



Original Research Article

Daily activity pattern in Assamese macaques inhabiting limestone forest, southwest Guangxi, China

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ABSTRACT

Daily activity patterns and micro-variations in specific behaviors are essential for understanding how primates meet their energetic and/or nutritional requirements while dealing with environmental change. However, such data regarding the Assamese macaques living in limestone forests has yet to be obtained. This study focused on the daily activity patterns and temporal distribution of feeding behaviors of Assamese macaques at the Nonggang National Nature Reserve in southwest Guangxi, China, using instantaneous scan sampling method. Our results indicated that the Assamese macaques included two feeding peaks and two resting peaks. However, the resting peaks in the fruit-rich season occurred at midday (10:00–12:00) and at dusk (17:00–19:00), whereas the resting peaks in the fruit-lean season occurred in the morning (7:00–9:00) and at dusk (18:00–19:00). Meanwhile, the intervals between the feeding peaks in the fruit-lean season were shorter than in the fruit-rich season. Moreover, fruit consumption generally peaked during the morning (37%). The consumption of young leaves during the morning was lower than that in the afternoon, likely being attributed to their higher water content. The implication of the findings is that Assamese macaques not only adjust their daily activity patterns and feedings to cope with the seasonal and micro-variations in temperature and dietary requirements, but also to adapt to their particular environment.

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1. Introduction

Determining the activity patterns and time budgets of animals is essential for understanding their behavioral characteristics (And and Dayan, 2003; Di Fiore and Rodman, 2001; Dunbar et al., 2009; Janson, 1992). Animals could reconstruct their activity patterns such as reducing resting times to cope with current environmental changes, thus conserving sufficient time/energy for their social relationships that strongly affect an individual's long term fitness (Dunbar and Dunbar, 1988; Silk, 2007; Silk et al., 2003). As demonstrated among gelada baboons (*Theropithecus gelada*), withdrawing from socializing in order

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to increase foraging times had a negative impact on the group's stability (Dunbar, 1992; Dunbar and Dunbar, 1998). Hence, activity patterns and time budgets can serve as significant predictors of their fates in particular habitats (Dunbar, 1992; Dunbar et al., 2009; Korstjens et al., 2010).

As social groups, primates vary in their activity patterns across taxa and habitats, even within congeners inhabiting different habitats (Chapman and Chapman, 1991; Dunbar et al., 2009; Fan et al., 2008; Hanya, 2004; Korstjens et al., 2010; Ma et al., 2014; Matsuda et al., 2014; Zhou et al., 2007). There are many variables that determine their activities, including endogenous timing systems coordinated by internal molecular oscillators (Hut and Beersma, 2011) and natural environments (Lincoln et al., 2003). In terms of natural settings, food-related factors, such as the abundance, quality, distribution, and seasonal variation of food resources, are the determinants shaping the temporal distribution of primates' daily activities (Hanya, 2004; Korstjens et al., 2010; Matsuda et al., 2009; Sha and Hanya, 2013). In general, primates adjusted their time spent to the four major activities (resting, moving, feeding, and socializing) in response to the fluctuation in food abundance (Bach et al., 2017; Fan et al., 2013; Guan et al., 2018; Hanya, 2004; Sha and Hanya, 2013). For instance, the eastern hoolock gibbons (*Hoolock leuconedys*) increased their resting and decreased moving in response to the fruit-lean seasons (Fan et al., 2013).

Ambient temperatures have been considered as significant predictor when modeling primates' daily activities and social interactions (Aujard et al., 1998; Fan et al., 2008, 2012; Hill and Dunbar, 2002; Huang et al., 2003; Matsuda et al., 2009). As emphasized by Dunbar et al. (2009) and Korstjens et al. (2010), primates alter their activity patterns in response to thermoregulatory demands, thus indicating that temperature is more important than other ecological factors. For example, the majority of diurnal primates are characterized by two feeding peaks (morning and afternoon) separated by one resting peak at noon (Chapman and Chapman, 1991; Fan et al., 2008; Huang et al., 2003; Ma et al., 2014; Matsuda et al., 2014; Raemaekers, 1978). The resting peak is in response to the normally high temperatures around midday (Huang et al., 2003, 2016; Hill et al., 2004), as demonstrated by the white-headed langurs (*Trachypitecus leucocephalus*) which increase their resting times during hotter temperatures (Huang et al., 2003).

