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Seasonal Variation in the Activity Patterns and Time Budgets of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China

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Abstract Activity patterns and time budgets are 2 important aspects of animal behavior that researchers use to investigate ecological influences on individual behavior. We collected data on activity patterns and time budgets in 1 group of François' langurs (*Trachypithecus francoisi*) from August 2003 to July 2004 in the Nonggang Nature Reserve, Guangxi Province, China, via instantaneous scan sampling method with 15-min intervals. The diurnal activity pattern of François' langurs showed morning and afternoon feeding peaks, with a midday resting peak. Seasonal change was apparent in the activity pattern: 2 significant feeding peaks occurred in the dry season and only 1 significant feeding peak in the rainy season. The group spent an average of 51.5% of the daytime resting. Feeding and moving accounted on average for 23.1% and 17.3% of the activity budget, respectively. Subjects spent little time on social activities, averaging 2% for grooming and 5.5% for playing. Their time budgets showed significant seasonal variation: they spent a greater proportion of time on feeding and less time on resting and grooming in the dry season than in the rainy season. They also differed among different sex-age classes: immatures spent more time playing, whereas adults devoted more time to resting, feeding, and grooming. Correlations between time budgets and food items or food availability clearly indicated that François' langurs might adopt an energy-maximizing strategy when preferred foods were scarce in the dry season.

Keywords activity patterns · François' langur · seasonality · time budgets · *Trachypithecus francoisi*

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Introduction

Activity patterns and time budgets are 2 important aspects of the temporal behavior of animals. They are directly related to metabolism and energetic constraints, which will often change in response to temporal variations in the environment (Bronikowski and Altmann 1996; Halle and Stenseth 2000; Hill 1999). Thus, comparisons of activity patterns and time budgets under different ecological conditions allow us to explore ecological influences on animal behavior, and behavior strategies.

Researchers have studied activity patterns in many primates (Bravo and Sallenave 2003; Clutton-Brock 1977b; Ding and Zhao 2004; Doran 1997; Huang *et al.* 2003; Passamani 1998). Primatologists have proffered several factors to explain the variations in activity patterns among diurnal primates, including variation in temperature and solar isolation (Chivers 1977; Hill *et al.* 2004; Huang *et al.* 2003; Richard 1977), stomach size and intestinal morphology (Clutton-Brock 1974; Lawes and Piper 1992), home range size, and resource dispersion and predictability (Li and Rogers 2004; Post 1981). The factors may interact and influence primate activity patterns.

Authors of numerous field studies have also documented that primates can regulate their time budgets in response to seasonal changes in food availability and climatic factors (Clutton-Brock 1974; Dasilva 1992; Di Fiore and Rodman 2001; Ding and Zhao 2004; Hanya 2004; Huang *et al.* 2003; Lawes and Piper 1992; Li and Rogers 2004; Marsh 1981; Oates 1987; Passamani 1998; Strier 1987; Watts 1988; Zhao 1999). For example, in some primates, the time allocated to feeding or foraging decreases when high-quality food is scarce and temperature is low (Ding and Zhao 2004; Hanya 2004). Opposite results are reported in other primates (Dunbar 1992; Huang *et al.* 2003, Oates 1987). Consequently, individuals will reduce resting and social activities in response to the increase of feeding time or to foraging time, which results in time-energy balances (Oates 1987). Furthermore, primate time budgets are also influenced by other factors, such as group size (Clutton-Brock and Harvey 1977; Janson and Goldmith 1995; Teichroeb *et al.* 2003), age and sex (Strier 1987; Fashing 2001; Li and Rogers 2004), reproductive condition (Strier 1987; Matsumoto-Oda and Oda 2001; Muruthi *et al.* 1991), and social dominance (Hemingway 1999; Whitten 1983).

François' langurs (*Trachypithecus francoisi*) are an endangered primate species. They range from the Red River in Vietnam across the Chinese border as far as the Daming Hills in Guangxi and Xingyi in Guizhou (Groves 2001). The langurs live in habitats characterized by Karst topography (Huang *et al.* 1983; Li 1993; Wu 1983). Groups are predominantly polygynous, and range from 5 to 13 individuals (Wu 1983). Some researchers have reported the François' langur diets (Huang *et al.* 1983; Li and Ma 1989; Zhou *et al.* 2006). However, less is known about their activity patterns and time budgets, which is important for understanding how they adapt to the specific habitat of Karst topography. We also provide important comparative information for the general study of dietary adaptation in the Colobinae as a whole.

