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ORIGINAL ARTICLE

The feeding ecology and dietary overlap in two sympatric primate species, the long-tailed macaque (*Macaca fascicularis*) and dusky langur (*Trachypithecus obscurus obscurus*), in Malaysia

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Abstract

Knowledge about the feeding ecology and dietary overlap of sympatric primates is essential for understanding how animals avoid or reduce interspecific competition. From April 2014 to March 2015, we investigated the feeding ecologies of two sympatric primates, a hindgut fermenter, the long-tailed macaque (*Macaca fascicularis*) and a foregut fermenter, the dusky langur (*Trachypithecus obscurus obscurus*), in a mixed landscape consisting of urban and agro-forested areas and forest fragments in Malaysia. We collected a total of 5570 and 4029 of feeding records for *M. fascicularis* and *T. o. obscurus*, respectively, using the 10-min scan sampling method. Food availability and seasonal changes in plant species consumed by both study groups were determined by vegetation surveys carried out across an area of 1.6 ha. A total of 113 and 130 plant species were consumed by *M. fascicularis* and *T. o. obscurus*, respectively. Leaves (51%) and fruits (40%) accounted for the majority of the feeding records in *T. o. obscurus*, whereas fruits (32%) and anthropogenic foods (27%) together with leaves (15%) and insects (6%) accounted for the majority of the feeding records for *M. fascicularis*. Throughout the year, there were 59 consumed plant species common to both species, and the dietary overlap was the highest for fruits. Although leaves were always more abundant than fruits in our study site, the amount of monthly fruit eating by the two species showed a significant correlation with that of fruit availability. Monthly fruit availability had a positive effect on overall monthly dietary overlap while flower and leaf availability had a negative effect. We showed that fruit was the preferred food resource of two sympatric species with different digestive systems. This could have implications for resource competition, interspecific competition, and niche separation, which should be investigated in more detail.

Keywords Long-tailed macaque · *Macaca fascicularis* · Dusky langur · *Trachypithecus obscurus obscurus* · Feeding ecology

Introduction

In both old and new-world forests, many primate species commonly occur sympatrically (Reed and Bidner 2004). An understanding of interspecific competition and niche separation is indispensable for explaining how these primates can coexist (Fleagle et al. 1999). In Southeast Asian forests,

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foregut- and hindgut-fermenting primates commonly coexist within the same habitats (e.g., MacKinnon and MacKinnon 1980; Matsuda et al. 2016; Singh et al. 2011; Ungar 1995). This may be due to the specialized stomachs of foregut fermenters (i.e., colobine monkeys), which are complex and multi-chambered, allowing them to process foods, where bacteria detoxify defensive chemicals and digest cellulose, allow them to exploit a diet of leaves in greater quantities than other sympatric hindgut-fermenting primates (Chivers 1994). However, contrary to earlier assumptions that colobines mostly exploit ubiquitous food sources such as leaves (Davies and Oates 1994; Kirkpatrick 1999), recent colobine studies have reported high levels of fruit and/or seed consumption (Koenig and Borries 2001; Vandercone et al. 2012), which may cause high interspecific competition for foods and niche overlap between foregut- and hindgut-fermenting primates. This indicates that dietary studies on coexisting primates with different physiological systems (foregut vs. hindgut fermenters) are important for further understanding the underlying mechanisms, e.g., resource competition and/or niche separation, in coexisting primates.

MacKinnon and MacKinnon (1980) focused on the effects of diet and seasonality on feeding behavior in coexisting populations of *M. fascicularis* and *T. o. obscurus* in secondary dipterocarp forest, finding a limited niche overlap in diet between the species. Another comparative study on the feeding ecologies of sympatric macaques (*M. silenus* and *M. radiata*) and colobines (*Semnopithecus entellus*) living in evergreen forests also showed little dietary overlap (Singh et al. 2011). In addition, Ungar (1995), who focused on the fruit preferences of four sympatric primates inhabiting a primary lowland rain forest showed a clear difference between colobines (*Presbytis thomasi*) and other monogastric primates, including *Hylobates lar, M. fascicularis* and *Pongo pygmaeus*; the colobines mostly consumed the seeds of dry fruits, whereas the other primates preferred consuming fruit flesh. In contrast, very little information is available about the coexisting mechanism such as resource competition and/or niche separation, in sympatric primates inhabiting the forest edge near adjacent urban areas, where both anthropogenic foods and cultivated plants with natural foods are available. Since colobines that inhabit such fragmented habitats are known to consume a high amount of both natural and cultivated plant fruits (Dela 2012), it is ecologically important to understand the dietary flexibility of coexisting macaques and colobines in such habitat.

