

# Niche separation of sympatric macaques, *Macaca assamensis* and *M. mulatta*, in limestone habitats of Nonggang, China

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**Abstract** Comparative studies of sympatric species are essential in understanding those species' behavioral and ecological adaptations as well as the mechanisms that can reduce resource competition enough to allow coexistence. We collected data on diet, activity budget and habitat use from two sympatric macaque species, the Assamese macaque (*Macaca assamensis*) and the rhesus macaque (*M. mulatta*), in a limestone seasonal rainforest of Nonggang Nature Reserve, southwestern Guangxi, China. Our results show that the two sympatric macaques differ in diet, activity budget, and habitat use: (1) out of the 131 plant species that were used by both macaque species as food over the year, only 15 plant species (11 %) were shared. Rhesus macaques used more plant species as major foods, and had higher dietary diversity and evenness indexes than Assamese macaques. (2) Assamese macaques fed predominantly on leaves, whereas rhesus macaques fed more selectively on fruits. The rhesus macaques' diet varied according to season, and was significantly correlated to season fluctuation in fruit availability. (3) Assamese

macaques devoted more time to resting, and less time to feeding than rhesus macaques (4) Assamese macaques were present mostly on the cliff, and tended to stay on the ground, whereas rhesus macaques were present mostly on the hillside, and showed preference to lower and middle canopy. The observed differences in diet and habitat use between the two macaque species represent behavioral patterns enabling their coexistence.

**Keywords** Assamese macaques · Rhesus macaques · Niche separation · Limestone habitat

## Introduction

Comparative studies of sympatric species are essential in understanding those species' behavioral and ecological adaptations as well as the coexistence mechanisms. According to niche theory, sympatric species should evolve adaptations that allow them to avoid or to reduce inter-specific competition for limited resources (Gause 1934; Pianka 1981). Niche separation appears to have evolved as a mechanism to reduce resource competition, and make the coexistence of different species possible. Three principal factors have been identified in determining niche separation of sympatric species, namely diet choice, spatial use of the habitat, and activity pattern (Schoener 1974; Tokeshi 1999; Schreier et al. 2009).

Over the last three decades, there has been an impressive accumulation of data on the diets of sympatric primates. These studies reveal considerable inter-specific dietary variation (MacKinnon and MacKinnon 1980; Ganzhorn 1989; Tutin and Fernandez 1993; Tomblin and Cranford 1994; Porter 2001; Nakagawa 2003; Powzyk and Mowry 2003; Sushma and Singh 2006; Nadjafzadeh and Heymann

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2008). Even within closely related sympatric species, selection of plant species and plant parts eaten may show a marked divergence (Cords 1986; Bennett and Davies 1994; Singh et al. 2011; Hadi et al. 2012). For example, in Kakamega, Kenya, *Cercopithecus mitis* were more folivorous and less frugivorous and insectivorous than *C. ascanius* (Cords 1986). Similarly, in the rain forests of the Western Ghats, South India, the diets of *Macaca radiata* and *M. silenus* mainly included plant species or parts that were exclusively used by each species (Singh et al. 2011). These differences are in fact even more marked when considering seasonality. For example, at Tinigua National Park, Colombia, dietary variation of four sympatric neotropical primates became more pronounced during the dry season characterized by low fruit availability (Stevenson et al. 2000).

Besides dietary variation, sympatric primates show differences in habitat use (Ganzhorn 1989; Nakagawa 1999, 2003; Nadjafzadeh and Heymann 2008; Singh et al. 2011; Hadi et al. 2012). Habitat differentiation may occur either by the use of qualitatively dissimilar habitats (Nakagawa 1999, 2003; Schreier et al. 2009), or by spatial separation within a single habitat type, such as the use of different strata of a forest canopy (Singh et al. 2011; Hadi et al. 2012) or various substrates for animal prey foraging (Nadjafzadeh and Heymann 2008). These variations represent ecological niche separation, allowing the coexistence of sympatric primates.

The rhesus macaque (*Macaca mulatta*) and Assamese macaque (*M. assamensis*) are distributed sympatrically in various habitats across South and Southeast Asia (Fooden 1980; Zhang et al. 2002). Despite similarities in body size and gut morphology between the two macaques (Chivers and Hladik 1980; Smith and Jungers 1997), their diets show considerable variation. Rhesus macaques are omnivores, and eat a wide array of plant and invertebrate materials, as well as foods from human activities, which enable them to live in natural and anthropogenic environments (Goldstein and Richard 1989; Richard et al. 1989). Compared to rhesus macaques, very little quantitative information is available concerning Assamese macaques' diets, except for some descriptive accounts from Ahsan (1994) and (Chalise 2003). They found that Assamese macaques were predominantly folivorous, but would eat fruits and flowers whenever they were available. It was expected that dietary variation between the two macaques would be an important characteristic involved in separating their feeding niches. Thus, comparative studies on the behavior and ecology of sympatric rhesus macaques and Assamese macaques are important for understanding their coexistence mechanisms. We also provide important comparative information for the general study of behavioral adaptation in macaques, especially for Assamese macaques.

In this paper, we compare the diet, activity budget and habitat use of rhesus macaques and Assamese macaques living sympatrically in the limestone hills of southwestern Guangxi, China. We aimed to: (1) determine how food resource use differs between them; (2) investigate how differences in diet influence their activity budget and habitat use; (3) determine whether differences in diet and habitat use can explain their coexistence.

## Methods

### Study sites and subjects

This study was conducted from October 2005 to September 2007 at Nonggang Nature Reserve (106°42'–107°4'E, 22°13'–22°33'N, Fig. 1), Guangxi Province, China. The reserve comprises three areas, Nonggang (5,426 ha), Longhu (1,034 ha), and Longshan (3,949 ha), which are separated by farmlands and villages. The reserve consists of limestone hills ranging from 400 to 600 m above sea level (Guangxi Forest Department 1993). The vegetation is characterized by limestone seasonal rainforest. Annual precipitation was 1,373 mm (October 2005–September 2006) and 952 mm (October 2006–September 2007). There are two seasons: a rainy season from April to September with >80 mm monthly rainfall, and a dry season in the remainder of the year with <80 mm monthly rainfall. (Zhou et al. 2007; Tang et al. 2011).

