Diet of the Assamese macaque Macaca assamensis in limestone habitats of Nonggang, China

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Abstract To enhance our understanding of dietary adaptations in macaques we studied the diet of the Assamese macaque Macaca assamensis in limestone seasonal rain forests at Nonggang Nature Reserve, China from September 2005 to August 2006. Our results show that although macaques fed on many plant species, 85.2% of the diet came from only 12 species, of which a bamboo species, Indocalamus calcicolus contributed to 62% of the diet. Young leaves were staple food items (74.1% of the diet) for Assamese macaques at Nonggang, and constituted the bulk of monthly diets almost year-round, ranging from 44.9% (July) to 92.9% (May). Young parts of Indocalamus calcicolus unexpanded leaves contributed to a large proportion of the young leaf diet in most months. Fruit accounted for only 17.4% of the diet, with a peak of consumption in July. We suggest that this highly folivorous diet may be related to the long lean season of fruit availability in limestone habitats as well as the utilization of cliffs of low fruit availability [Current Zoology 57 (1): 18–25, 2011].

Key words Assamese macaque, Macaca assamensis, Diet, Limestone habitat

Many studies have revealed dietary variation among primates (Campbell et al., 2007; Yeager and Koll, 2000). Macaque species have been described as primarily frugivorous (Caldecott, 1986; Yeager, 1996; O’Brien and Kinnaird, 1997; Andrews, 2003; Riley, 2007). For example, O’Brien and Kinnaird (1997) reported that crested black macaques Macaca nigra spent 66% of feeding time on fruits. A study of tonkean macaques M. tonkeana in Sulawesi, Indonesia, showed that fruits accounted for 76.7%-84.4% of their diets (Riley, 2007). However, evidence is steadily accumulating that leaves contribute a large proportion of diet in some species (Zhao, 1996; Hanya, 2004). For example, Japanese macaques M. fuscata in the coniferous forest of Yakushima spent 45% of feeding time on leaves, and feeding time on fruits was only 13% (Hanya, 2004). Even within a species and population, considerable dietary variation in terms of plant species and parts eaten may occur (Hanya et al., 2003; Harris and Chapman, 2007). For example, Hanya et al. (2003) found variation in diet amongst Japanese macaques inhabiting different altitudinal zones. Much of these differences can largely be explained as differences in the temporal availability and spatial distribution of fruit resources (Hanya et al., 2003; Hanya, 2004).

The Assamese macaque Macaca assamensis is classified as Near Threatened by the 2008 IUCN Red List (Boonratana et al., 2008). They are distributed in Nepal, Sikkim, Bhutan, India, northern Thailand, and southernmost China (to the upper Mekong in Tibet, and in the east into southern Guizhou). They live in many different habitats including monsoon evergreen broadleaf forest, deciduous broadleaf forest, mixed broadleaf and conifer forest, and conifer forest (Zhang et al., 1997). Some studies have been undertaken on the diet of Assamese macaques in the highlands of Nepal, Bhutan and India, and have concluded that they are primarily folivorous (Ahsan, 1994; Chalise et al., 2003). However, systematic study on the behavior and ecology of this species in China is rare, which is important for supplementing the biology of the species, and also provide comparative information for the general study of behavioral adaptation in macaques. Here, we present data on the diet of Assamese macaques at Nonggang Nature Reserve, southern China. We first summarize data on dietary composition, and then describe seasonal changes in diet.

1 Materials and Methods

1.1 Study site and animal

Nonggang Nature Reserve is located in southwest Guangxi province, China (106°42′–107°4′E, 22°13′–
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and comprises three areas, Nonggang (5426 ha), Longhu (1034 ha), and Longshan (3949 ha), separated by farmlands and villages. The reserve consists of limestone hills with elevations 300-700 m above sea level (Guangxi Forestry Department, 1993). Our research site lies in northwestern of Nonggang (Fig. 1). Vegetation is characterized as limestone seasonal rain forest (Shu et al., 1988). Vegetation differs across the area due to differences in soil and surface water availability. Most large fruiting trees are found in valley basins and on hillsides rich in wet soil. The cliffs and hilltops consist of bare rock, and are covered by small drought-enduring trees (Liang et al., 1988). Annual precipitation during the study period (September 2005–August 2006) was 1372 mm. The area encounters two seasons, a rainy season from April and September with > 80 mm monthly rainfall and a dry season with < 80 mm monthly rainfall (Fig. 2).