We examined the feeding ecology of two sympatric hindgut- and foregut-fermenting primates, long-tailed macaques (*M. fascicularis*) and dusky langurs (*T. o. obscurus*), in the mixed landscape consisting of urban and agro-forested areas and forest fragments of Bangi Permanent Forest Reserve, Selangor, Malaysia (Md-Zain et al. 2010). *M. fascicularis* is one of the most widespread primate species, occurring in a broad variety of habitats, and has been well studied not only in Malaysia but also in other countries, where they are highly opportunistic omnivores/frugivores (Aldrich-Blake 1980; Gumert et al. 2011; Md-Zain et al. 2011; Sha and Hanya 2013a). Ecological knowledge of *T. o. obscurus*, with a distribution restricted to peninsular Malaysia, is less complete (Md-Zain and Ch’ng 2011). A single study in a secondary dipterocarp forest described them as a folivore with a high preference for leaves from the upper forest canopy (Curtin 1980). To gain a more complete picture of the coexisting mechanisms in primates with different physiological systems (i.e., *M. fascicularis* and *T. o. obscurus*), with special reference to the forest edge habitat near adjacent urban areas (where it is ecologically important to understand primate dietary flexibility but has never been studied), we sought to (1) describe the basic feeding ecologies and monthly differences in diets between the species, (2) describe the relationship between resource availability and the feeding behavior of each species, and (3) compare diet composition and dietary overlap between the two species. Finally, we discussed the dietary flexibility of coexisting macaques and colobines in this type of forest.

Methods

Study site and animals

This study was conducted in mixed landscape and forest fragments of the Bangi Permanent Forest Reserve, Selangor, Malaysia (Fig. 1, 101°45′E, 2°54′N), continuously from April 2014 to March 2015, except in August. The study area is hilly, with the highest point reaching 80 m above sea level, and includes the main campus of the Universiti Kebangsaan Malaysia (UKM), intercity roads, foothill oil palm cultivations, and human premises. The monthly rainfall distribution and temperatures were obtained from a nearby weather station at the UKM (station name: Pekan Bangi Lama, station ID: 2817180). The mean minimum and maximum temperatures were approximately 24.7 and 32.0 °C, respectively, and total annual precipitation at the site was 2157 mm. The UKM Permanent Forest Reserve, although fragmented, still harbors important plant resources, including over 500 species of seed plants (Mat Salleh 1999). *M. fascicularis* and *T. o. obscurus* commonly inhabit the area with pig-tailed macaques (*M. nemestrina*) and pale-thighed langurs (*Presbytis siamensis siamensis*) encountered more infrequently (Md-Zain and Abdullah 2008).

One multimale–multifemale group of *M. fascicularis* and a one-male–multifemale group of *T. o. obscurus* were habituated to observers, and some members of the groups with distinctive features such as unusually short tail lengths, missing and deformed hand digits, a hunchback,

Fig. 1 Map of the study area showing major landmarks within the study site, forest, and urban/edge habitats

and distinct skin color were identified individually. The group of *M. fascicularis* included 49 individuals: 12 adult males, 14 adult females, 11 subadults, eight juveniles, and four infants. The group of *T. o. obscurus* included 18 individuals: one adult male, seven adult females, four subadults, three juveniles, and three infants.

Behavioral data collection

We collected behavioral data from the adults and subadults in the *M. fascicularis* and *T. o. obscurus* groups continuously during our daily observation period, which lasted from 08:00 (or the time when the groups were found) until 18:30 (or the time when the groups were lost). We followed each focal group alternately for at least 3 days a month. During the observation periods, we conducted scan sampling at 10-min intervals (Altmann 1974). The total observation times for *M. fascicularis* and *T. o. obscurus* were 406.5 h and 373.1 h, respectively, and the monthly observation times periods were 29.5–59.0 h (mean, 37.0 h) and 29.9–42.4 h (mean, 34.5 h), respectively. The observation periods per day for *M. fascicularis* and *T. o. obscurus* were 10.2 ± SD 0.32 h and 10.4 ± SD 0.5 h, respectively. We recorded the activity (feeding, moving, and resting) of all visible adults and subadults. Feeding included handling, masticating, or swallowing food items. The food items consisted of leaves, fruits, flowers, anthropogenic foods (i.e., food waste), and others. Food plants were taxonomically identified in situ. If a food plant species was unknown, leaves, fruits, and/or flowers were collected for identification at the UKM by Mr. Ahmad Fitri Zohari.

Vegetational and phenological survey

We set up ten quadrats of 40 × 40 m (i.e., 1.6 ha) in our study site. The vegetative plots were set up as follows: seven of the quadrats were in the edge of secondary forest while three were set up in agroforest for timber and bird food (Idilfitri and Mohamad 2012), as it is known to form part of home ranges of the focal groups according to a previous study by Md-Zain et al. (2011). In each quadrat, we marked trees with a DBH (diameter at breast height) ≥ 10 cm. We taxonomically identified all marked trees to species level if possible with the support of the Herbarium Universiti Kebangsaan Malaysia. At the end of each monthly survey, except for August 2014, we recorded the phenology of the 349 marked plants in the ten plots by examining each plant for the presence of leaves, fruits, and flowers. In the monthly phenological survey, food availability was determined as the leafing, fruiting, and flowering ratio (number of leafing, fruiting, and flowering plants/total number of monitored plants).