Conventional approaches have mainly examined the influence of climatic conditions, food and nutrient demands, and predation on activity patterns (Carlson et al., 2013; Cowlishaw, 1997; Fan et al., 2008, 2012; Guan et al., 2018; Hill and Dunbar, 2002; Hanya, 2004; Hill et al., 2004; Matsuda et al., 2009; Zhou et al., 2007). However, the majority of previous studies have examined the annual and/or monthly variations among animals, with limited focus on micro-variations in specific behaviors (Carlson et al., 2013). Information regarding such micro-variations is, in fact, crucial for understanding how primates interact with their environment and distribute their energy/time (Carlson et al., 2013; Ma et al., 2014; Matsuda et al., 2014; Raemaekers, 1978). For instance, the temporal distribution of feeding behavior can vary in order to meet the energy needs during different time periods (Fan et al., 2008; Ma et al., 2014; Raemaekers, 1978). Most primates prefer to consume fruits in the morning to compensate for the energy deficiency from the previous night's rest (Chapman and Chapman, 1991), which is demonstrated by several primates, including Cao Vit gibbons (*Nomascus nasutus*) (Ma et al., 2014), spider monkeys (*Ateles geoffroyi*) (Chapman and Chapman, 1991), and lar gibbons (*Hylobates lar*) (Raemaekers, 1978).

Assamese macaques (*Macaca assamensis*) are listed as Near Threatened in the IUCN Red List. They can be found in Bangladesh, Bhutan, southwestern China, northeastern India, Lao PDR, Myanmar, Nepal, northwestern Thailand, and northern Vietnam (Boonratana et al., 2008). In China, they inhabit monsoon evergreen broadleaf forests, deciduous broadleaf forests, mixed broadleaf and conifer forests, and conifer forests (Zhang, 1997). In southwest Guangxi, China, the Assamese macaques are restricted to limestone forests, where surface water is nearly absent (Chen, 1988; Hu, 1988; Jiang et al., 1993; Wada et al., 2010). Such habitats have forced the macaques to exclusively depend on the water from food (Huang et al., 2015, 2016; Zhou et al., 2011). Moreover, the temperatures in limestone forests dramatically fluctuate throughout the day hours (Huang et al., 2003; Larson, 2000).

Several studies have been conducted on the ecology of Assamese macaques in limestone forests, which primarily focus on their dietary adaptations (Huang et al., 2015, 2016; Zhou et al., 2011, 2018), activity budgets (Li et al., 2018; Zhou et al., 2007), and ranging behaviors (Li et al., 2017; Zhou et al., 2014), with the emphases on their seasonal variations. However, data regarding their daily activity patterns and temporal distribution of feeding behaviors has yet to be obtained. Therefore, in the present study, we collected such data to examining the ecological adaptation of the Assamese macaques in the Nonggang National Nature Reserve in southwest Guangxi, China, by testing the following predictions:

- 1) Temperatures during the fruit-rich months (April to October) are higher than those in the fruit-lean months (November to March) (Huang et al., 2015). Due to their need in the high temperature avoidance, the Assamese macaques in the limestone forests should have more pronounced midday resting peak during the fruit-rich months than in the fruit-lean months.
- 2) Fruits, particularly mature fruits, are richer in sugar and more rapidly converted into energy than leaves (Richard, 1985). Animals are generally in need of compensation for the energy deficiency caused by previous night's resting (Chapman and Chapman, 1991). Due to the fact that they are folivorous while still preferred to fruits (Huang et al., 2015; Zhou et al., 2018), the Assamese macaques in the limestone forests should consume more fruits during the morning than in the afternoon.
- 3) Free-standing water on the rock surfaces is nearly absent in limestone forests (Hu, 1988; Larson, 2000). Meanwhile, young leaves contain more water than fruits (Richard, 1985). Due to their heavy dependences on food water (Huang et al., 2016) and the higher temperatures at noon than morning hours, the Assamese macaques in the limestone forests should consume more young leaves during the afternoon than in the morning.

2. Methods

2.1. Study site and animals

This study was conducted at the Nonggang National Nature Reserve in southwest Guangxi, China (22° 29' 25" N, 106° 53' 33" E), between September 2012 and August 2013. This seasonal tropical rainforest consists of limestone hills, with an altitude ranging from 400 m to 600 m above sea level (Guangxi Forestry Department, 1993). The 10 most dominant plant families in the reserve include: *Euphorbiaceae*, *Moraceae*, *Ebenaceae*, *Tiliaceae*, *Poaceae*, *Meliaceae*, *Sterculiaceae*, *Verbenaceae*, *Rubiaceae*, and *Sapindaceae*. Among the 10 most common tree species, *Diospyros siderophylla* is the dominant one, followed by *Streblus indicus*, *Vitex kwangsiensis*, *Excentrodendron tonkinense*, *Ficu shispida*, *Diospyros eriantha*, *Pterospermum heterophyllum*, *Maclura tricuspidata*, *Cleistanthus saichikii*, and *Cleistanthus petelotii* (Huang et al., 2015).