Our study site lies in the northwestern portion of Nonggang (Fig. 1). In this study, we selected one group of rhesus macaque ( $N = 22$ ) and two groups of Assamese macaque (Group 1,  $N = 15$ ; Group 2,  $N = 12$ ) who ranged nearest to our temporary camp. The three study groups' home ranges overlapped with each other. The rhesus macaque group was composed of 2 adult males, 7 adult females, 10 subadult individuals of unidentified sex, and 3 infants. Group 1 of the Assamese macaques consisted of 2 adult males, 4 adult females, 4 adult individuals of unidentified sex, and 5 juveniles, and Group 2 had 2 adult males, 4 adult females, 2 adult individuals of unidentified sex, and 4 juveniles.

### Ecological sampling

We conducted vegetation surveys in the main study area at the onset of behavioral data collection. We used a stratified random sampling method for the placement of vegetation plots. We placed 13 plots (50 × 10 m) in the main study area, including 4 at the valley basins and 9 on the hillsides. The plots covered most of the vegetation types described by Shu et al. (1988). Within the plots, all trees with ≥5 cm diameter at breast height were tagged. In total, we

**Fig. 1** Map of Nonggang Nature Reserve showing the study site and surrounding area



monitored 312 trees from 30 families at monthly intervals, and recorded the presence of young leaves, fruits, and flowers.

#### Data collection

We conducted behavioral observations of the Assamese macaque groups for 58 days (3–9 days each month) from October 2005 to September 2006. We observed the rhesus macaque group for 65 days (3–13 days each month) from October 2006 to September 2007. W.H. and T.H.X. collected behavioral data. To ensure consistent methodology, we conducted detailed training before we started to collect data. Each day, data collection began when the monkeys were first encountered, and ended when they disappeared or entered the sleeping sites. We observed monkeys with binoculars and a spotting scope at a distance of 10–200 m. We used scan sampling (Altmann 1974) with 15-min intervals. Each scan lasted 5 min, followed by 10 min of inactivity until the next scan began. We recorded the activity of each individual seen during each scan. We watched each individual for 5 s after detection, and recorded its behavior and canopy height during that

interval. The behaviors included 4 activity categories: resting, moving, feeding, and social behavior (e.g. grooming and playing). The canopy heights were divided into 5 strata: ground, lower ( $\leq 5$  m), middle<sup>-</sup> ( $>5$  m,  $\leq 10$  m), middle<sup>+</sup> ( $>10$  m,  $\leq 15$  m) and upper canopy ( $>15$  m). To avoid sampling bias toward certain individuals or a particular age-sex class, we tried to collect behavioral records on as many different individuals as possible during a scan so that all individuals in the focal group were included, but we sampled no individual more than once. When the individual was feeding, we recorded plant species and parts eaten, e.g., young leaf, mature leaf, fruit, flower, seed, or other (e.g. petiole and stem). During the study period, a total of 6,525 behavior records were obtained from 1,666 scan samples for Assamese macaques, of which there were 1,259 feeding records. We collected 5,506 behavior records from 1,372 scan samples for rhesus macaques, of which there were 1,712 feeding records. We also recorded the location of the focal group in different zones of the hill every 30 min to analyze habitat use. We visually divided the hill into 4 zones: valley basin, hillside, cliff, and hilltop. The zones only indicate relative differences in height and gradient.

## Data analysis

We expressed the relative abundance of different plant parts as the percentage of trees bearing the plant parts of interest each month, regardless of the size of the canopy (Britt et al. 2002). Because few records were collected in September or October 2005 for Assamese macaque groups, and in October 2005, December 2005, and April 2006 for the rhesus macaque group, we excluded data in these months from later analyses. We also excluded records for dependent infants and juveniles because these animals were not acting independently. We determined the percentage of different plant species in the diet of each study group by calculating the percentage of feeding records devoted to them among annual total feeding records. Food category composition was expressed as the percentage of different plant parts in the monthly diet of the study group using monthly total feeding records. In calculating the activity budget, we first determined time allocation to each activity for each scan, expressed as the percentage of scanned individuals engaging in each activity category among the total number recorded in a scan. We averaged the scan budgets in a month to construct monthly activity budget. Habitat and canopy height use was expressed as the percentage of monthly location records occurring in each zone and strata. Annual food category composition, activity budget and habitat use were obtained by averaging the monthly percentages.

To compare inter-specific variation in dietary diversity, we calculated the Shannon–Weaver diversity index and evenness index on the basis of consumption of plant species. The Shannon–Weaver diversity index is calculated as  $H' = -\sum P_i \times \ln P_i$  (where  $P_i$  is the proportion of feeding records of the  $i$ th plant species). The evenness index is calculated as  $J = H'/H_{\max} = H'/\ln N$  (where  $N$  is the number of species eaten). To calculate niche overlap between the two macaque species, we used Pianka's index with the formula:

$$O_{jk} = \frac{\sum P_{ij}P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}}$$

where  $O_{jk}$  is the overlapping index between species  $j$  and  $k$ , and  $P_{ij}$  and  $P_{ik}$  are the percentage of utilization of  $i$  resource category ( $i$  = habitat, diet) by species  $j$  and  $k$  respectively. Pianka's index varies between 0 (total separation) and 1 (total overlap) (Pianka 1973).

The Mann–Whitney U test was used to examine inter-specific variations in the overall and seasonal pattern of time budget, use of different food categories, zones of the limestone hills and canopy height. We used Spearman rank correlations to test the relationship between the abundance and consumption of different plant parts. All tests were 2-tailed, with a significance level of 0.05.

## Results

### Diet

A total of 131 plant species were used by the two macaque species as foods over the year. Assamese macaques consumed 69 species and rhesus macaques ate 77 species. Among the food species, 15 species were shared by both (11 % of total food species). In the rainy season, 79 plant species were consumed by the two macaque species. Assamese macaques and rhesus macaques consumed 40 and 49 species, respectively, with 10 species shared by both (13 %). In the dry season, 76 plant species were eaten by the two macaque species. Assamese macaques and rhesus macaques consumed 39 and 48 species, respectively, with 11 species shared by both (14 %). The Pianka's index, describing the dietary overlap between the two macaque species, was 0.34, 0.47, and 0.38 in the rainy season, the dry season and over the year, respectively.

When the comparison was limited to major foods (those that accounted for >1 % of all feeding records) there was a more marked difference between the species. Major foods contributed to a large proportion of the total diet (Assamese macaque: 85.2 %; rhesus macaque: 83.7 %, Table 1). In total, rhesus macaques used more plant species as major foods than Assamese macaques. Annual diversity and evenness of use of major food plants was higher for rhesus macaques ( $H = 2.408$ ,  $J = 0.804$ ) than for Assamese macaques ( $H = 1.164$ ,  $J = 0.468$ ). This indicates that Assamese macaques concentrated on fewer food species than rhesus macaques: the top 10 food species accounted for 82.8 % of the Assamese macaque diet, but only for 67.4 % of the rhesus macaque diet. In particular, *Indocalamus calciculus*, a small bamboo, contributed to 62 % of the annual diet of Assamese macaques. The major foods of the two macaque species showed little overlap (Table 1), and only two plant species (*Indocalamus calciculus* and *Ficus microcarpa*) were shared by Assamese macaques and rhesus macaques.