Data analysis

We tested for differences in the time spent feeding (%) on plant parts by *M. fascicularis* and *T. o. obscurus* and the mean monthly dietary overlap for each plant part (i.e., leaves, fruits, and flowers) using a Mann–Whitney *U* test with Bonferroni correction ($p = 0.05/N$; where N is the number of comparisons made). The dietary overlap of the primate species was calculated using the Holmes–Pitelka index, $\mathrm{Di} = \sum \mathrm{Si}$, where Di is the total percent overlap and Si is the percent overlap between shared food items (Holmes and Pitelka 1968). We tested for a correlation between the monthly availability of each plant part (leaves, fruits, and flowers) for the two primate species, using Spearman's rank correlation coefficient. A linear model was used to examine whether the monthly mean proportion of time spent feeding on each plant part (i.e., leaves, fruits, and flowers) was affected by the monthly food availability of each plant part. The proportion of the monthly mean time spent feeding on each plant part was logit transformed [log $(p/1-p)$] and treated as a normally distributed response variable. The other factors (monthly availability of fruit, leaves, and flowers) were treated as explanatory variables. We examined a set of models with all possible combinations of the explanatory variables and ranked them by the corrected version of the Akaike information criterion (AIC) for small sample sizes, called the AICc (Burnham and Anderson 2002). Following guidelines published for wildlife research (Johnson and Omland 2004), we selected as the best-supported models those with a ΔAIC(c) score ≤ 2, where ΔAIC(c) = AIC(c) − minimum AIC(c) within the candidate model set (Burnham and Anderson 2002). In other words, if the AIC(c) in a model is less than two units larger than in the best model, it was also discussed and reported. The same procedure (i.e., linear model) was used to examine whether the monthly proportion of dietary overlap (but logit transformed) between two primate species was affected by the monthly food availability of each plant part. Since logit transformation is not applicable to zero values, we did not perform an analysis on the food availability of flowers, including seven data points in which the proportion of the dietary overlap was zero. These analyses were performed in R ver. 3.1.0 (R Development Core Team 2014) using the *dredge* function in the *MuMIn* package, ver. 1.9.13 (Bartoń 2013).

Behavioral data collection is non-invasive, and our research was conducted following the protocols approved by the Department of Wildlife and National Park Malaysia. In addition, the protocols adhere to all the legal requirements of Malaysia.

Results

Vegetation characteristics and food availability

We marked 349 trees (119 species, 82 genera, 40 families) within our vegetation plots. The five most abundant families were Meliaceae (13.4% of all plants), Leguminosae (4.4%), Moraceae (3.7%), Myrtaceae (3.5%), and Euphorbiaceae (3.4%). The five most abundant tree species were *Azadirachta excelsa* (26.7% of all trees), *S. koetjape* (3.4%), *Aidia densiflora* (3.4%), *Macaranga gigantea* (2.3%), and *Archidendron jiringa* (2.3%). The vegetation survey area covered 0.16 ha, or approximately 0.45% and 1.14% of the study groups' home ranges for *M. fascicularis* and *T. o. obscurus*, respectively. The cumulative number of plant species sampled did not reach an asymptote (Fig. 2), indicating that the edges of secondary forest are still growing and have high plant species diversity. Moreover, it was clear that the sampling effort would not be adequate to cover all the species.

Of the 349 trees marked within the plots, 238 (68.2%) and 167 (47.9%) were plant species that we observed *M. fascicularis* and *T. o. obscurus* to use as food sources, respectively. This included 211 (*M. fascicularis*) and 165 (*T. o. obscurus*) trees containing leaves (60.5 and 47.3%), 189 and 134 containing fruits/seeds (54.2 and 38.4%), and 150 and 131 containing flowers (43.0 and 37.5%), respectively. Food availability (potential food plants) for *M. fascicularis* and *T. o. obscurus*, determined as the leafing, fruiting, and flowering ratio (number of leafing, fruiting, and flowering plants/total number of monitored plants) in the monthly phenological survey fluctuated seasonally, with a similar pattern (Fig. 3a, b). The monthly availability of leaves, fruits, and flowers of *M. fascicularis* was significantly correlated with that of *T. o. obscurus* (leaves: $rs = 0.97$ and $p < 0.01$; fruits: $rs = 0.98$ and $p < 0.01$; flowers: $rs = 0.98$ and $p < 0.01$). Leaves were abundant throughout the year but with two peaks in July 2014 and March 2015. The availability of flowers was always lower than that of leaves and fruits, except in January and March 2015. The availability of fruits was generally higher from May to July 2014 and lower from January to February than in the remaining months.