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

Fig. 2  Monthly rainfall and abundance of young leaves, fruit and flowers at Nonggang Nature Reserve between September 2005 and August 2006
At least six social groups of Assamese macaques inhabit the study area. In this study, most behavioral data were collected from Group 1 and Group 2 who ranged nearest to our temporary camp. Group 1 consisted of 15 individuals (two adult males, four adult females, four adult individuals of unidentified sex, and five juveniles) at the start of this study, and increased to 17 individuals due to the birth of two infants in June 2006. Group 2 had 12 individuals (two adult males, four adult females, two adult individuals of unidentified sex, and four juveniles) at the start of this study and two infants were born in June and July 2006.

1.2 Ecological sampling

We conducted vegetation surveys at the onset of behavioral data collection. We used a stratified random sampling method for placement of vegetation plots. We placed 13 plots (50 m × 10 m) in the main study area, including four at valley basins and nine on hillsides. The plots covered most of the vegetation types described by Shu et al. (1988). Within plots we tagged all trees with a diameter ≥ 5 cm at breast height (DBH), and measured DBH. Each month we visually inspected all tagged trees for the presence of young leaves, fruit, and flowers to evaluate seasonal changes in the availability of potential food resources.

1.3 Behavioral observation

Field observations were done from September 2005 to August 2006. Because of difficult land physiognomy, we were unable to conduct full-day consecutive behavioral sampling for most days. Each sampling day, data collection began when the monkeys were first encountered and ended when the monkeys disappeared or entered sleeping sites. Instantaneous scan sampling was used (Altmann, 1974). Scans 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 predominant behavior during that interval. To avoid sampling bias toward certain individuals of a particular age-sex class, we collected 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. Because some individuals inevitably could not be found because of the dense vegetation, only a fraction of the group could be sampled during most scans.

We classified five general activities: resting, moving, feeding, social grooming, and playing. When monkeys were feeding we recorded the plant part eaten, including young leaf, mature leaf, fruit, flower, and others (e.g. petiole, root and bark). If possible, specimens of plant species eaten were collected for later identification by the Institute of Botany, Chinese Academy of Sciences (Guilin, Guangxi).

1.4 Data analysis

We expressed the relative availability of different plant parts as the percentage of trees bearing the plant parts of interest each month, regardless of the size of the canopy. The percentage of time spent consuming each plant species was calculated from the number of feeding records for plant species divided by the total number of feeding records. Monthly diet composition was expressed as the percentage of feeding records devoted to different food items among monthly total feeding records. Annual diet composition was obtained by averaging monthly percentages. We excluded records for dependent infants and juveniles (n = 200) from analysis because they were not foraging independently and infant and juvenile mouthing of prospective foods often cannot be differentiated from actual feeding.

We used a Spearman rank correlation coefficient test was used to examine correlations between the availability of plant parts of interest and rainfall. A Wilcoxon signed-rank test was used to examine inter-group variation in the overall pattern of use of different plant parts. Because few records were collected in September and October 2005 we excluded data in these months for comparisons of inter-group variations and later analysis. We used Mann-Whitney’s U test to examine seasonal variation in the availability of plant parts of interest and the consumption of various items. All tests were two tailed, with significance levels of 0.05.

2 Results

2.1 Phenology

A total of 312 trees of 56 species were monitored within 13 vegetation plots. The availability of young leaves and flowers reached their highest level in April 2006. A peak of fruit availability was observed in June and July 2006 (Fig. 2). Compared to the dry season, the availability of young leaves, fruits and flowers was higher in the rainy season, but only the difference in the availability of fruit was statistically significant (young leaf: Z = -1.604, n1 = 6, n2 = 6, P = 0.109; fruit: Z = -2.330, P = 0.020; flower: Z = -0.855, P = 0.393). A significant and positive correlation was found between monthly fruit availability and rainfall (r = 0.719, n = 12, P = 0.008)

2.2 Food plant species

During the study period a total of 6525 behavior re-
cords were obtained from 1666 scan samples, with an average of 3.9 individuals per scan. We made 1259 feeding records (monthly mean = 122, $SD = 95$, range = 65 to 324), of which there were 1094 records of identified food species, and 1198 for identified food items. Macaques were observed to forage on 69 plant species (Table 1). Not counting eight unidentified species, the range of food included 34 families, 59 species of tree, eight species of vine, and two species of herb. Tree species accounted for 93.2% of total feeding records, vines for 3.1%, and herbs for 3.7%.

Though the macaques consumed a large number of plant species, only 12 species such as *Indocalamus calcicolus*, *Ficus nervosa*, *Guihaia argyrata*, *Sinosideroxylon pedunculatum*, *Canthium dicoccum*, *Burretiodendron hsienmu*, *Croton euryphyllus*, *Ficus microcarpa*, *Ventilago calyculata*, *Berchemia floribunda*, *Lepionurus sylvestris*, and *Sapium rotundifolium* accounted for >1% each of all feeding records, and contributed to 85.2% of the total diet (Table 1). Of these 12 species, *Indocalamus calcicolus* accounted for 62.0% of the total diet. Thus, the macaques concentrated on a few species, but opportunistically consumed a large number of other plant species.