We collected data on climate including minimum/maximum temperatures and rainfall. Based on the findings, the mean monthly minimum temperature was 14.9 °C (ranging from 6.1 °C in January to 19.9 °C in July), whereas the mean monthly maximum temperature was 26.5 °C (ranging from 15.9 °C in January to 31.3 °C in June). The total rainfall during this research period was 1,055 mm (Huang et al., 2015). Moreover, one group of Assamese macaques was observed, which initially consisted of 14 individuals (2 adult males, 6 adult females, 6 juveniles), but increased to 16 members after the birth of 2 infants.

2.2. Behavioral data collection

Behavioral observations were conducted from September 2012 to August 2013 after 3 months habituation. For the full-day observations, we located the study group in/near their sleeping sites at dawn and observed the group until dusk. For the partial-day observations, we observed the macaques whenever we encountered the group and ended the observations when the group either disappeared or could not be seen after entering their sleeping sites.

During the observations, behavioral data was collected using instantaneous scan sampling method (Altmann, 1974). The sampling intervals were set as 15-min. For each sampling, a 5-min scan recorded the behaviors of any individuals in sight, followed by 10 min of inactivity. Moreover, during the first 5 s of each sampling, the predominant behavior of each sampled individual was noted. If the macaque was engaged in more than one behavior, then the animal was observed for additional seconds until a predominant behavior was identified (Fan et al., 2012). The group was scanned from left to right (or clockwise) in order to avoid any bias toward a particular individual and/or activity (Huang et al., 2017). Overall, we yielded 17,186 individual records (monthly $1,432 \pm 402$) from 3,616 scan samplings (monthly 301 ± 81), with an average of 4.8 individuals per scan. In total, the group of macaques was observed for 904 h (see Table 1).

The group's activities were categorized into four classes: resting, moving, feeding, and socializing. Resting included instances in which the animal was inactive, usually sitting or lying down but not engaging in social activities; this behavior also included the cases of auto-grooming occurred during resting. Moving included movements such as walking, running, climbing, and jumping, in which resulted in change of spatial position. Feeding included manually or orally manipulating food items. Socializing included social grooming and playing. More specifically, when the individual was feeding, the plant species and parts eaten, including young leaves, mature leaves, flowers, fruits, seeds, barks, petioles, stems, were recorded. When the food items could not be discerned, they were recorded as "unknown". For any unidentified plant species in the field, specimens were collected (along with auxiliary photos) for subsequent identification by the Guangxi Institute of Botany, Chinese Academy of Sciences.

2.3. Data analysis

For the data analysis, we used hourly activity-time budgets to express the group's activity patterns (Fan et al., 2012; Zhou et al., 2007). The time budgets were presented as the proportion of the time spent on certain activities (i.e. percentage of

Table 1
Information for behavioral scanning on Assamese macaques.

Month	No. of sampling days	No. of observation hours	No. of scans	No. of records
September/2012	8	44	176	904
October	9	55	220	1155
November	12	84	336	1755
December	11	81.75	327	1559
January/2013	14	106.75	427	1952
February	6	52.5	210	964
March	13	103	412	2095
April	14	96.25	385	1804
May	8	58.5	234	1061
June	9	75.25	301	1478
July	12	78.25	313	1309
August	8	68.75	275	1150
In total	124	904	3616	17186
Average	10.3	75.33	301.3	1432.2
SD	2.7	20.36	81.4	402.0

sample points for specific activities). As stated earlier, four predominant activities (resting, moving, feeding, and socializing) were used to analyze the group's patterns. Moreover, the analysis only included four samplings per hour, while the infants' records were excluded because they were unable to act independently. For each scan, we first divided the number of individuals devoted to various activities by the total number of individuals recorded in the scan. Then, by averaging the four scans, the hourly activity-time budget was determined, which provided the data for the monthly activity-time budget. The data for each hour was averaged to correct for potential bias from the uneven monthly observation records. Finally, the seasonal time budget was constructed according to the mean values of the relevant months.