Based on monthly percentages of feeding records for different food categories, there was marked inter-specific variation in annual food category composition (Fig. 2). Assamese macaques consumed more young leaves and flowers (young leaf:  $Z = -2.531$ ,  $n_1 = 10$ ,  $n_2 = 9$ ,  $P = 0.010$ ; flower:  $Z = -2.010$ ,  $P = 0.044$ ), whereas rhesus macaques ate more fruits than Assamese macaques ( $Z = -2.206$ ,  $P = 0.028$ ). There was significant difference in food category utilization by the two macaque species when comparison was limited to the rainy season or the dry season (Fig. 2). In the rainy season, Assamese macaques consumed more young leaves ( $Z = -2.193$ ,  $n_1 = 4$ ,  $n_2 = 5$ ,  $P = 0.032$ ); rhesus macaques consumed more fruits than Assamese macaques ( $Z = -2.193$ ,  $P = 0.032$ ).

**Table 1** Plant species used for major foods by the two sympatric macaque species in the Nonggang Nature Reserve

Plant species eaten	Family	Assamese macaque		Rhesus macaque	
		Parts eaten <sup>a</sup>	% (F) <sup>b</sup>	Parts eaten <sup>a</sup>	% (F) <sup>b</sup>
<i>Aristolochia longgangensis</i>	Aristolochiaceae			FR, B, ST	1.92
<i>Berchemia floribunda</i>	Rhamnaceae	YL, F, P	1.37		
<i>Burretiodendron hsienmu</i>	Tiliaceae	YL	1.55		
<i>Canthium dicoccum</i>	Rubiaceae	YL, ML, F, FR	2.28		
<i>Capparis cahtohiesis</i>	Capparaceae			YL, ML, FR	1.10
<i>Carvota ochlandra</i>	Palmaceae			YL, FR	12.18
<i>Clausena anisum</i>	Rutaceae			FR	5.19
<i>Clausena emarginata</i>	Rutaceae			YL, ML, FR	1.29
<i>Croton euryphyllus</i>	Euphorbiaceae	YL	1.55		
<i>Cuscuta chinensis</i>	Convolvulaceae			ST	1.96
<i>Dracontomelon duperreanum</i>	Anacardiaceae			YL, FR	7.23
<i>Embelia scandens</i>	Myrsinaceae			YL, ML	5.54
<i>Ficus gibbosa</i>	Moraceae			YL, ML, FR	2.27
<i>Ficus glaberrima</i>	Moraceae			ML, FR	1.36
<i>Ficus microcarpa</i>	Moraceae	YL, FR	1.46	YL, ML, FR	5.36
<i>Ficus nervosa</i>	Moraceae	YL, ML, F, FR	4.01		
<i>Ficus obscura</i>	Moraceae			FR	3.40
<i>Guihaia argyratea</i>	Palmae	F, P	3.64		
<i>Indocalamus calciculus</i>	Bambusoideae	YL	62.02	YL	11.00
<i>Iondes ovalis</i>	Icacinaceae			FR	3.97
<i>Lepionurus sylvestris</i>	Sapotaceae	YL, ML	1.18		
<i>Pithecellobium clypearia</i>	Mimosaceae			YL, ML	3.16
<i>Poffhos repens</i>	Araceae			YL, FR	1.28
<i>Polygonum chinense</i>	Polygonaceae			FR	1.13
<i>Pueraria thunbergiana</i>	Papilionaceae			YL, ML, ST	10.39
<i>Sapium rotundifolium</i>	Euphorbiaceae	FR	1.18		
<i>Sinosideroxylon pedunculatum</i>	Sapotaceae	YL, FR	3.55		
<i>Spondia lakonensis</i>	Anacardiaceae			YL, FR	2.74
<i>Urobotrya latisquama</i>	Opiliaceae			YL, ML, FR	1.18
<i>Ventilago calyculata</i>	Rhamnaceae	YL	1.37		

<sup>a</sup> Parts eaten: YL young leaf, ML mature leaf, FR fruit, S seed, F flower, P petiole, ST stem

<sup>b</sup> % (F): percentage of total feeding records

In the dry season, Assamese macaques consumed more flowers than rhesus macaques ( $Z = -2.491$ ,  $n_1 = 5$ ,  $n_2 = 5$ ,  $P = 0.016$ ). Additionally, there was marked variation in the species of different categories consumed by each macaque species. For example, there was no overlap in which plant species provided the main fruit resources for rhesus macaques and Assamese macaques (Table 1).