Food habits

We collected a total of 5570 and 4029 feeding records for *M. fascicularis* and *T. o. obscurus*, respectively. The total number of plant species consumed within the feeding records was 113 (82 genera, 43 families; Appendix I)

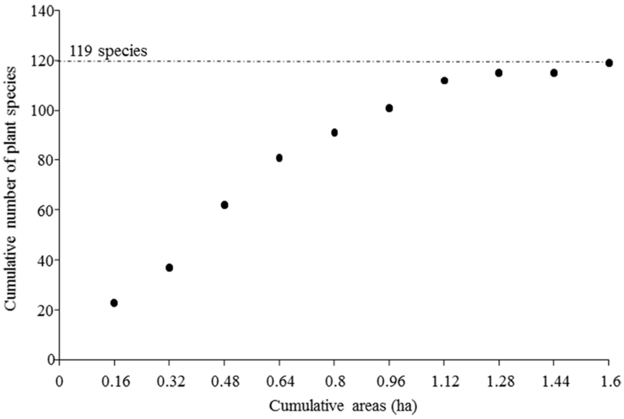

Fig. 2 Cumulative number of plant species found from Plot 1 to Plot 10

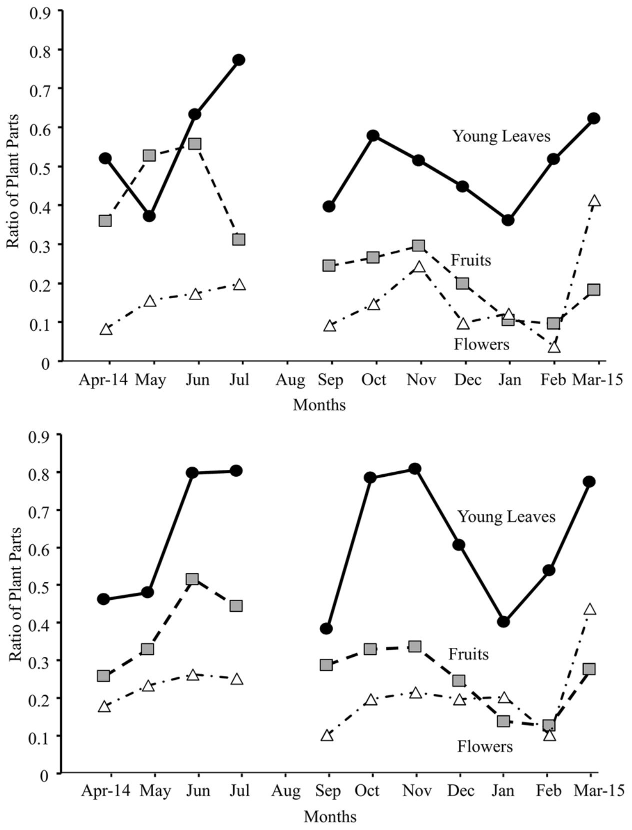

Fig. 3 Monthly fluctuation of young leafing, fruiting, and flowering ratio for plant species consumed by *M. fascicularis* (*top*) and *T. o. obscurus* (*bottom*) from April 2014 to March 2015. No observation was performed in August

Table 1 Percentage of time spent feeding on food items by *M. fascicularis* and *T. o. obscurus*

Food items	*M. fascicularis*	*T. o. obscurus*
Fruits and seeds	31.9 + 9.2%	40.1 + 13.8%
Leaves	16.1 + 4.6%	51.2 + 15.42%
Flowers	5.5 + 4.3%	7.8 + 7.5%
Others (red soil and fungi)	4.3 + 2.6%	0.81 + 1.0%
Anthropogenic foods	26.9 + 7.4%	0%
Insects	15.3 + 8.3%	0%

Percentage is the mean values per month with standard deviation

for *M. fascicularis*. The five most consumed species were *Elaeis guineensis* (11%), *Ficus variegate* (4%), *Melastoma malabathricum* (3.1%), *Schizostachyum jaculans* (3.1%), and *Acacia mangium* (2.7%). In comparison, a total of 130 plant species (85 genera, 43 families; Appendix II) were consumed by *T. o. obscurus*: the five most consumed species were *Adenanthera pavovina* (9.9%), *Archidendron dulce* (5.7%), *Sandoricum koetjape* (4.9%), *F. variegate* (4.7%), and *Endospermum diadenum* (4.4%). Both *M. fascicularis* and *T. o. obscurus* frequently consumed leaves, fruits/seeds, and flowers, although only *M. fascicularis* fed on anthropogenic foods and insects. Overall, for *M. fascicularis*, 31.9% of the feeding records were for fruits/seeds (27.8%/4.1%), 26.9% were for anthropogenic foods, 16.1% were for leaves (young leaf: 40.2%; mature leaf: 12.6%; both young and mature leaf: 47.1), 15.3% were for insects, 5.5% were for flowers, and 4.3% were for other food items, including red soil and fungi (Table 1). The number of plant species providing leaves, fruits, and flowers were 48, 57, and 32, respectively. Meanwhile, for *T. o. obscurus*, 51.2% of the feeding records were for leaves (young leaf: 36.1%; mature leaf: 4.7%; both young and mature leaf: 56.1; unknown: 3.1), 40.1% were for fruits/seeds (34.6%/5.5%), 7.8% were for flowers, and < 1% were for other food items, including red soil and unknown food items (Table 1). The number of plant species providing leaves, fruits, and flowers were 104, 45, and 34, respectively.