2.3 Food items

Because there was no significant difference in diet between the two main study groups ($Z = -0.674$, $n = 5$, $P = 0.500$) we pooled their dietary data for analysis. Assamese macaques were highly folivorous, and young leaves accounted for 74.1% of the total diet, of which young parts of *Indocalamus calcicolus* unexpanded leaves contributed to 77.7% of feeding records for young leaves (Fig. 3). Fruit accounted for 17.4% of the total diet, and the majority of fruit in the diet came from

Table 1  Plant species consumed by Assamese macaques at Nonggang Nature Reserve between September 2005 and August 2006

| Family       | Species                      | Life form | Parts eaten | Number of month used | %d(F) |
|--------------|------------------------------|-----------|-------------|----------------------|-------|
| Vitaceae     | *Ampelopsis brevipedunculata*| Vine FR   | 1           | 0.09                 |
|              | *Ampelopsis cantiensii*      | Vine FR   | 1           | 0.46                 |
|              | *Tetrastigma planicaude*     | Vine YL,ST| 1           | 0.36                 |
| Verbenaceae  | *Vitex kwangsiensis*         | Tree FR   | 1           | 0.09                 |
| Ulmaceae     | *Trema cannabina*            | Tree YL   | 1           | 0.09                 |
| Tiliaceae    | *Burretiodendron hsienmu*    | Tree YL   | 5           | 1.55                 |
|              | *Hainania trichosperma*      | Tree YL   | 2           | 0.46                 |
| Verbenaceae  | *Vitex kwangsiensis*         | Tree FR   | 1           | 0.09                 |
| Ulmaceae     | *Trema cannabina*            | Tree YL   | 1           | 0.09                 |
| Tiliaceae    | *Burretiodendron hsienmu*    | Tree YL   | 5           | 1.55                 |
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| Ulmaceae     | *Trema cannabina*            | Tree YL   | 1           | 0.09                 |
| Tiliaceae    | *Burretiodendron hsienmu*    | Tree YL   | 5           | 1.55                 |
|              | *Hainania trichosperma*      | Tree YL   | 2           | 0.46                 |