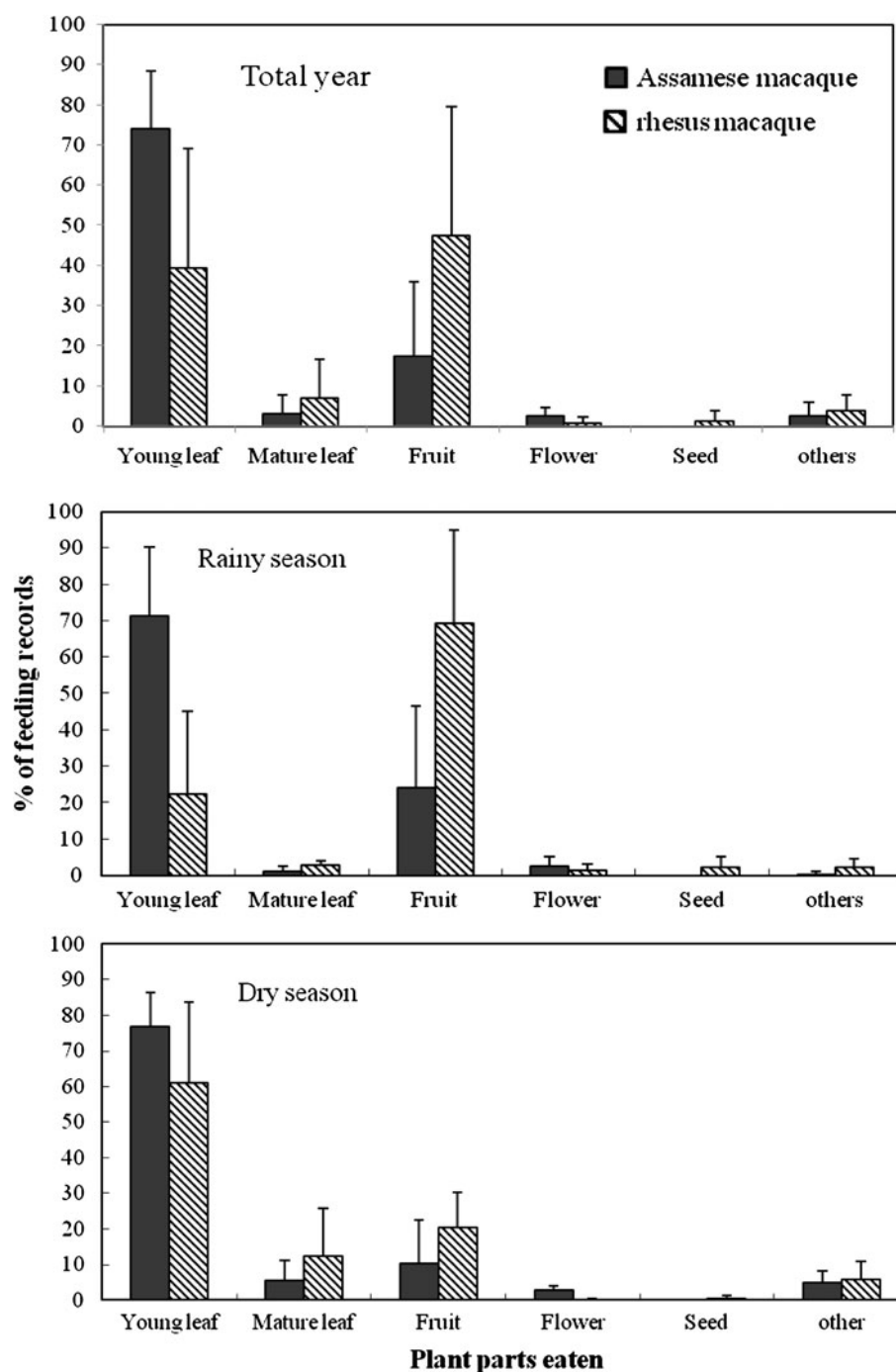
#### Seasonal changes in abundance and use of food categories

At Nonggang, the abundance of young leaves, fruits, and flowers showed similar seasonal changes between the two study periods, with lower abundance in the dry season than

in the rainy season (Fig. 3). There was marked inter-specific variation in seasonal dietary shift (Fig. 4). Rhesus macaques ate more fruits in the rainy season than in the dry season ( $Z = -2.205$ ,  $n_1 = 4$ ,  $n_2 = 5$ ,  $P = 0.027$ ). There was a significant and positive correlation between fruit consumption and abundance ( $r_s = 0.840$ ,  $n = 9$ ,  $P = 0.005$ ). In contrast, rhesus macaques consumed more young leaves in the dry season than in the rainy season ( $Z = -1.960$ ,  $P = 0.050$ ). A significant and negative correlation was found between the consumption of fruits and young leaves ( $r_s = -0.967$ ,  $n = 9$ ,  $P < 0.001$ ). Young leaves contributed to a large proportion of the monthly diet of Assamese macaques almost year-round (Fig. 4), and their consumption showed no significant seasonal variation



**Fig. 2** The pattern of use of different plant parts over the year and in the rainy and dry season by the two sympatric macaque species in the Nonggang Nature Reserve