We collected a total of 1,184 and 856 fruit eating records of *M. fascicularis* and *T. o. obscurus*, respectively. The exploitation of ripe fruits, both ripe and unripe fruits, and unripe fruits accounted for 90.8, 5.4, and 3.8% of the fruit-eating records of *M. fascicularis*, respectively. *M. fascicularis* consumed only fruit flesh during 60.7% of fruit eating while consuming both fruit flesh and seeds during 39.3% and only seeds during 0% (see Table 2 in details). On the other hand, the exploitation of ripe fruits, both ripe and unripe fruits, unripe fruits, and unknown accounted for 67.5, 18.0, 13.7, and 0.8% in *T. o. obscurus*, respectively. *T. o. obscurus* consumed only fruit flesh during 41.08% of fruit eating while consuming both fruit flesh and seeds during 42.3% and only seeds during 15.8% (see Table 2 in details).

Comparison between two primate species throughout the year

T. o. obscurus generally spent more time consuming fruits/seeds, leaves, and flowers than did *M. fascicularis*, though *M. fascicularis* spent much more time feeding on insect and anthropogenic foods. The mean time spent feeding on leaves differed significantly between the two species ($Z = 7.00$, $p < 0.001$), although there was no significant differences in terms of eating flowers ($Z = 0.72$, $p = 0.468$); it should be noted that the difference in the time spent feeding on fruits/seeds tended towards significance ($Z = 1.96$, $p = 0.050$). Throughout the year, the number of shared items and the absolute percentage dietary overlap between *T. o. obscurus* and *M. fascicularis* were 59 (45 genera, 32 families) and 24.3%, respectively. Overall, the dietary overlap was the highest for fruits. The mean monthly dietary overlap index for consumed fruits (mean, 16.9%, SD, 10.08) was significantly higher than that for leaves (mean, 8.30%, SD, 4.58) and flowers (mean 1.05, SD 2.26), and that for leaves

Table 2 Time allocated to the consumption of ripe or unripe fruits and to three fruit parts (i.e., flesh only, flesh and seed, and seed only) in *M. fascicularis* and *T. o. obscurus*

M. fascicularis								
Ripe (90.8%)			Unripe (3.8%)			Ripe + unripe (5.37%)		
Flesh	Flesh and seed	Seed	Flesh	Flesh and seed	Seed	Flesh	Flesh and seed	Seed
57	33.8	0	2.7	1.1	0	0.98	4.4	0
T. o. obscurus								
Ripe (67.5%)			Unripe (13.7%)			Ripe + unripe (18.0%)		
Flesh	Flesh and seed	Seed	Flesh	Flesh and seed	Seed	Flesh	Flesh and seed	Seed
32.6	27.7	7.1	2.98	2.05	8.67	5.42	12.5	0

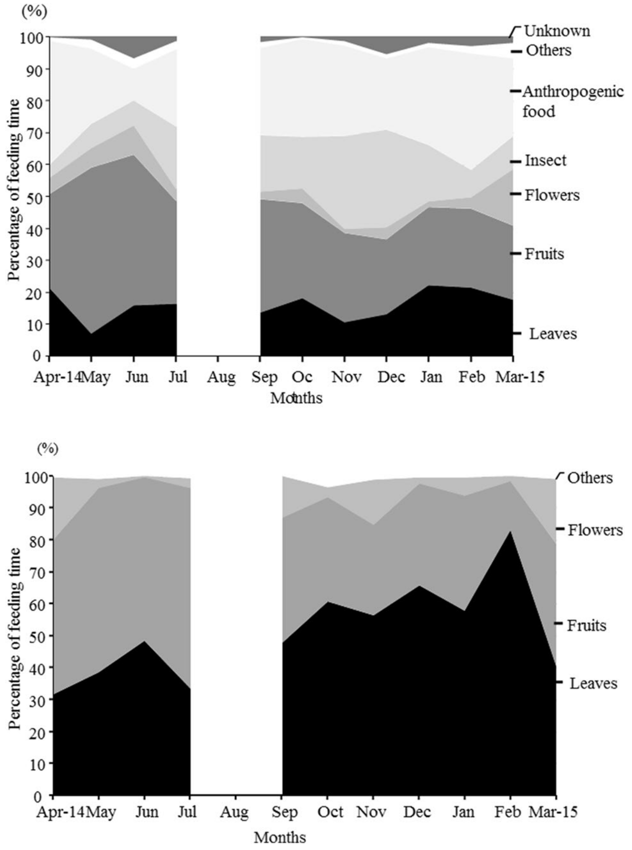

Fig. 4 Seasonal changes in the diet composition of *M. fascicularis* (*top*) and *T. o. obscurus* (*bottom*); the values represent the monthly feeding times spent on each food category