The temporal distribution of the group's feeding behaviors was determined by calculating the hourly dietary composition (i.e. percentage of sample points for feeding) (Huang et al., 2016). For this purpose, we first divided the number of individuals devoted to feeding on certain items in each scan by the total number of individuals recorded in the scan. Then, this value was divided by the proportion of individuals engaged in feeding to determine the percentage of feeding time spent on specific items. The data for each hour was also averaged to correct for potential bias from the uneven scans recorded throughout the day. Finally, the average value of the percentage of feeding time spent on specific items in the same hour was used to represent the dietary composition across daytime hours. It is important to note that this study only featured the group's feeding activities in regard to young leaves and fruits, since such items dominated their diet throughout the entire research period (Huang et al., 2015, 2016; Zhou et al., 2011, 2018). Moreover, the hours of the day between 06:00 and 19:00 was divided into morning and afternoon using 12:00 as the boundary (Huang et al., 2016).

Following Huang et al. (2015), the research period in the present study was divided into a fruit-rich season and a fruit-lean season according to monthly fruit abundance. For phenology monitoring, we randomly selected 200 trees from 20 food species (i.e., 10 individuals per species), based on previous studies (Zhou et al., 2011, 2018) and a three-month pilot study (Li et al., 2017). At the end of each month, we visually inspected the sampled trees for the presence of food (e.g., young leaves, flowers, and fruit), the abundance of which was scored on a 5-point scale. The monthly food availability index (FAI) for the young leaves, flowers, and fruits was calculated by integrating the density, basal area, and phenology score of the sampled trees. Consequently, the fruit-lean season was determined to be from November 2012 to March 2013 (with a fruit FAI of <500), while the fruit-rich season was the remainder of the research period (with a fruit FAI of >500) (Huang et al., 2015).

All of the variables were tested via the one-sample Kolmogorov-Smirnov test to examine normality. The results indicated that a few variables of hourly activity-time budgets deviated from a normal distribution. Thus, the Kruskal-Wallis test was used to examine the variations in hourly activities. Then, a cluster analysis (based on Euclidean distance) was conducted for resting, moving, feeding, and socializing in order to identify any relevant peaks and variations in such activities, if the variation in specific activity across daytime hours was detected. Following Matsuda et al. (2014), the statistical significance of any differences between the sampling units was examined by the analysis of similarity (ANOSIM). For this purpose, the matrix was permuted 10,000 times. We used an independent samples *t*-test in order to examine any variations in the dietary composition between the morning and afternoon hours. R software (version 3.3.2) was used to perform the statistical analysis. All of the tests were two-tailed (except for the dietary composition comparison (one-tailed)), with significance levels of 0.05.

3. Results

3.1. Diurnal activity patterns and seasonal variations

The activities of resting, feeding, and socializing showed significant variations across daytime hours (see Fig. 1, Table 2). Overall, the Assamese macaques included two resting peaks (6:00–7:00, 18:00–19:00) (ANOSIM, $r = 0.581$, $p = 0.003$) and two feeding peaks (8:00, 15:00–17:00) ($r = 0.389$, $p = 0.014$). The macaques generally entered their sleeping sites and stopped diurnal activities after 20:00. Their socializing patterns indicated no significant peak ($r = 0.270$, $p = 0.197$). As for moving, the group maintained a stable trend across daytime hours, without marked hourly variation (see Table 2).

However, the activity patterns during the fruit-rich and fruit-lean months revealed marked variations across daytime hours (see Fig. 2 and Table 2). More specifically, there were two significant resting peaks in the fruit-rich season, occurring at midday (10:00–12:00) and at dusk (17:00–19:00) ($r = 0.448$, $p = 0.005$) (see Fig. 2). There were also two resting peaks in the fruit-lean season, occurring in the morning (7:00–9:00) and at dusk (18:00–19:00) ($r = 0.407$, $p = 0.014$) (see Fig. 2). Meanwhile, the feeding peaks occurred twice in both seasons (see Fig. 2). Moreover, during the fruit-rich season, the macaques concentrated on feeding from 7:00–9:00 and from 15:00–17:00 ($r = 0.868$, $p < 0.001$), whereas during the fruit-lean season, the group focused on feeding from 9:00–11:00 and from 14:00–16:00 ($r = 0.521$, $p = 0.003$), with shorter intervals between the peaks than in the fruit-rich season. As for the other activities, there was no significant socializing peak in the fruit-rich season ($r = 0.136$, $p = 0.175$) and no moving peak in the fruit-lean season ($r = 0.168$, $p = 0.123$).