(to be continued on the next page)
| Family            | Species                     | Life form | Parts eaten\(^a\) | Number of month used | \(\% (F)^b\) |
|-------------------|-----------------------------|-----------|--------------------|----------------------|--------------|
| Moraceae          | Schefflera glomerulata      | Tree      | YL                 | 1                    | 0.09         |
|                   | Ficus cyrtophylla           | Tree      | FR                 | 2                    | 0.46         |
|                   | Ficus gibbosa               | Tree      | FR                 | 2                    | 0.46         |
|                   | Ficus glaberrima            | Tree      | FR                 | 1                    | 0.09         |
|                   | Ficus microcarpa            | Tree      | YL, FR             | 7                    | 1.46         |
|                   | Ficus nervosa               | Tree      | YL, ML, FR, F      | 11                   | 4.01         |
|                   | Ficus sp.                   | Tree      | FR                 | 2                    | 0.36         |
|                   | Ficus sp.                   | Tree      | FR                 | 1                    | 0.09         |
|                   | Ficus virens                | Tree      | FR                 | 2                    | 0.27         |
|                   | Ficus wightiana             | Tree      | YL, FR, P          | 4                    | 0.91         |
|                   | Pseudostreblus indica       | Tree      | FR                 | 1                    | 0.18         |
|                   | Species 2                   | Tree      | YL                 | 1                    | 0.18         |
| Mimosaceae        | Acacia pennata              | Tree      | S                  | 1                    | 0.18         |
| Menispermaceae    | Diplolcistis glaucescens    | Vine      | YL                 | 1                    | 0.09         |
| Meliaceae         | Aphanamixis grandifolia     | Tree      | YL, FR             | 2                    | 0.55         |
|                   | Species 3                   | Tree      | FR                 | 1                    | 0.27         |
| Melastomataceae   | Memecylon scutellatum       | Tree      | FR                 | 1                    | 0.09         |
| Linaceae          | Tirpitzia ovoida            | Tree      | FR                 | 1                    | 0.18         |
| Leguminosae       | Pithocellium Brycepia       | Tree      | YL                 | 1                    | 0.09         |
| Lauraceae         | Cinnamomum saxatile         | Tree      | YL, P              | 3                    | 0.55         |
| Icacinaceae       | Apodytes dimidiata          | Tree      | YL, FR             | 2                    | 0.18         |
|                   | Lodes ovalis                | Vine      | FR                 | 3                    | 0.55         |
| Guttifceae        | Garcinia paucinervis        | Tree      | S                  | 1                    | 0.82         |
| Gramineae         | Species 4                   | Herb      | S                  | 1                    | 0.09         |
| Fagaceae          | Quercus glauca              | Tree      | FR                 | 1                    | 0.09         |
| Euphorbiaceae     | Alchornea trewioides        | Tree      | FR                 | 1                    | 0.09         |
|                   | Bischofia javanica          | Tree      | YL                 | 1                    | 0.09         |
|                   | Croton euryphylus           | Tree      | YL                 | 4                    | 1.55         |
|                   | Sapium rotundifolium        | Tree      | FR                 | 4                    | 1.18         |
|                   | Species 5                   | Tree      | FR                 | 1                    | 0.09         |
|                   | Trigonostemon thyrsoideus   | Tree      | YL                 | 1                    | 0.09         |
| Ebenaceae         | Diospyros siderophyllus     | Tree      | FR                 | 4                    | 0.46         |
| Bambusoideae      | Dendrocalamus minor         | Tree      | YL                 | 2                    | 0.18         |
|                   | Indocalamus calciculus      | Tree      | YL                 | 12                   | 62.02        |
|                   | Phyllostachys bambusoides   | Tree      | YL                 | 1                    | 0.09         |
| Aristolochiaceae  | Aristolochia cinnabararia   | Vine      | R                  | 1                    | 0.09         |
| Araliaceae        | Schefflera octophylla       | Tree      | YL                 | 2                    | 0.18         |
| Apocynaceae       | Trachelospermum brevistylum | Tree      | YL, FR             | 5                    | 0.73         |
| Anacardiaceae     | Pistacia weinmannifolia     | Tree      | YL                 | 1                    | 0.09         |
|                   | Species 6                   | Tree      | YL                 | 1                    | 0.18         |
| Alangiaceae       | Alangium chinense           | Tree      | YL                 | 1                    | 0.18         |
|                   | Species 7                   | Herb      | F                  | 2                    | 0.18         |
|                   | Species 8                   | Tree      | YL                 | 1                    | 0.09         |

\(^a\) Parts eaten: YL, young leaf; ML, mature leaf; FR, fruit; S, seed; F, flower; P, petiole; ST, stem.

\(^b\) \(\% (F)\): percentage of total feeding records
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Fig. 3 Annual diet composition for Assamese macaques at Nonggang Nature Reserve

four plant species: *Ficus nervosa*, *Ficus microcarpa*, *Sinocalamus calciculus*, and *Canthium dicoccum*, which accounted for 55.7% of fruit feeding records. The consumption of mature leaves, flowers and other items (petioles, barks and roots) was low and accounted for 3.3%, 2.7% and 2.5%, respectively.

2.4 Seasonal Changes in Food Items

Young leaves constituted the bulk of Assamese macaque monthly diet almost year-round, ranging from 44.9% in July to 92.9% in May (Fig. 4), and their consumption showed no significant seasonal variation ($Z = -0.313$, $n_1 = 5$, $n_2 = 5$, $P = 0.754$). Young parts of *Indocalamus calciculus* unexpanded leaves contributed a large proportion of the young leaf diet in most months except for February, April and May (Fig. 4). Macaques ate more fruit when it was abundant in the rainy season, with peak consumption in July, but no significant seasonal variation was found in fruit consumption ($Z = -0.838$, $P = 0.421$). The consumption of flowers also showed no significant seasonal variation ($Z = -0.105$, $P = 0.917$), and was even across months, except for July and August, in which there was no feeding record for flowers. Although there was no significant seasonal variation in the consumption of mature leaves ($Z = -1.509$, $P = 0.131$), mature leaf consumption concentrated in the dry season months, with a peak in February. Macaques significantly increased the consumption of other items (e.g. petiole, root and bark) in the dry season than in the rainy season ($Z = -2.117$, $P = 0.034$) (Fig. 4).

3 Discussion

The diet of Assamese macaques at Nonggang Nature Reserve was highly folivorous. Leaves accounted for 77.4% of total feeding records, whereas fruit only constituted 17.4% of total feeding records. This pattern is in accordance with reports from other study sites (Ahsan, 1994; Chalise et al., 2003). For example, the diet of Assamese macaques in Bangladesh comprised more leaves (46%) than fruit (23%) (Ahsan, 1994). Chalise et al. (2003) also reported that Assamese macaques in Nepal were predominately leaf eaters.