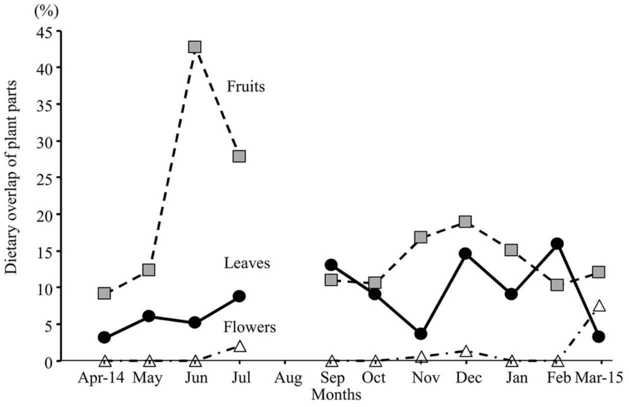

Fig. 5 Monthly fluctuation of dietary overlapping index for each plant part eaten

was significantly higher than that for flowers: fruits vs. leaves: $Z = 2.73$ and $p < 0.01$; fruits vs. flowers: $Z = 4.04$ and $p < 0.001$; leaves vs. flowers: $Z = 3.70$ and $p < 0.001$.

Monthly variation in diet

We found that flower eating by both *M. fascicularis* and *T. o. obscurus* was constantly low throughout the study period (Fig. 4). On the other hand, leaf and fruit eating was almost always higher in *T. o. obscurus* than in *M. fascicularis*, and insect and anthropogenic food was only consumed by *M. fascicularis*. The best-fit model predicting fruit eating by *M. fascicularis* showed only a positive effect of fruit availability ($y = -0.6507 + 1.319x$); the ΔAICc score of the second model was > 2. The best-fit models predicting leaf and flower eating by *M. fascicularis* were both null models. Similar to *M. fascicularis*, the best-fit model predicting fruit eating by *T. o. obscurus* included only a positive effect of fruit availability ($y = -0.5706 + 1.656x$); it should be noted that the second model was a null model. Indeed, the best-fitting models predicting leaf eating and flower eating by *T. o. obscurus* were both null models.

Comparison between two primate species

The amount of monthly overlap for three plant parts (i.e., fruit, flowers, and leaves) fluctuated seasonally. The dietary overlap for leaves and flowers was small and showed a relatively even distribution across the seasons, although that for fruits was unevenly distributed, with clear peaks in June/

July 2014, (63.4 and 41.4%, respectively; Fig. 5). In June and July, when the dietary overlap of fruits was extremely high, both primate species consumed the cultivated fruits *Nephelium lappaceum* and *Sandoricum koetjape* except *Ochanostachys amentacea*. The best-fit model predicting the amount of monthly dietary overlap for the consumed fruits included only a positive effect of fruit availability ($y = -0.7541 + 1.295x$); the second model was a null model (Fig. 6). Conversely, the best-fitting model to explain the dietary overlap of leaves, which was evaluated using the AIC(c) criterion, included fruit and flower availabilities (Table 3), although the ΔAIC(c) values of some other models were also < 2.0. The dietary overlap of leaves increased with decreasing fruit and flower availabilities (Fig. 6).

Discussion

This study described the feeding ecologies of *T. o. obscurus* and *M. fascicularis* inhabiting a forest edge adjacent to an urban area. Our findings on the dietary composition of *T. o. obscurus* are similar to those found in a lowland evergreen dipterocarp forest, Kuala Lompat, Peninsular Malaysia—leaves: 58%, fruits: 32%, flowers: 7%, and others: 3% (Curtin 1980)—although our *T. o. obscurus* study group consumed more plant species (130 vs. 87) than reported by Curtin (1980). However, it would be impossible to compare the number of consumed plant species directly between the two studies because the sampling methods differed.

On the other hand, our *M. fascicularis* study group showed a typical dietary composition, as reported in Singapore (Sha and Hanya 2013a) and Bali, Indonesia (Brotcorne 2014), where the animals live on the forest edge with an adjacent urban area; fruits, anthropogenic foods/food waste, and insects were the most important food sources. In this study, *M. fascicularis* fed on 17 of the same genus of plant species reported by Sha and Hanya (2013b), with $> 70\%$ of species (25 out of 36 species) recorded available or consumed by *M. fascicularis*. Distinctive diet choices by *M. fascicularis* in forest edges are evident, as some fruits are mostly derived from cultivated and herbaceous plants. The sympatric *T. o. obscurus* did not consume the anthropogenic food sources, although they also consumed leaves and seeds derived from urban/cultivated plants, suggesting different nutritional benefits for hindgut- and foregut-fermenting primates. Higher sugar and carbohydrate contents in the anthropogenic foods (e.g., rice, bread, and biscuits) present as an energy bonus (Strum 2010), as human foods were higher in calories and lower in fiber than natural foods (Forthman-Quick and Demment 1988). However, it is difficult to determine whether the exploitation of anthropogenic foods by *M. fascicularis* in our study site is due to the natural food