3.2. Temporal variations in feeding behaviors

The feeding behaviors of the Assamese macaques distinctly varied across daytime hours. According to Fig. 3, young leaves accounted for 69.2% of the total feeding time in the morning (with a minimum (62.1%) at 6:00) and 76.5% of the total feeding time in the afternoon (with a maximum (82.3%) at 15:00). Conversely, fruit consumption accounted for 27.2% of the feeding time during the morning and 19.0% of the feeding time in the afternoon, with a maximum (37.0%) at 6:00 and a minimum

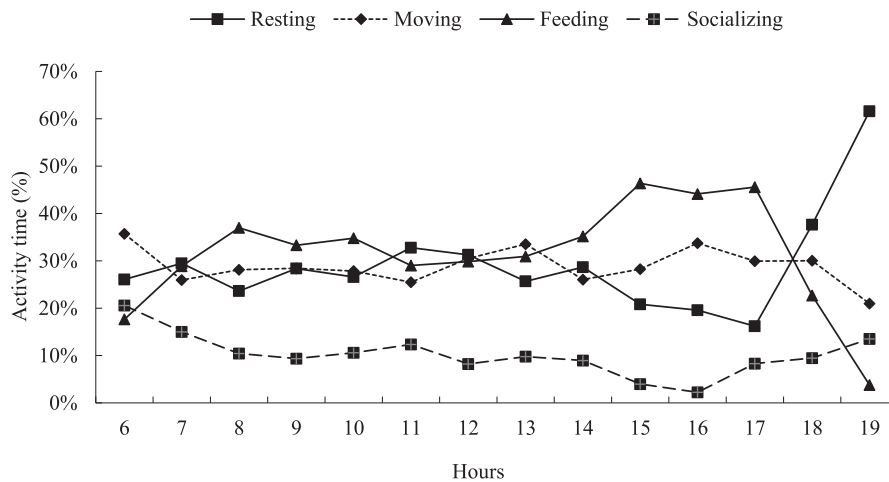


Fig. 1. Annual activity patterns of the Assamese macaques.

Table 2

Variations in activity patterns of Assamese macaques across daytime hours (Kruskal-Wallis test, $df = 13$).

		Resting	Moving	Feeding	Socializing
Annual	χ^2	37.032	14.861	43.104	24.122
	p	<0.001	0.316	<0.001	0.030
Fruit-rich season	χ^2	35.427	10.903	29.729	25.909
	p	0.001	0.619	0.005	0.017
Fruit-lean season	χ^2	35.273	25.46	43.053	20.843
	p	0.001	0.020	<0.001	0.076

(10.9%) at 15:00. Meanwhile, the consumption of young leaves during the morning was lower than that in the afternoon ($t = -2.764$, $df = 12$, $p = 0.009$), whereas the consumption of fruits during the morning was higher than that in the afternoon ($t = 2.400$, $df = 12$, $p = 0.017$).

In the fruit-rich season, young leaves accounted for 58.8% of the total feeding time during the morning and 68.9% of the total feeding time in the afternoon. Moreover, fruit consumption accounted for 38.1% of the feeding time during the morning and 28.7% of the feeding time during the afternoon. Finally, the consumption of young leaves during the morning was lower than that in the afternoon ($t = -2.754$, $df = 12$, $p = 0.009$), while the consumption of fruits during the morning was higher than that in the afternoon ($t = 2.480$, $df = 12$, $p = 0.014$). However, during the fruit-lean season, there was no significant difference in the feeding times devoted to young leaves and fruits during the morning and afternoon (young leaves: $t = 1.780$, $df = 11$, $p = 0.051$; fruits: $t = -1.411$, $df = 11$, $p = 0.092$) (see Fig. 3).

