit Availability

We assessed resource availability in the home range of the study group along seven transects. Three of these were oriented in the north–south direction (one of them 1 km long, two of 500 m each) and four were oriented east–west (each 500 m in length). Each transect was 20 m wide and together, the seven transects covered 18 % of the home range area. We marked all trees with diameter at breast height (DBH) ≥10 cm and lianas present on the trees along the seven transects. We recorded 2439 trees belonging to 107 species.

Every month, we monitored the phenological state of the trees and the lianas. Based on the percentage of crown area covered by fruit, 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 a Fruit Availability Index (FAI) for each month using the following formula

$$\mathrm{FAI} = \sum_{i=1}^{n} D_i\, B_i P_{im}$$

where D_i is the density of a particular species i in the home range, B_i is the mean basal area of trees of species i (cm^2), P_{im} is the mean phenology score of fruit in species i in a given month m, and n is the number of species considered in the study (Albert *et al.* 2013).

Fruit and Seed Traits

We collected specimens of fruits eaten by rhesus macaques and fruits of other species which were present in our phenology transects and recorded their morphological characteristics. We typically collected intact fruits that had fallen on the ground but we also collected specimens of certain species, e.g., *Syzygium formosa*, *Bridelia retusa*, directly from the trees. We selected fruits that were in the same state of ripeness in which we observed the rhesus macaques feeding on them. We recorded fruit traits of only those species for which we could collect at least 30 intact samples. In all, we observed fruit and seed traits of 80 species of which 43 species were included in the diet of the macaques. In accordance with our sample size, we considered a limited number of fruit traits, namely, kind of edible tissue, fruit protection, number of seeds, seed protection, and fruit and seed lengths (Kunz and Linsenmair 2010; McConkey *et al.* 2002). The choices of most of the variables were dictated by our predictions: fruit and seed lengths representative of fruit and seed sizes, fruit and seed protection representative of external protection, and kind of edible tissue. Alongside these, we also documented seed number as rhesus macaque preference for single or multiseeded fruits would have direct implications for the species' seed dispersal effectiveness in terms of number of seeds dispersed per visit to a tree (Schupp *et al.* 2010). Fruit and seed lengths were measured by a digital caliper (measurement accuracy: 0.01 mm).

Statistical Analyses

We calculated preference indices (S_i) for all the species that were consumed by rhesus macaques using the formula (McConkey *et al.* 2002)

$$S_i = \frac{f_i}{a_i}$$

We calculated the preference index of each species taking into account only those months of the year in which it was available. For example, if species i was in fruit during the months A, B, C, then f_i would be ratio of number of dietary scans in which the macaques fed on fruits of species i to the total number of dietary scans in which they fed on all fruits in months A, B, C and a_i would be the ratio of number of trees or lianas of taxon i that were in fruit to the total number of trees or lianas that were in fruit during these months. A preference index of >1.1 indicated that the species was preferred and we considered preference indices from 0.9 to 1.1 to be representative of neutral preference in keeping with the 95 % confidence interval of binomial proportions.

We calculated preference indices for each of the fruit traits using the same formula used for calculating preference indices for fruit taxa. Here f_i = ratio of number of dietary scans in which the macaques fed on fruits with particular trait i to the total number of dietary scans and a_i = ratio of number of trees or lianas that had fruits with trait i to the total number of trees or lianas that were in fruit during the study period (McConkey *et al.* 2002). In this case also, we considered preference indices from 0.9 to 1.1 to be representative of neutral preference and a preference index of >1.1 indicated that the trait was preferred.

We used generalized linear modeling to understand the influence of fruit or seed traits on the consumption of a fruit species by rhesus macaques (N = 80 species). For this analysis, the dependent variable was occurrence of a species in the diet (0 = not eaten, 1 = eaten) (Kunz and Linsenmair 2010) and the predictor variables were fruit length, fruit protection, kind of edible tissue, number of seeds, seed length, and seed protection. We also conducted a similar analysis to examine the influence of fruit-seed traits on species preference for the high and low fruit availability periods (N = 80 species). In this case, the preference indices of the species were the dependent variables whereas the preference indices of each of the fruit/seed traits considered in the study were the predictor variables. For all the analyses, we first checked for autocorrelation between the predictor variables, ran multiple models, and determined the best fit models using second-order Akaike's Information Criterion (AICc). Then using MuMIn on R, we averaged the best fit models to understand the influence of fruit traits on fruit consumption and fruit preference.