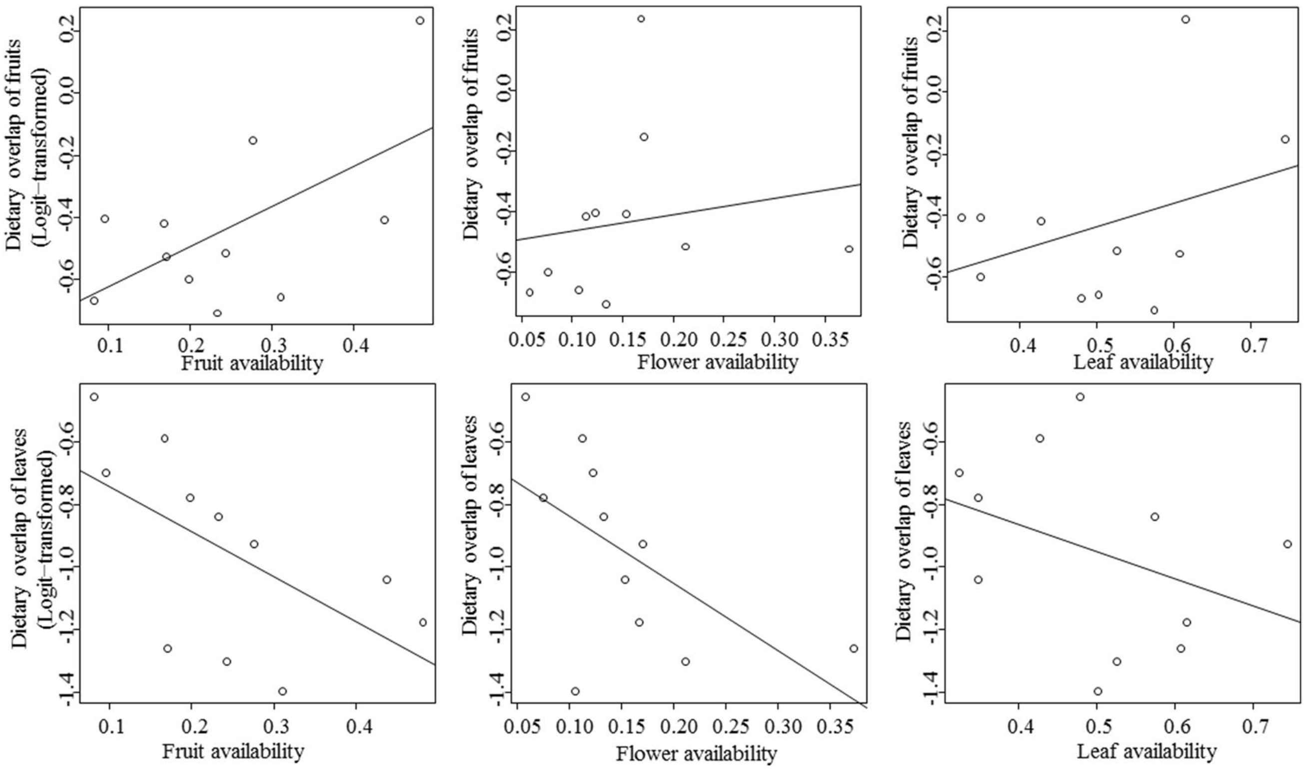

Fig. 6 Relationship between food availabilities (fruits, flowers, and leaves) and dietary overlap of fruits (*top*) and leaves (*bottom*)

Table 3 Summary of model selection using linear models to investigate whether the fruit and leaf eating of species and the dietary overlap of consumed fruits and leaves was affected by the food availabilities such as fruits, flowers, and leaves

Model	AICc	AICc weight	Intercept	Df	Log-likelihood	Flower availability	Fruit availability	Leaf availability
Time spent in fruit eating by *M. fascicularis*								
1	−11.6	0.864	−0.6507	3	10.535		1.319	
2	−6.5	0.067	−0.6095	4	10.599		1.331	−0.08532
3	−6.5	0.066	−0.6377	4	10.582	−0.08793	1.324	
4	0.8	0.002	−0.6108	5	10.614	−0.05393	1.331	−0.06615
Null	2.5	0.001	−0.2744	2	1.479			
Time spent in fruit eating by *T. o. obscurus*								
1	4	0.644	−0.5706	3	2.718		1.656	
Null	7	0.141	−0.186	2	−0.763			
Dietary overlap for the consumed fruits								
1	6.3	0.47	−0.7541	3	1.584		1.295	
Null	7.2	0.29	−0.4371	2	−0.862			
Dietary overlap of leaves eating								
1	8.3	0.334	−0.3346	4	3.174	−1.943	−1.301	
2	9.2	0.214	−0.6202	3	0.112	−2.157		
3	9.2	0.212	−0.5966	3	0.101		−1.444	
Null	10	0.145	−0.9501	2	−2.245			

resource scarcity or a high dependence on anthropogenic foods, as we did not survey the availability of anthropogenic foods in our study site. Further efforts should be made into elucidating the effect of anthropogenic foods on the diet of *M. fascicularis*.