4. Discussion

Over a one-year period, the present study focused on the daily activity patterns and temporal distribution of feeding behaviors among the Assamese macaques. The findings showed that the macaques had two resting peaks in both the fruit-rich season and the fruit-lean season. However, the first peak was at midday in the former and in the morning during the latter. Thus, Prediction 1 is supported. This seasonal difference could be attributed to the temperature and humidity fluctuations, which is consistent with other diurnal primates (Chapman and Chapman, 1991; Huang et al., 2003; Matsuda et al., 2014; Robinson, 1984). Assamese macaques had a more pronounced resting peak during midday hours in the fruit-rich months characterized by high temperature and humidity. The midday resting peak allowed the macaques to maintain energy during high temperatures, promoted the digestion of foods eaten during the morning (Huang et al., 2003; Richard, 1985), and reduced water loss caused by perspiration (Aujard et al., 1998). It was also observed that the macaques in the fruit-lean season had a resting peak within the first hour of leaving their sleeping sites. Again, this could be linked to their thermoregulation strategy and the low-calorie content of the food available to them, i.e., young bamboo leaves (Huang, 2017; Richard, 1985). We also found that during the fruit-lean season, the temperatures were generally lower than in the fruit-rich months (Huang et al., 2015). As a result, the macaques basked in the sun before harvesting food, which is consistent with the results of previous studies on sympatric primates (Huang et al., 2003, 2006; Zhou et al., 2007). This strategy helped them to not only conserve energy but also deal with the poor food quality and the low atmospheric temperatures (Guan et al., 2018).

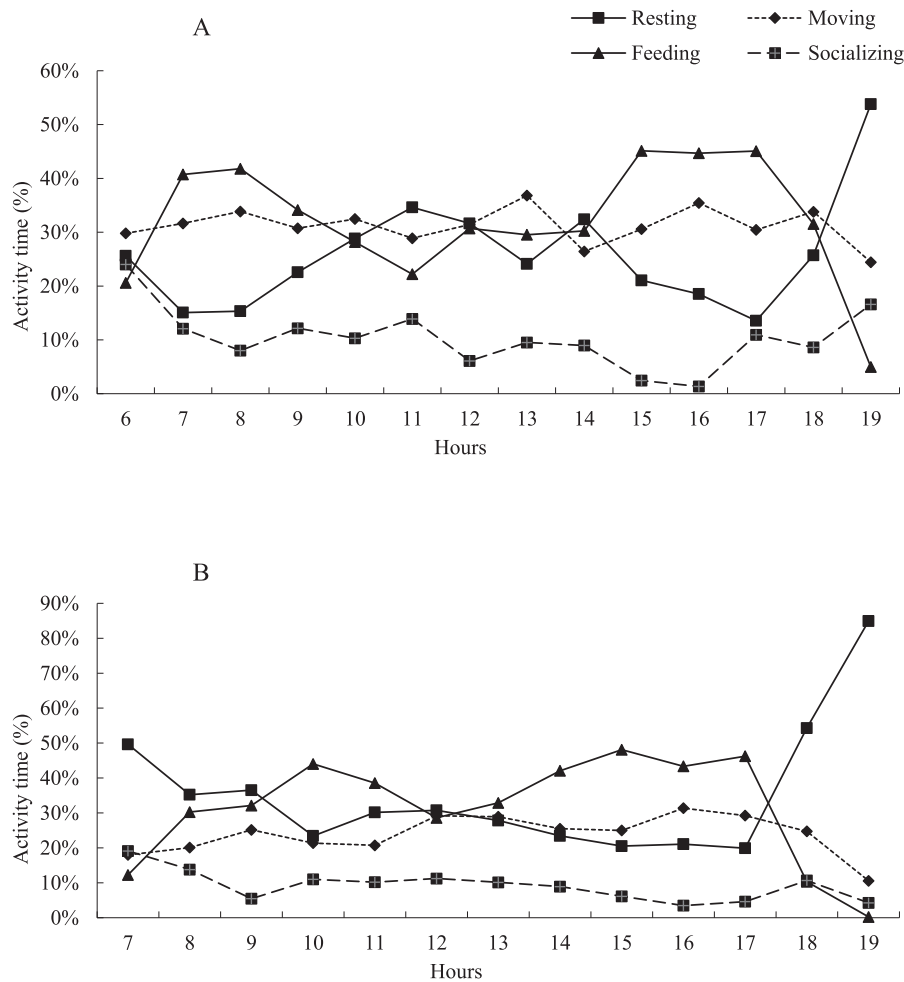


Fig. 2. Activity patterns of the Assamese macaques during the fruit-rich season (A) and fruit-lean season (B).

Moreover, during the fruit-lean months, we observed many cases in which the macaques remained stationary and/or performed social grooming in the morning.