We initially used generalized linear modeling to determine which fruit traits predict whether the seeds of a species would be destroyed. For this analysis, the dependent variable was occurrence of seed predation for a species (0 = not predated, 1 = predated) (Kunz and Linsenmair 2010) and the predictor variables were fruit length, fruit protection, kind of edible tissue, number of seeds, seed length, and seed protection. However, when we ran the generalized linear models in R, the algorithm did not converge. Also, as long as edible tissue was a predictor variable in any model, all the models had $r = 1$ and $P < 2.26 \times 10^{-16}$. We believe this was due to the small sample size (only six of the 43 species in our dataset were subjected to predation). We therefore calculated correlation coefficients between the response variable and each of the predictor variables individually (Zar 2010).

We conducted all the analyses using R version 3.2.0 (R Core Team 2015).

Results

Fruit Availability

The Fruit Availability Index (FAI) ranged from 99,765 in April to 1,266,063 in June (mean = 470,001 ± SD 443,939, $N = 12$ mo). Based on this index, we considered May to September to be the high fruit availability period and October to April as the low fruit availability period (Fig. 2).

Dietary Observations

We collected a total of 77,355 scan records in 2865 scans (amounting to 716.25 h of observations) and 600 focal sampling records (300 h). Rhesus macaques fed on fruits

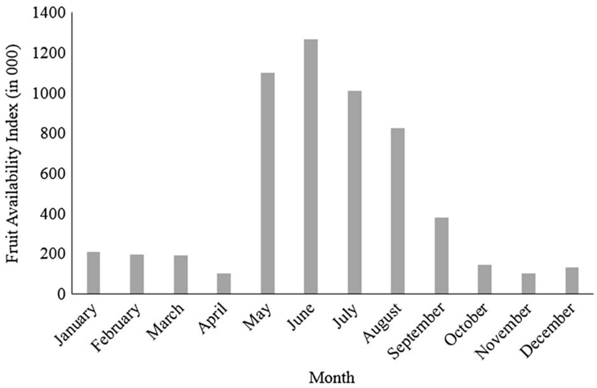

Fig. 2 Monthly variation in fruit availability at the Buxa Tiger Reserve from July 2012 to June, 2013.

(79.4 %), flowers (5.8 %), leaves (12.5 %), and insects (2.4 %) (*N* = 44,866 dietary scan records). They consumed the fruits of 49 species and fruits came from three different sources: trees (73.5 %), lianas (20.4 %), and shrubs (6.1 %) (*N* = 49 species). Fruit lengths (mean = 46.1 ± SD 84.8 mm; range: 5–500 mm; *N* = 43 fruit species), seed numbers (mean = 50.3 ± SD 94.5; range: 1–250; *N* = 43 fruit species), and seed lengths (mean = 10.4 ± SD 10.6 mm; range: 0.01–47.8 mm; *N* = 43 fruit species) varied considerably. Consumed fruit species varied in their fruit and seed protection as well as the type of edible tissue (dry fibrous, juicy soft, and juicy fibrous pulps).

Preference for Fruit Species

The mean preference index during high fruit availability was 2.3 (± SD 0.46, *N* = 5 months), with a maximum of 2.6 in June and a minimum of 1.6 in September. During low fruit availability, November had the lowest mean preference index (0.9) and January the highest (2) (mean preference index = 1.42 ± SD 0.41, *N* = 7 mo). Across the year, *Artocarpus chaplasha* (7.5) had the highest preference index whereas *Elaeocarpus floribundus* (0.1) had the lowest (Table I).