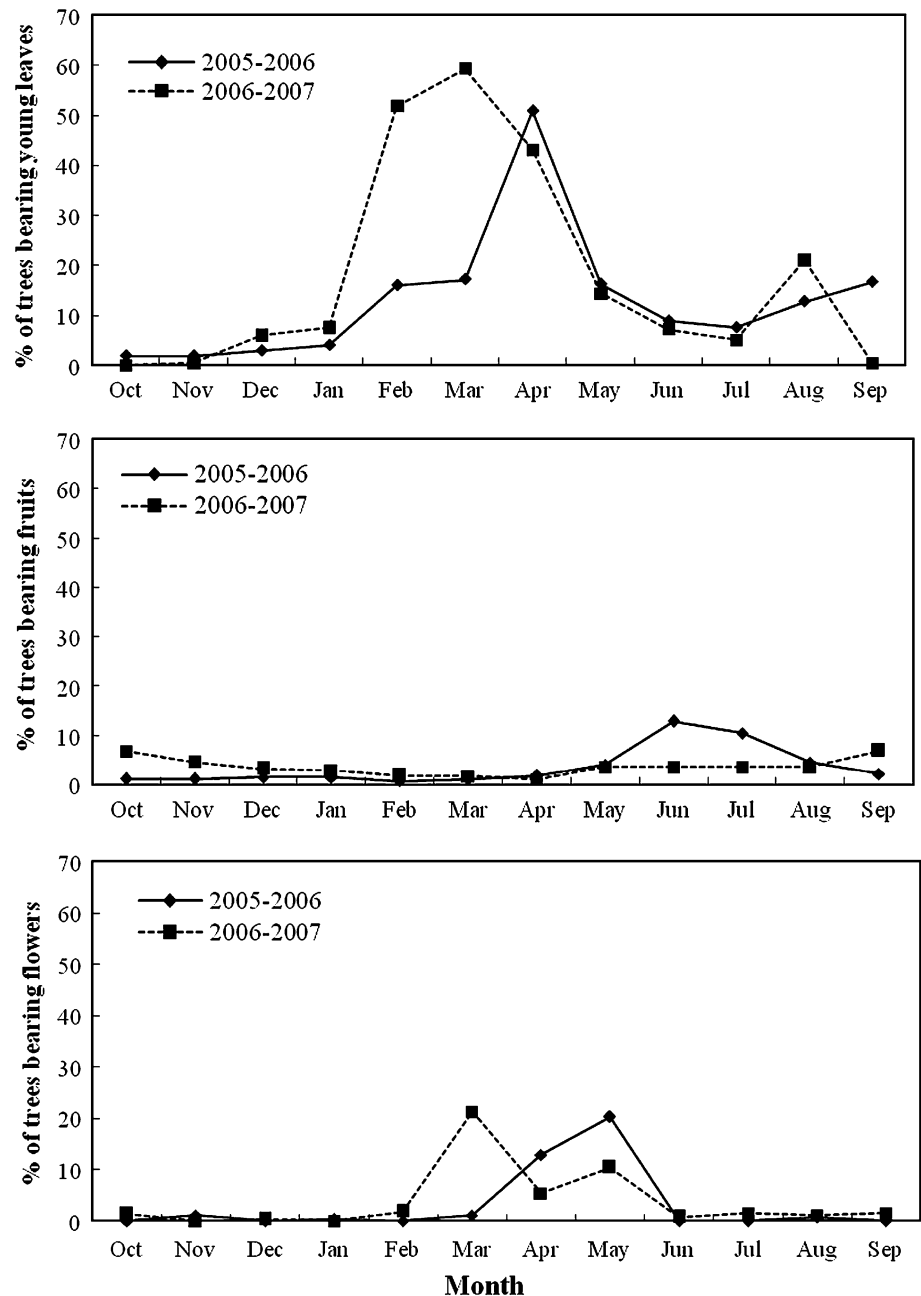


( $Z = -0.313$ ,  $n_1 = 5$ ,  $n_2 = 5$ ,  $P = 0.754$ ). Assamese macaques consumed more fruits when they were abundant, with a peak in July, but no significant seasonal variation was found in fruit consumption ( $Z = -0.838$ ,  $P = 0.421$ ). There was no significant correlation between young leaf consumption and abundance ( $r_s = 0.406$ ,  $n = 10$ ,  $P = 0.244$ ), as well as between fruit consumption and abundance ( $r_s = 0.393$ ,  $P = 0.261$ ).

#### Activity budget

There was significant variation in activity budgets of the two macaque species (Fig. 5). Assamese macaques spent more time resting ( $Z = -2.224$ ,  $n_1 = 10$ ,  $n_2 = 9$ ,  $P = 0.027$ ), whereas rhesus macaques devoted more time to feeding than Assamese macaques ( $Z = -3.021$ ,  $P = 0.001$ ). There was also significant difference in

**Fig. 3** Monthly abundance of young leaves, fruits and flowers in Nonggang study site during 2005–2007



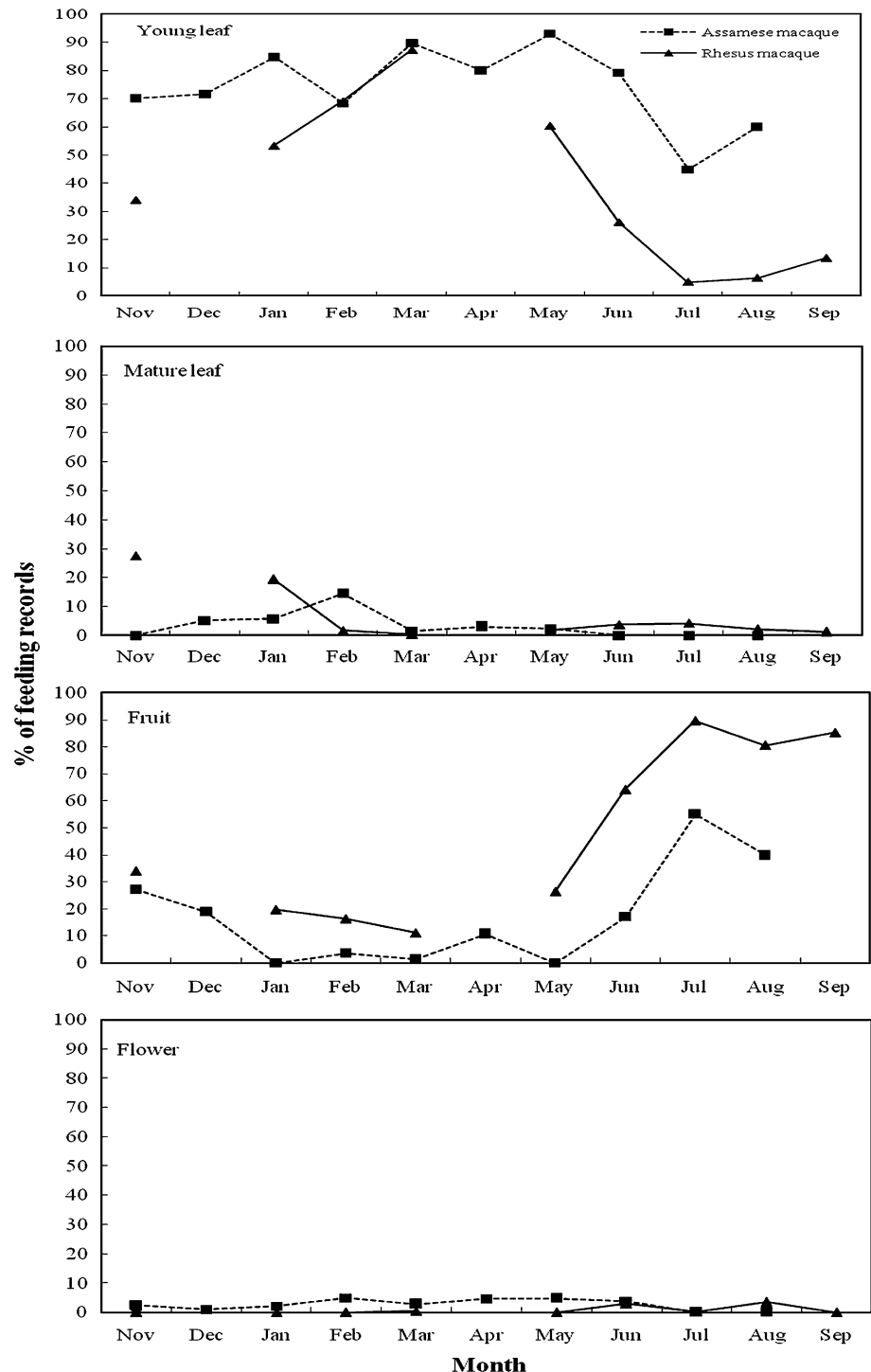
activity budgets of the two macaque species when comparison was limited to the rainy season (Fig. 5). In the rainy season, rhesus macaques spent more time feeding, and less time resting than Assamese macaques (feeding:  $Z = -2.236$ ,  $n_1 = 4$ ,  $n_2 = 5$ ,  $P = 0.036$ ; resting:  $Z = -2.236$ ,  $P = 0.036$ ). However, no significant variation was found in the dry season (feeding:  $Z = -1.776$ ,  $n_1 = 5$ ,  $n_2 = 5$ ,  $P = 0.095$ ; resting:  $Z = -1.358$ ,  $P = 0.222$ ).