As for their feeding intensity, the macaques maintained similar attributes in both seasons. This pattern could again be linked to the low-calorie, young bamboo leaves, and the reduced fruit intake during the fruit-lean months (Huang et al., 2015; Zhou et al., 2011, 2018). Assamese macaques in the limestone forests consume young leaves of *B. saxatilis* year-round, and decreased fruit intakes but increased young leaf consumptions in the fruit-lean months (Huang et al., 2015). The calorie content in bamboo leaves was extremely lower than most of other plant species (Chongtham et al., 2011; Huang, 2017). Moreover, the genus *Bonia* was characterized by their solitary unexpanded leaf needles that were used by macaques (Huang et al., 2015). The Assamese macaques thus ate large amount of bamboo to meet their energetic and nutritional requirements, which probably forced them to maintain a stable rhythm of feeding to ensure adequate energy intake. Regarding the two feeding peaks in the morning and afternoon, they could once again be based on the need to avoid the limestone forest's high temperatures that generally peak around noon (Huang et al., 2003; Larson, 2000). A similar strategy has been found among sympatric primates. For instance, both the Francois langurs (*T. francoisi*) and the white-headed langurs tend to rest during the hottest hours of the day and initiate physical activities when the temperature drops, which is considered as an effective strategy for karst primates when coping with the high ambient temperature in the limestone forests (Huang et al., 2003, 2006; Zhou et al., 2007).

Socializing patterns of the study group revealed no significant peak; however, the variations in socializing pattern across daytime hours were significant when using annual and fruit-rich season records. This pattern could be, at least partly, linked to the seasonal variation in the day length. Previous studies confirm that animals must allocate sufficient time to socializing,