Preference for Fruit Traits

Rhesus macaques showed preference for large fruits (fruit length), rind-like skin (fruit protection), juicy soft pulp (kind of edible tissue), medium to large seeds (seed length), and seeds that were true stones (seed protection) (Table II). *Artocarpus chaplasha*, the fruit taxon with the highest preference index, was the only species included in the diet with a rind-like skin. Re-analysis of the data excluding *A. chaplasha* showed that rhesus macaques preferred fruits with skins that could be pierced by a fingernail, juicy edible tissue, medium to large seeds, and seeds that were true stones (Table II). Macaques did not feed on fruits with latex, dehiscent fruits, and those with thorny surfaces. They showed no preference for dry fibrous pulp or fruits that had no discernible pulp, fruits with >50 seeds, and small seeds and fruits that had skin that could not be easily pierced. These patterns did not vary when we carried out the analysis without *A. chaplasha* (Table II).

Influence of Fruit Traits on Inclusion of Fruit Species in Rhesus Macaque Diet, Fruit Species Preference, and Seed Predation

The average model (Table III) derived from component models (Table SI) to determine the fruit traits that influenced inclusion of fruit species in rhesus macaque diets had the following predictor variables: kind of edible tissue, fruit length, and seed protection. Of these, only the kind of edible tissue was significant, with macaques feeding on fruits with juicy soft tissue (*P* = 0.04) (Table SII).

The best fit model (derived from component models, Table SIII) to determine which traits influenced fruit preference in the high fruit availability period contained two parameters: kind of edible tissue (*P* = 0.01) and fruit protection (*P* = 0.008) (Table IV, Table SIV). Macaques preferentially fed on fruits with juicy soft edible tissue and soft-skinned species (which can be easily pierced by a fingernail).

Table I Preference indices for fruit species fed on by rhesus macaques in Buxa Tiger Reserve between July 2012 and June 2013

Species	Family	Preference index	Kind of preference
Amoora rohituka	Meliaceae	0.20	Not preferred
Anogeissus latifolia	Combretaceae	0.20	Not preferred
Anthocephalus chinensis	Rubiaceae	2.50	Preferred
Antidesma diandrum	Phyllanthaceae	2.20	Preferred
Artocarpus chaplasha	Moraceae	7.50	Preferred
Baccaurea sapida	Phyllanthaceae	3.00	Preferred
Beilschmedia gammieana	Lauraceae	4.60	Preferred
Bridelia retusa	Phyllanthaceae	1.10	Neutral
Careya arborea	Lecythidaceae	0.30	Not preferred
Casearia spp.	Salicaceae	1.90	Preferred
Chisocheton paniculatus	Meliaceae	6.00	Preferred
Cissus elongata	Vitaceae	1.10	Neutral
Crataeva unilocularis	Capparaceae	0.50	Not preferred
Dillenia indica	Dilleniaceae	0.40	Not preferred
Elaeocarpus floribundus	Elaeocarpaceae	0.10	Not preferred
Elaeocarpus varuna	Elaeocarpaceae	4.80	Preferred
Eurya acuminata	Pentaphylacaceae	1.40	Preferred
Ficus benghalensis	Moraceae	0.90	Neutral
Ficus benjamina	Moraceae	0.40	Not preferred
Ficus racemosa	Moraceae	0.30	Not preferred
Ficus spp.	Moraceae	0.80	Not preferred
Gmelina arborea	Lamiaceae	0.90	Neutral
Leea spp.	Vitaceae	0.30	Not preferred
Liana 2		0.80	Not preferred
Liana 3		0.10	Not preferred
Liana 6		0.40	Not preferred
Liana 7		0.76	Not preferred
Mangifera indica	Anacardiaceae	1.80	Preferred
Mangifera sylvatica	Anacardiaceae	1.20	Preferred
Phyllanthus emblica	Phyllanthaceae	0.88	Not preferred
Polyalthia simiarum	Annonaceae	2.00	Preferred
Premna benghalensis	Lamiaceae	2.70	Preferred
Spondias mangifera	Anacardiaceae	1.82	Preferred
Syzygium cumini	Myrtaceae	1.00	Neutral
Syzygium formosa	Myrtaceae	1.80	Preferred
Talauma hodgsonii	Magnoliaceae	0.70	Not preferred
Zanthoxylum budrunga	Rutaceae	0.60	Not preferred
Ziziphus mauritiana	Rhamnaceae	3.60	Preferred

Preference indices of 0.9 – 1.1 indicate neutral preference.