#### Habitat use

The overall habitat categories used by the two macaque species are shown in Fig. 6. In most location records, the

two macaque species were observed to be present on the limestone hill. However, there was significant inter-specific variation in the use of different zones of the limestone hill (Fig. 6). We observed rhesus macaques more often on the hillside and in the valley (hillside:  $Z = -3.676$ ,  $n_1 = 10$ ,  $n_2 = 9$ ,  $P < 0.001$ ; valley:  $Z = -2.633$ ,  $P = 0.043$ ), whereas Assamese macaques used the cliff more frequently than rhesus macaques ( $Z = -3.676$ ,  $P < 0.001$ ). Similarly, Assamese macaques used the hill-top more frequently than rhesus macaques, but the difference is not statistically significant ( $Z = -1.675$ ,  $P = 0.113$ ). Similar patterns of habitat utilization by the two macaque species were found in both the rainy season

**Fig. 4** Monthly percentage of feeding records devoted to different food items in the diet of two sympatric macaque species in the Nonggang Nature Reserve



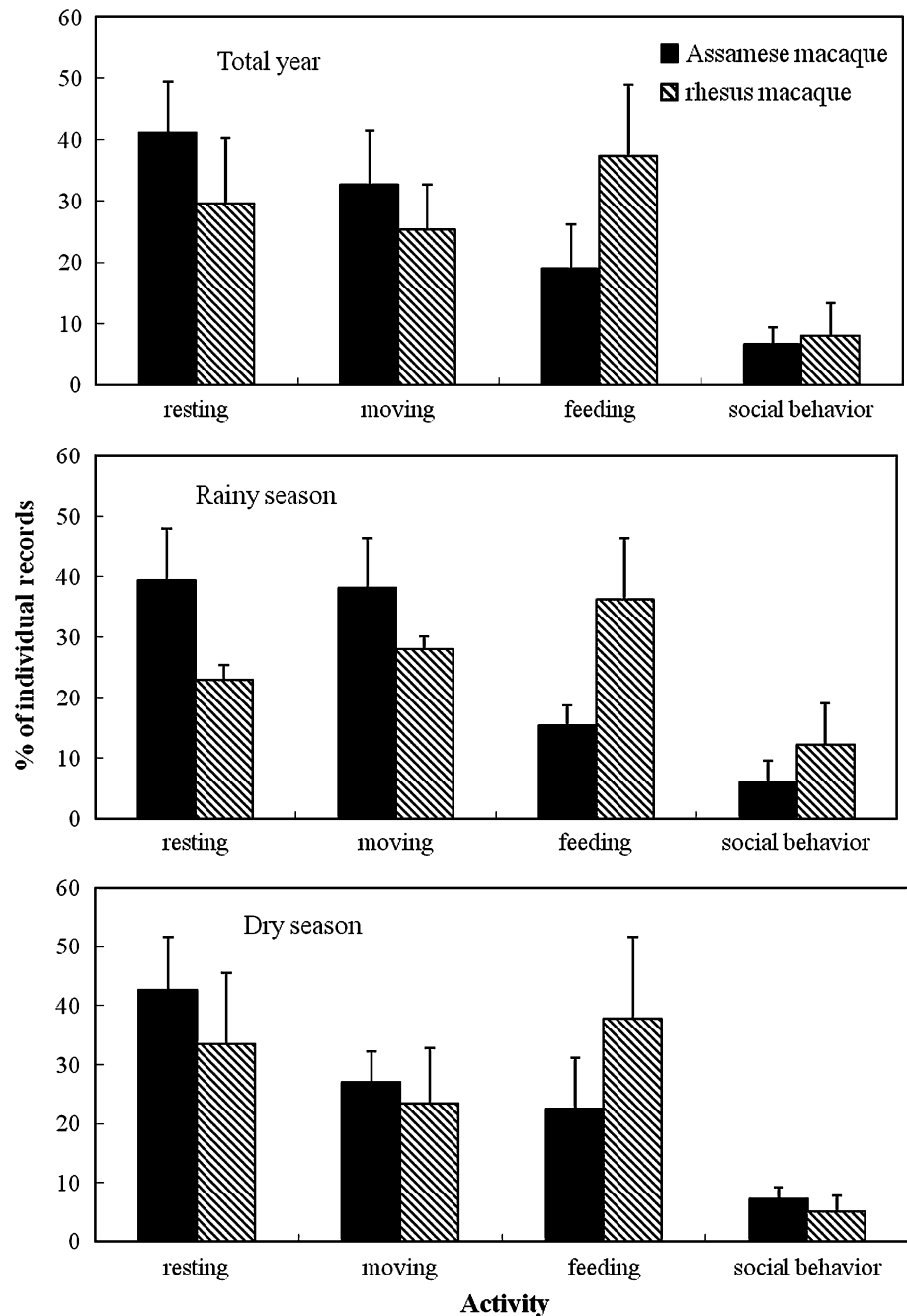
and the dry season (Fig. 6). Pianka's index, describing the habitat overlap between the two macaque species, was 0.40, 0.19 and 0.29 in the rainy season, the dry season and over the year, respectively.

There was also significant difference in the use of forest strata between the two macaque species (Fig. 7). Assamese macaques spent more active time on the ground ( $Z =$

$-3.674$ ,  $n_1 = 10$ ,  $n_2 = 9$ ,  $P < 0.001$ ), whereas rhesus macaques used lower and middle canopy heights more frequently than Assamese macaques (lower:  $Z = -2.531$ ,  $P = 0.010$ ; middle<sup>-</sup>:  $Z = -3.103$ ,  $P = 0.001$ ; middle<sup>+</sup>:  $Z = -3.429$ ,  $P < 0.001$ ). A similar pattern of canopy utilization by the two macaque species was found in both the rainy season and the dry season (Fig. 7).



**Fig. 5** Activity budgets of the two sympatric macaque species over the year and in the rainy and dry season in the Nonggang Nature Reserve