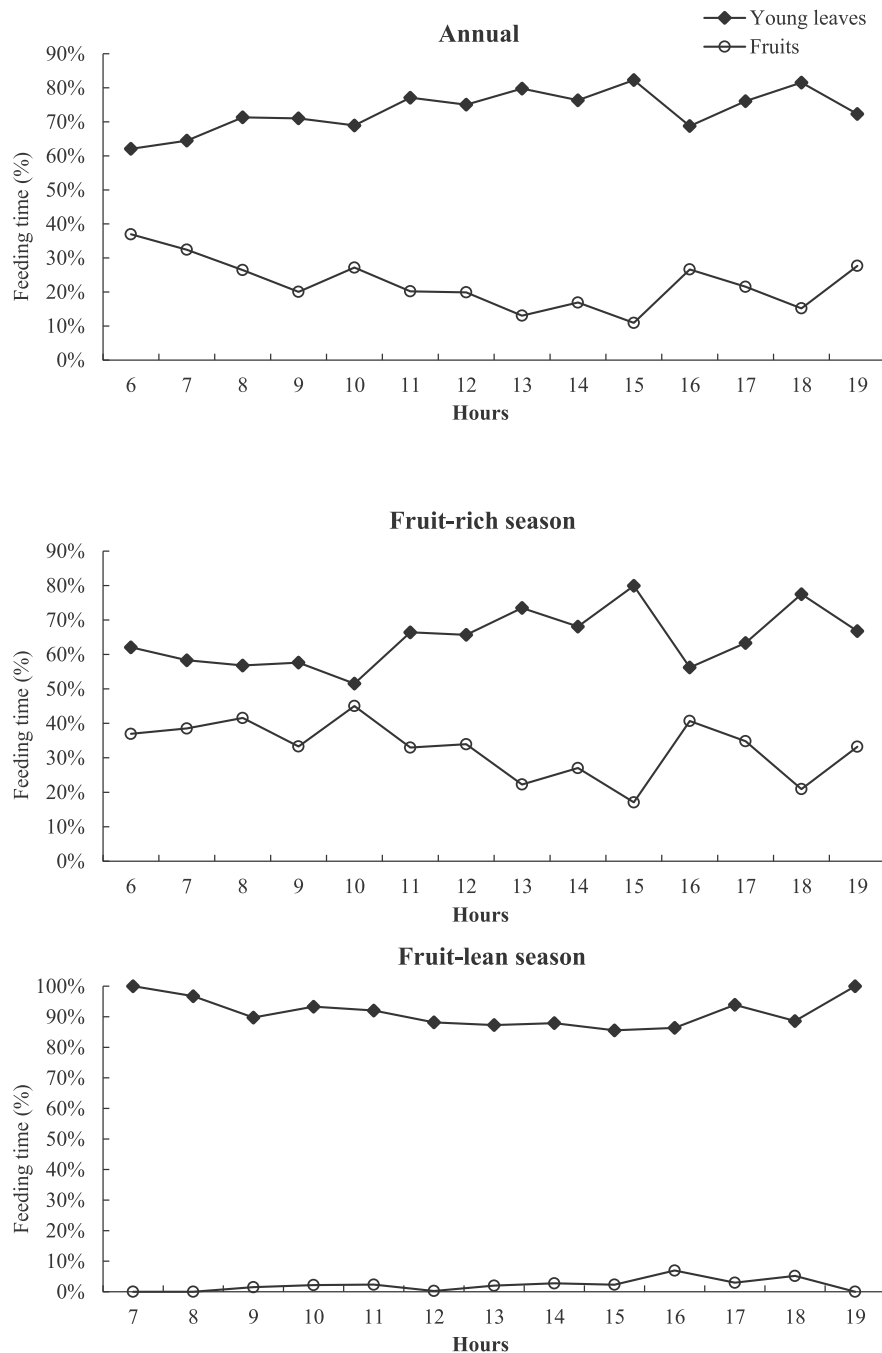


Fig. 3. Feeding times devoted to young leaves and fruits during various daytime hours.

which is essential for grouping patterns (Dunbar, 1992; Dunbar and Dunbar, 1998; Dunbar et al., 2009). For example, being forced to draw on socializing strongly influenced the gelada baboons' group instability, even permanently fission when too much socializing is compromised (Dunbar, 1992; Dunbar and Dunbar, 1998). In this study, the Assamese macaques socialized with similar frequency during the fruit-lean season that had shorter day lengths, contrary to the cases during the fruit-rich months that featured longer day lengths. This pattern likely aims them preserving grouping intensity. Actually, these macaques' monthly activity time engaging in grooming were exclusively driven by the day length (unpublished data). Moreover, grooming, the social activity most frequently occurred, is a relatively low-energy activity (Dunbar and Dunbar, 1998; Dunbar et al., 2009), largely facilitating them conserving energy during the cold fruit-lean months.

Overall, the macaques consumed more fruits and less leaves in the morning, compared to the afternoon. Thus, both prediction 2 and 3 are supported. Such actions are in accordance with other primates, such as *Ateles geoffroyi* (Chapman and Chapman, 1991), *Cebus olivaceus* (Robinson, 1984), *Pan troglodytes* (Carlson et al., 2013), *Hylobates lar* (Raemaekers, 1978), *Nasalis larvatus* (Matsuda et al., 2014), and *Nomascus nasutus* (Ma et al., 2014). Based on the fact that fruits are richer in sugar, more easily digestible, and more rapidly converted into energy than leaves (Chapman and Chapman, 1991; Richard, 1985), primates generally prefer fruits (rather than low-energy and high-fiber leaves) in order to compensate for the energy deficiency caused by the preceding night's rest. For example, the black crested gibbon (*Nomascus concolor jingdongensis*) (Fan et al., 2009), the Cao Vit gibbon (Ma et al., 2014), and the hoolock gibbon (*Hoolock hoolock*) (Ahsan, 2001) eagerly select fruits to raise their blood glucose levels in the early morning. Similarly, the Assamese macaques consumed more fruits in the morning, except during the fruit-lean season when the fruits were nearly absent.

The consumption of more young leaves in the afternoon could be attributed to their higher water content. As stated earlier, since limestone forests are characterized by an extreme lack of surface water (Huang et al., 2003), karst primates are forced to find other ways to deal with their hydration needs. Almost all sympatric primates, such as the white-headed langur, the Francois langur, and the rhesus macaque (*Macaca mulatta*), exclusively depend on water from their foods (Huang et al., 2003, 2006; 2015, 2016; Tang et al., 2011). As for the Assamese macaques, they not only consumed young leaves for their nutritional needs, but also for their water content, particularly during the afternoon (Huang et al., 2016; Huang, 2017). Meanwhile, since the leaves are generally more difficult to digest than fruits, eating more leaves shortly before entering sleeping sites likely could assist themselves to reduce the distance travelled with a stomach full of leaves (Chapman and Chapman, 1991). In addition, the long stationary nights' resting periods actually aided their digestion (Chapman and Chapman, 1991; Richard, 1985).

In summary, the Assamese macaques in this study had variations in their resting and feeding peaks in order to deal with thermoregulation and nutritional requirements. They consumed more fruits in the morning to offset the energy deficit, and consumed more leaves in the afternoon to meet nutritional and hydration needs. The implication of the findings is that Assamese macaques adjust their daily activity patterns not only to cope with the seasonal and micro-variations in temperature and dietary requirements, but also to adapt to their particular habitat.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00709>.

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