Table II Preference for different fruit trait categories in rhesus macaques in Buxa Tiger Reserve between July 2012 and June 2013

Fruit trait (Reference)	Description	Preference index including *Artocarpus chaplasha*	Preference index excuding *Artocarpus chaplasha*
Fruit length (Kunz and Linsenmair 2010)	≤10 mm	1.00	1.00
	>10 mm and ≤30 mm	0.82	0.81
	>30 mm	1.38	1.03
Fruit protection (modified from McConkey *et al.* 2002)	Can be pierced by fingernail	1.31	1.31
	Cannot easily be pierced by fingernail	0.38	0.38
	None (dehiscent fruits)	0.00	0.00
	Orange-like rind	4.53	0.89
	Thorny surface	0.00	0.00
Edible tissue (modified from McConkey *et al.* 2002)	Dry fibrous	0.29	0.29
	Juicy fibrous	1.37	1.37
	Juicy soft	2.02	1.73
	No discernible pulp	0.00	0.00
Seed length (Kunz and Linsenmair 2010)	≤5 mm	0.41	0.41
	>5 mm and <20 mm	1.30	1.30
	>>20 mm	1.50	1.50
Seed protection (modified from McConkey *et al.* 2002)	No discernible testa	0.58	0.58
	Latex	0.00	0.00
	Testa can be broken	1.08	0.68
	True stone	2.35	2.26
Seed number	1	0.98	0.98
	2–10	1.12	1.10
	11–50	1.15	0.34
	>50	0.57	0.57

The average model (derived from components models, Table SV) to determine which traits influenced fruit preference in the period of low fruit availability contained two parameters: kind of edible tissue and fruit length (Table IV). Only the kind of edible tissue was significant ($P < 0.001$) (Table SVI); during this period, macaques also preferentially fed on fruits with juicy soft edible tissue.

Table III Component models of the average model for fruit traits that influenced consumption by rhesus macaque in Buxa Tiger Reserve between July 2012 and June 2013

Predictor variables	df	Log likelihood	AICc	δ AICc	Weight
Kind of edible tissue, fruit length, seed protection	8	–30.73	79.48	0	0.67
Kind of edible tissue, seed protection	7	–32.67	80.89	1.41	0.33

Table IV Component models of the average model for fruit traits that influenced fruit preference by rhesus macaques in Buxa Tiger Reserve in high (May, 2013 to September, 2013) and low fruit availability periods (October, 2012 to April, 2013)

Period of fruit availability	Predictors	df	Log likelihood	AICc	δ AICc	Weight
High	Kind of edible tissue, fruit protection	4	–76.89	162.8	0	1
Low	Kind of edible tissue	3	–57.09	120.78	0	0.66
	Kind of edible tissue, fruit length	4	–56.52	122.07	1.29	0.34

The kind of edible tissue ($r = 0.9$, $P < 0.001$) and fruit length ($r = 0.6$, $P < 0.001$) correlated significantly with the occurrence of seed predation ($N = 43$ species), while no other fruit traits did (Table SVII). None of the fruits that rhesus macaques acted as seed predators for had any discernible pulp and four of these species were >30 mm in length.

Discussion

In the present study, rhesus macaques were able to handle fruits and seeds of all sizes, as we had predicted, but showed preference for large seed sizes. It has been suggested that in areas of tropical and subtropical Asia where deforestation is common and where the native fauna is depleted, disturbance-tolerant macaques such as *Macaca mulatta* may potentially be the only seed dispersers, especially for species with large fruits or seeds that cannot be handled by other disturbance-tolerant frugivores such as birds or bats due to their limited gape size (Albert *et al.* 2014; Lucas and Corlett 1998). Our results showed that rhesus macaques may be able to disperse many species with large seeds owing to preferential feeding on such seeds.