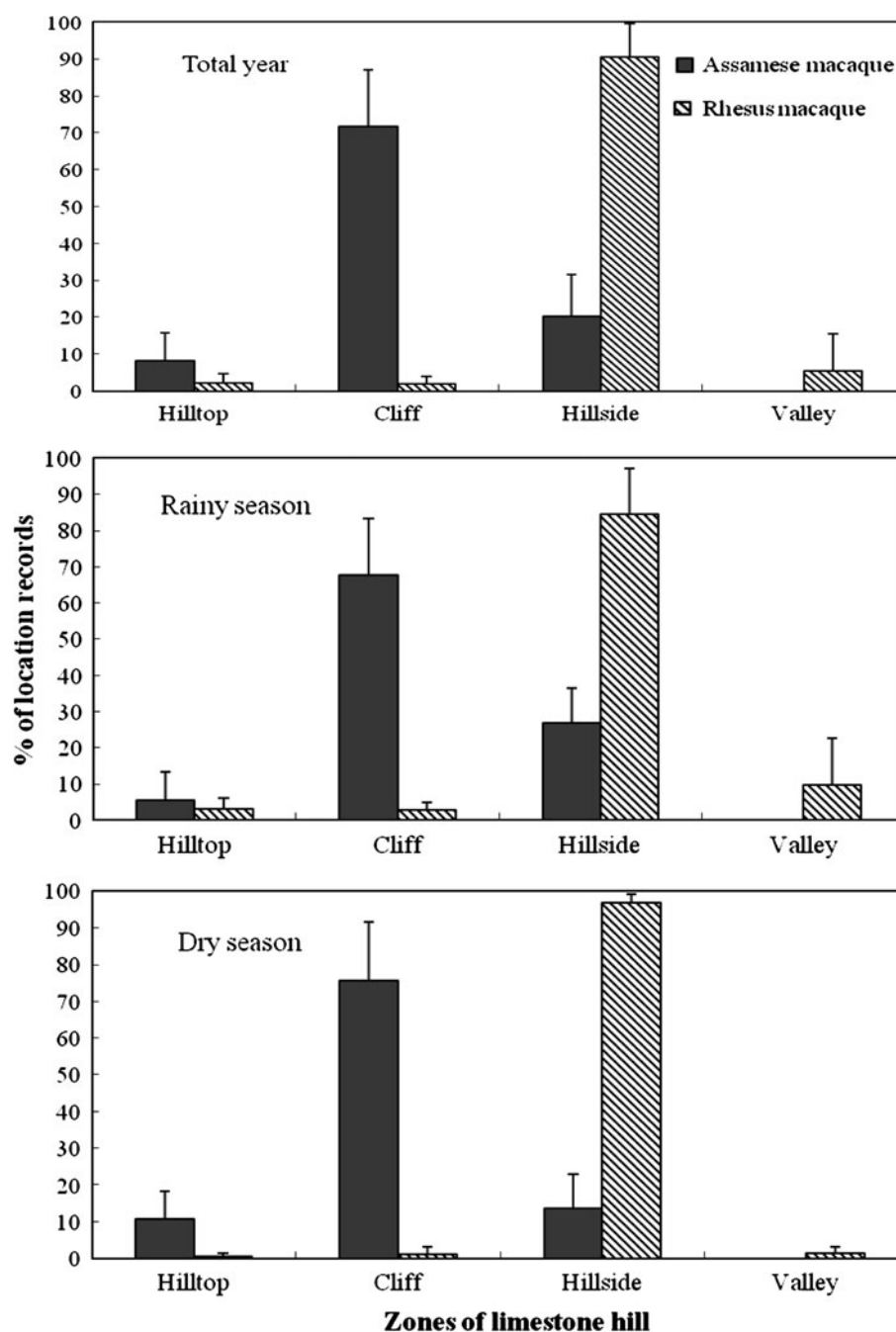


## Discussion

It is expected that closely related sympatric species employ processes that lead to niche separation that make the coexistence of species possible. In this study, although a total of 131 food species were consumed by the two macaque species, only 15 species (11 %) were shared by both. This degree of dietary overlap is much lower than that of 42 % reported for sympatric *Macaca leonina* and *M. mulatta* in Bangladesh (Feeroz 2012), as well as those for other sympatric primate species (e.g. 77 % for

*Cercopithecus ascanius* and *C. mitis* in Kakamega forest, Cords 1986; 43 % for *Procolobus badius* and *Colobus guereza* in the Kaibul National Park, Uganda, Chapman and Pavelka 2005; 40 % for *Presbytis potenziani* and *Simias concolor* on Mentawai Islands, Indonesia, Hadi et al. 2012). This small degree of dietary overlap is also reflected by the relatively low value of Pianka's index (0.38) for the two macaque species. A similar dietary overlap index of 0.32 was reported in a study on sympatric *Macaca silenus* and *M. radiata* in the rain forests of the Central Western Ghats (Singh et al. 2011). This small degree of dietary

**Fig. 6** The pattern of use of different zones of the limestone hills over the year and in the rainy and dry season by the two sympatric macaque species at Nonggang Nature Reserve



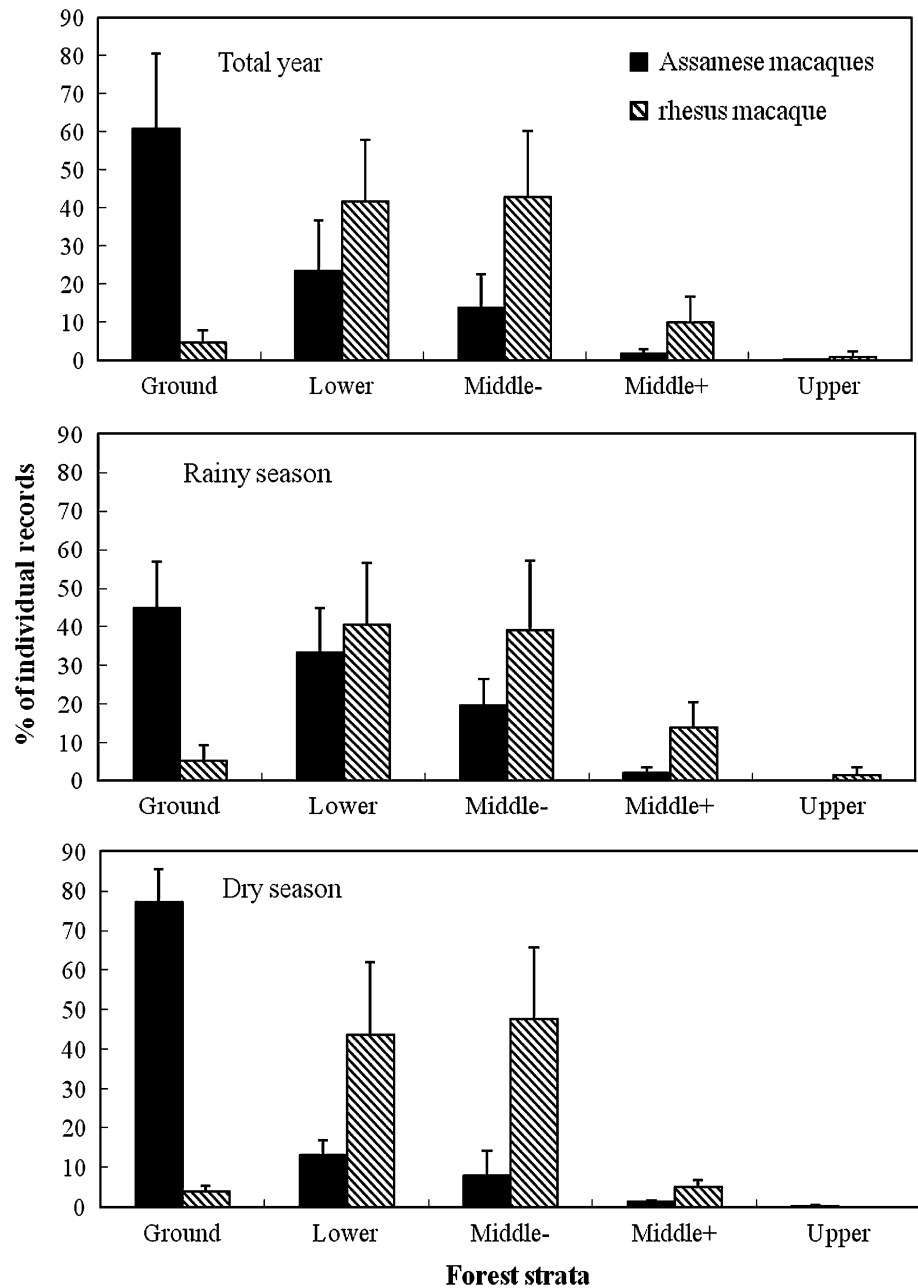
overlap may play an important role in explaining niche separation between the two macaque species.