In this study, we showed that both *M. fascicularis* and *T. o. obscurus* consumed relatively high amounts of fruits/seeds; notably, foregut-fermenting *T. o. obscurus*, which is considered a folivorous animal (Curtin 1980), tended to spend more time eating fruit compared to the hindgut-fermenting *M. fascicularis*, which is considered to be omnivorous/frugivorous (Lucas and Corlett 1991). Contrary to earlier assumptions that foregut-fermenting primates (i.e., colobines) mainly exploit ubiquitous food sources such as leaves, recent colobine studies have revealed high levels of fruit and/or seed consumption in response to local conditions, for example, *T. o. obscurus*: 40.1% (this study); *P. potenziani*: 55.4% for fruit eating (Hadi et al. 2012); *Colobus guereza*: 33–44% (Fashing 2001); *P. rubicunda*: 30–84% (Davies 1991; Hanya and Bernard 2012; Ehlers Smith et al. 2013); *T. vetulus*: 53.7–60.1% (Dela 2007); and *Semnopithecus entellus*: 23–29.1% (Vandercone et al. 2012). Notably, in our study, over 65% of fruit eating involved the consumption of ripe fruits, and in the majority of cases, the fruit flesh containing more sugar was likely eaten (Table 2). It is believed that colobines avoid sugary food sources (i.e., ripe fruits), which can result in a decrease in fermentation efficiency or cause acidosis, and in extreme cases can even result in death (Collins and Roberts 1978; Kay and Davies 1994). However, not only our study species but also other colobines, for example, *T. auratus* (Kool 1993), *Presbytis entellus* (Koenig et al. 1998), *Semnopithecus vetulus* (Dela 2012), and *Piliocolobus tephrosceles* (Danish et al. 2006), reportedly include ripe fruits as an important food source. Nonetheless, the detailed digestive mechanism by which these colobines can deal with such sugary sources in their forestomaches and avoid harmful fermentation is poorly known (Danish et al. 2006). In future studies, feeding trials and/or digestibility measured by an in vitro gas production method using ripe fruits, as performed using leaves by Matsuda et al. (2017), together with the investigation of forestomach microbiome analyses (e.g., Amato et al. 2016; Hayakawa et al. 2018) would be helpful in explaining colobines' digestive mechanism for such sugary items.

Although leaves were always more abundant than fruits in our study site, the amount of monthly fruit eating by *M. fascicularis* and *T. o. obscurus* only showed a significant correlation with fruit availability, indicating that both species prefer feeding on fruits when they are available. In this study, the percentage of time spent on leaf eating did not show a clear pattern in relation to leaf availability, supporting the strong fruit preference described in other colobine studies, for example, *T. auratus* by Kool (1993), *Nasalis larvatus* by Matsuda et al. (2009), and *P. rubicunda* by Hanya and Bernard (2012, 2015). Thus, although the digestive systems of *M. fascicularis* and *T. o. obscurus* are different, fruits would be their key food source.

Monthly dietary overlap between *M. fascicularis* and *T. o. obscurus* in our study showed a positive effect of monthly fruit availability. In addition, contrary to previous studies showing that colobines prefer unripe fruits while macaques prefer ripe fruits, *T. o. obscurus* consumed a relatively high amount of ripe fruits in this study. In theory, this suggests that their fruit preference mainly leads to contest (or direct) competition for resources rather than scramble (indirect) competition, especially when fruits are abundant and cultivated fruits are available. The dietary overlap with the resource competition between the two species in this study might be more the result of cultivated plants than of natural forest species, suggesting that resource competition becomes higher and niche separation becomes ambiguous between foregut- and hindgut-fermenting primates living in forest edge near adjacent urban areas.

On the other hand, there would also be a possibility that their resource competition is low, as we did not observe the two species to feed on fruits on the same tree, nor did we observe clear conflict or aggressive behaviors between the two species (F.R., pers. obs.), although we did not do alternative evaluation, the degree of food competition between the two sympatric species in our study site. Although the fruits were preferred by the two species in our study site, to avoid food competition, *T. o. obscurus* would flexibly shift to leaves due to their special digestive system while *M. fascicularis* could shift to anthropogenic foods, which *T. o. obscurus* would not be able to consume.

We succeeded in clarifying the detailed feeding ecologies of two sympatric primates, showing their similar dietary preference despite their different physiological systems, although they appeared to avoid or reduce interspecific competition for essential resources. However, to understand the mechanism of coexistence of the two sympatric primates in our study site, further research focusing on the detailed resource competition level to quantify their interspecific competition and niche separation including their ranging patterns is needed.

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