The kind of edible tissue was an important determinant of fruit consumption by rhesus macaques with the species mainly feeding on fruits with juicy-soft pulp. Preference for juicy-soft pulp has been reported for other primate species such as howler monkeys, guenons, and gibbons (Julliot 1996; McConkey *et al.* 2002; Sourd and Gautier-Hion 1986). Fruit trait analysis also indicated that rhesus macaques preferred fruits with rind-like skin. However, *Artocarpus chaplasha* was the only preferred fruit taxa that had this particular kind of fruit protection. *A. chaplasha* has a very short fruiting season (June–August), but the macaques fed almost exclusively on this species during this period. We contend that the high preference index of this species reflects this exclusive feeding and that the fruit traits preference results were skewed because of the presence of *A. chaplasha* in the dataset. Also, scan sampling as an observational methodology tends to overestimate conspicuous behaviours such as feeding (Gonzalez and Stevenson 2009), and because *A. chaplasha* was the largest fruit included in rhesus macaque diet, *A. chaplasha* feeding observations may have been more visible to us than feeding observations on smaller plant parts.

Our analysis excluding *Artocarpus chaplasha* from the dataset showed that macaques preferred fruits with skins that could be easily pierced by a fingernail. We thus conclude that although rhesus macaques consumed husked or protected fruits, contrary to our prediction, they preferred soft-skinned fruits. Preference for soft-skinned fruits is in contrast with other primates such as capuchins, which prefer husked fruits (Janson, 1983) but similar to gibbons (Ungar 1995). Differences in preferred traits of primates have been noted in other studies also. For example, unlike most Neotropical and Old World primates which preferentially feed on red-colored fruits, olive baboons (*Papio anubis*) feed on brown and green fruits that other cercopithecines avoid (Kunz and Linsenmair 2010). In addition to the many possible explanations for differences in fruit trait preference across studies that we reviewed earlier, chemical composition of fruits may also influence fruit preference (Leighton 1993). For example, fruit preference in baboons and some species of spider monkeys is a function of protein content (Felton *et al.* 2009; Whiten *et al.* 1991) whereas that in white-bellied spider monkeys (*Ateles belzebuth*) is dependent on lipid content (Dew 2005). Analysis of nutritional content and secondary metabolites of fruits included in rhesus macaque diet would provide a clearer understanding of the basis of fruit choice by this species (*sensu* Ungar 1995).

Inclusion of particular fruits in the diet of a primate may also be contingent on competition with other sympatric primates. For example, gibbons (*Hylobates lar*) in Ketambe, Sumatra, fed on fruits that varied in traits from gibbons (*Hylobates muelleri* × *agilis*) in Barito Ulu, Indonesia (McConkey *et al.* 2002; Ungar 1995). Such variation has been attributed in part to competition between gibbons and orangutans (*Pongo pygmaeus*) and long-tailed macaques (*Macaca fascicularis*) in Ketambe as opposed to those in Barito Ulu, where there is much lesser abundance of other frugivorous primates (McConkey *et al.* 2002). As rhesus macaques are the only primate species inhabiting Buxa Tiger Reserve, the results of our study are free of this confounding factor.

The macaques in the study group destroyed the seeds of only six species and acted as potential seed dispersers for 41 of them (Sengupta *et al.* 2014). In accordance with our prediction, species subjected to seed predation had traits distinctly different from those which were targeted for their pulp; unlike the latter, they were dry, fibrous, and had no discernible pulp. In general, the macaques showed no preference for fruits without discernible pulp. However, we suggest the use of generalized linear modeling with a larger sample size to confirm results in this respect. Macaques, as a taxonomic group, are often dismissed as effective seed dispersers primarily because they have been documented as seed destroyers (Corlett 2004; Datta and Rawat 2008; Ganesh and Davidar 2001). An interesting avenue for further research would be to examine if the fruit traits of seeds destroyed by various macaque species are similar to those seen in this study.