Fig. 4 Monthly percentage of feeding records devoted to different food items for Assamese macaques between November 2005 and August 2006
Although our study site is located in a sub-tropical area (Guangxi Forestry Department, 1993), fruit consumption of Assamese macaques at Nonggang is much lower than tropical macaques such as Macaca fascicularis: 66.7% (Yeager, 1996), M. nigra: 66% (O’Brien and Kinnaird, 1997), M. brunnescens: 90.4% (Andrews, 2003), and M. tonkeana: 76.7-84.4% (Riley, 2007), and more similar to temperate species such as Macaca fuscata yakui: 13% (Hanya, 2004) and M. mulatta: 9% (Goldstein and Richard, 1989). The difference is, at least partly, explained by the seasonal scarcity of fruit in limestone habitats. Many studies have shown a strong correlation between rainfall and fruit production in limestone habitats, and that little fruit is available in the dry season from October to March (Li and Roger, 2006; Zhou et al., 2006). Thus, it seems that the lean period when fruit is uncommon is longer in this region than in the tropics where fruit is more or less available year round (Yeager, 1996; Riley, 2007). Furthermore, Assamese macaques at Nonggang spent most maintenance activities on the cliffs and hilltops of limestone hills (unpublished data), which consist of bare rock, and are covered by small drought-enduring trees. Similarly, the habitat of Assamese macaques in Nepal are characterized by steep slopes and rocky areas with patchy forest. They frequently forage in open bushy and shrubbery lands with low fruit availability (Chalise et al., 2003). This further decreases fruit availability for Assamese macaques.

Within the genus Macaca, Assamese macaques at Nonggang rely on fiber-rich foods most heavily (77.4% of the diet). This value is even higher than the average of 24 species of colobines, which are forestomach-fermenting primates (52%, Kirkpatrick, 1999). Macaques have an enlarged caecum and colon as the primary fermentation chamber, which enhances their digestive abilities to digest large amounts of fiber-rich foods (Lambert, 1998; Hayan, 2004). Our data and this physiological fact suggest that Assamese macaques may have an ability to digest large amounts of fiber-rich food. Although Assamese macaques at Nonggang relied heavily on fibrous foods, they were mostly young leaves (95.7% of the total fibrous foods), and mature leaves accounted for only 4.3% of the total fibrous foods. This is similar to other folivorous primates (e.g Colobine: young leaves account for 69% of the total fibrous foods, Kirkpatrick, 1999; Alouatta palliata: 87%, Estrada et al., 1999; Propithecus diadema: 65%-73%, Hemmingsway, 1998). Compared with mature leaves, young leaves are preferred foods for primates because they have higher nutritional quality such as for protein and are lower in fiber and secondary compounds (Richard, 1985).

Although the availability of young leaves decreased markedly from October to January (Fig. 2), a high level of young leaves was maintained in the diet of Assamese macaques almost year-round. This can be mostly accounted for by the macaques feeding on young parts of Indocalamus calcicolus (Rubiaceae) unexpanded leaves. This food item accounted for 77% of the Assamese macaque young leaf diet, and formed the bulk of the diet in most months. Probably, this plant species plays a crucial role in the feeding ecology of Assamese macaques in limestone habitats. This bamboo is very abundant on the cliffs and hilltops of limestone hills (Liang et al., 1988), and unexpanded leaves eaten by macaques are available almost year-round (personal observation). Thus, they may provide a long-term stable food resource for Assamese macaques in limestone habitats. However, it is still unclear why the macaques show such a preference for the young parts of unexpanded leaves from Indocalamus calcicolus. Obviously, more nutritional data are needed to compare these leaves with alternatives.

Dietary flexibility may permit primates to live in a variety of habitats. When high-quality food such as fruit is scarce, primates can use fiber-rich foods as fallback foods (Marshall and Wrangham, 2007). Accumulated evidence shows the folivory of Macaca species (e.g. Zhao, 1996; Hanya, 2004) is originally frugivorous. This dietary flexibility according to habitat may be one of reasons why the genus Macaca is more widely distributed than any other nonhuman primate genus. For example, Japanese macaques can use a large amount of mature leaves in response to long-term seasonal reduction in fruit in temperate regions (Hanya, 2004). Similarly, there is a long lean period when fruit is uncommon in limestone habitats. Monkeys may also need to develop the ability to cope with fiber-rich food so as to survive in such environments. Although physiological investigation is needed, the fact that Assamese macaques rely heavily on leaves as fallback foods suggests an adaptation that has allowed Assamese macaques to survive in limestone habitats.

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