This small degree of dietary overlap may be reflected by inter-specific difference in habitat use. There are significant differences in plant species among different zones of the limestone hills because of the differences in temperature, humidity and soil available to plants (Liang et al. 1988), decreasing, in principle, the number of foods shared by the two macaque species who showed different preference to different zones of the limestone hills. The degree of specialization on particular foods can also influence dietary

similarity between species (Cords 1986). Compared to rhesus macaques, Assamese macaques concentrated more foraging efforts on only a few food species, especially *Indocalamus calciculus*, which contributed to 62 % of the diet. This is also reflected in lower dietary diversity and evenness indexes of Assamese macaques than those of rhesus macaques. Thus, Assamese macaques appear to have narrower dietary niche than rhesus macaques, decreasing the number of foods that can be shared by species.

Another major dietary difference, which may explain niche separation between the two macaque species, was

**Fig. 7** The pattern of use of different canopy heights over the year and in the rainy and dry season by the two sympatric macaque species at Nonggang Nature Reserve



found in the analysis of food category composition. Young leaves constituted the bulk of the Assamese macaque diet, whereas rhesus macaques consumed more fruits. Even in terms of fruit consumption, the two macaque species had different preferences. Similar dietary differences have also been reported in other closely related sympatric primate species (Cords 1986; Hadi et al. 2012). For example, on the Mentawai Islands, *Presbytis potenziani* preferred to feed on fruits, while *Simias concolor* fed more on leaves (Hadi et al. 2012). Thus, feeding on a leaf- vs a fruit-based diet may represent niche separation among closely related sympatric species.

Pyke et al. (1977) proposed that in fluctuating environments, resource overlap between potential competitors should decrease during the period of resource scarcity, as has been found in many primate communities (e.g. *Ateles belzebuth* and *Lagothrix lagothricha*, Stevenson et al. 2000; *Macaca silenus* and *M. radiata*, Singh et al. 2011). In contrast, we found a higher degree of dietary overlap between the two macaque species in the dry season, a period of low fruit availability. This may be related to different foraging strategies adopted by the two macaque species in response to seasonal resource availability. In rhesus macaques, seasonal variation in diet was

significantly correlated with seasonal fluctuation in food availability. Rhesus macaques significantly increased fruit consumption as it became more available. When fruit became rare in the dry season, they consumed larger quantities of young leaves. Other Asian macaques have been known to respond to fruit shortages in this way (Su and Lee 2001; Kummar et al. 2007; Hanya et al. 2011). Young leaves were the stable, main part of Assamese macaques' diet year-round, which was further supplemented mainly by fruits. Thus, a higher degree of dietary overlap was more likely to occur during the period of low fruit availability, presumably because both species were forced to resort to the same food resources.

There were significant differences in activity budgets between the two macaque species, especially in the rainy season: rhesus macaques spent more time on feeding, and less time on resting than Assamese macaques. These differences may be explained by the greater reliance of rhesus macaques on fruits in the rainy season. Fruits are distributed in discrete patches (Richard 1985). Thus, rhesus macaques devoted more time to foraging in large fruit patches. In contrast, a prolonged period of resting is helpful for digestion of fibrous foods, such as leaves, by Assamese macaques (Lambert 1998). However, it cannot be ruled out that another factor, such as difference in feeding rate, may also influence the activity budgets of the two macaque species.

Our finding of low competition over resources between the two macaque species is further supported by our results on inter-specific difference in habitat use, even though the study macaque groups' home ranges overlapped with each other. In contrast to rhesus macaques, who showed preferences for hillsides, Assamese macaques tended to stay on the cliffs and hilltops. This small degree of habitat use overlap is reflected by the relatively low value of Pianka's index (0.29) for the two macaque species. Moreover, rhesus macaques spent most of their active time in the lower and middle canopy, while Assamese macaques were most frequently seen on the ground. Similar differences in canopy use has been observed in sympatric *Macaca fascicularis* and *M. nemestrina* in east Kalimantan (Rodman 1991), as well as in sympatric *M. leonina* and *M. mulatta* in Bangladesh (Feeroz 2012).

The variations in habitat and canopy use may in large part be related to differences in food preferences. In this study, fruits contributed to the highest proportion of the rhesus macaque's diet. Most large fruiting trees are found in the valley basins and on the hillsides rich in wet soil (Liang et al. 1988). Thus, rhesus macaques preferred hillsides, the location of most large fruiting trees. Assamese macaques, in contrast, tended to stay on the cliffs and hilltops where their staple food species, *Indocalamus callicolus*, is abundant (Liang et al. 1988). Moreover, *Indocalamus callicolus* is a small bamboo. Assamese macaques

always plucked unexpanded leaves from this bamboo and ate them on the ground. The variation in canopy use between the two macaque species may also be reflected by the differences in vegetation and structure among different zones of the limestone hill. For example, the Assamese macaque's semi-terrestrial habit is explained by their preference for cliff-hilltop areas, characterized by steep cliff-rocky surfaces and less vegetation.

In summary, sympatric Assamese macaques and rhesus macaques at Nonggang exhibit species-specific differences in diet (food species and food category preferences) and habitat use, as reflected by a low dietary and habitat use overlap value, which appears to reduce competition for food resources and allows them to be sympatric.

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