Comparative studies of woolly and spider monkeys have shown fruit availability is the primary determinant of diet diversity in frugivores (Peres 1994; Russo *et al.* 2005). A frugivore may consume a particular fruit in great quantities but this may be reflective of the abundance of that fruit rather than preference on the part of the frugivore (McConkey *et al.* 2002). During the high fruit availability period in our study, >70 % of the fruit species included in the diet had the preferred fruit traits —skins that could be easily pierced by fingernail and juicy soft edible tissue— whereas during the low fruit availability period, only 45 % of the consumed species had the preferred trait-juicy edible tissue. Thus, fruit availability influenced fruit preference in rhesus macaques and they used a specific suite of fruit characteristics to guide fruit consumption during the high fruit availability period. This highlights the dietary flexibility of rhesus macaques as compared to other frugivorous primates such as gibbons, which not only exercise choice when fruits are abundant but also preferentially feed on heavier fruits during periods of fruit scarcity (McConkey *et al.* 2002).

Rhesus macaques could potentially disperse a broad range of fruit species, but fruits with juicy-soft edible tissue, skins that can be easily pierced by a fingernail and medium to large seeds that are true stones have a higher probability of being dispersed. Among the preferred species, *Elaeocarpus varuna*, *Chisocheton paniculatus*, *Beilschmedia gammeiana*, *Polyalthia simiarum*, *Syzygium formosa*, *Spondias mangifera*, *Mangifera sylvatica*, and *Mangifera indica* have all these characteristics and thus, rhesus macaques may be particularly important seed dispersers for these species (these account for almost 20 % of the fruit taxa dispersed by rhesus macaques). Rhesus macaques may also be important seed dispersers for *Artocarpus chaplasha*, the species with the highest preference index; in fact, in a study conducted in the same area, rhesus macaques removed as many as 62 fruits of *A. chaplasha* from the canopy during focal tree watches (104 h), nine times as many as those removed by frugivorous birds in Buxa Tiger Reserve (Sekar 2014). Our results further suggest that dehiscent, multiseeded fruits with dry fibrous pulp have a very low probability of being dispersed by *Macaca mulatta*. Some species with these traits such as *Schima wallichii*, *Chukrasia tabularis*, *Holarrena antidysenterica*, *Albizia lucida*, *Toona ciliata*, and *Oroxylum indicum* were abundant in the study area but we never observed the macaques feeding on them. Irrespective of overall fruit availability, rhesus macaques may act as potential seed dispersers for a broad range of species as long as they have juicy soft edible pulp. As >42 % of the trees/lianas that we documented for this study had similar edible tissue, rhesus macaques may particularly be important as seed dispersers in the Buxa Tiger Reserve.

The fruit traits of a taxon will be influenced by all the frugivores it interacts with (Herrera 2002; Russo *et al.* 2005), and a single frugivore will likely exert less selective pressure on a taxon that is dispersed by a large number of frugivores as compared to taxa that are dispersed by a small number of specific frugivores. Hence further investigations into all the frugivore guilds that affect the dispersal of fruit taxa preferred by rhesus macaques would provide a more complete understanding of the importance of the rhesus macaque in influencing the fruit traits of the species it feeds on. We also suggest that studies such as the present one be conducted across years and habitats (Russo *et al.* 2005) to understand the consistency of interactions between primates and fruits with specific traits and hence to determine the degree of selective pressure (if any) exerted by the former on fruit traits.

Acknowledgments The authors thank the West Bengal Forest Department for granting necessary permits for the study. Suresh Roy and Netra Prasad Sharma provided invaluable assistance during field work and Tanumay Datta gave helpful inputs with respect to data analysis. This study was supported by the Department of Science and Technology, Government of India (contract grant number: SB/SO/AS-128/2012). The authors would also like to thank Dr. Setchell and the two anonymous reviewers for their extremely valuable inputs which helped improve the manuscript.

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