We here describe the diurnal activity patterns and activity budgets of the François' langur in the Nonggang Nature Reserve, and examine how they vary seasonally. We then explore how diet and various environmental variables, such as food availability

and rainfall, influence their activity budgets, and offer an assessment of François' langur behavior strategy.

Methods

Study Site and Langur Groups

Nonggang Nature Reserve is located in the southwest of Guangxi province, China (106°42′-107°4′E, 22°13′-22°33′N), and comprises 3 areas—Nonggang (5426 ha), Longhu (1034 ha), and Longshan (3949 ha)— which are separated by farmlands and villages (Fig. 1). The reserve consists of limestone hills with elevations 300–700 m above sea level (Den 1988). The vegetation is characterized as seasonal rain forest (Shu *et al.* 1988). There are many endemic plant species that occur only on limestone hills, such as *Burretiodendron hsienmu, Cephalomappa sinensis, Garcinia paucinervis, Parashorea chinensis var. kwangsiensis, Walsura robusta, Urobotrya*

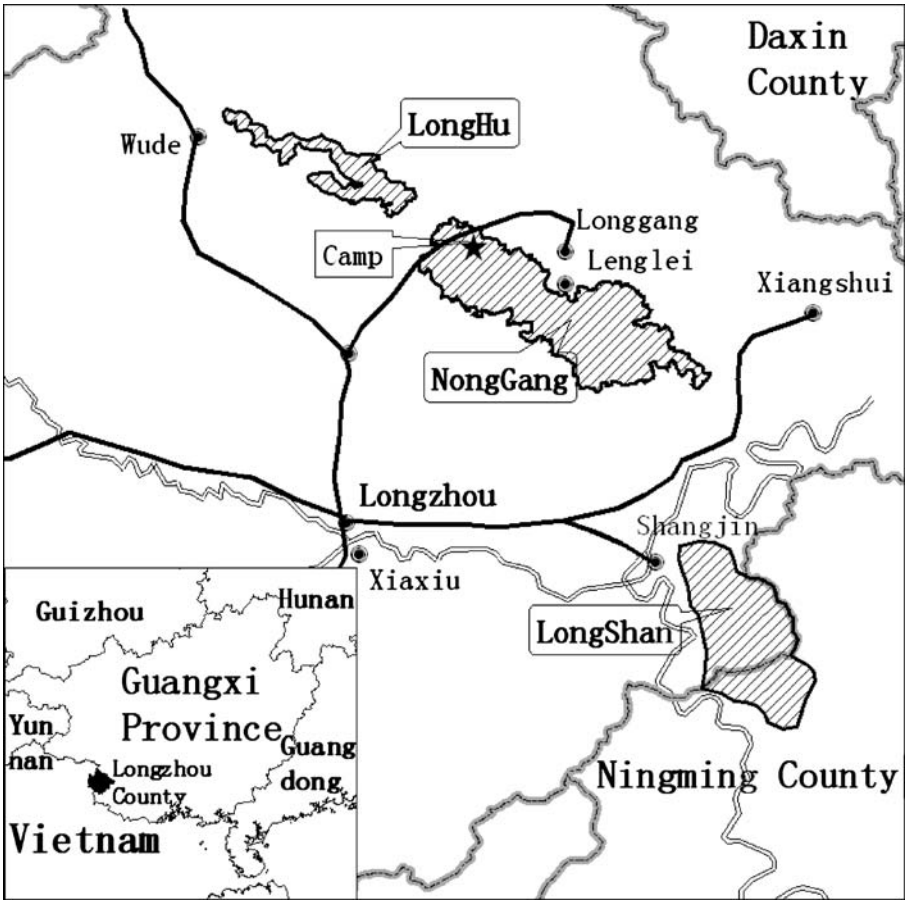

Fig. 1 Map of Nonggang Nature Reserve showing the study site and surrounding area.

latisquama, and *Cleistanthus petelotii*. Rainfall was seasonal with a distinct rainy season between April and September, and annual precipitation during study period (August 2003-July 2004) was 977 mm (Zhou *et al.* 2006).

We conducted our field research in the northwestern portion of Nonggang from April 2003 to July 2004. The main study area is about 200 ha. Two social groups of François' langurs lived in the main study area. Our focal group (group 1) had been semihabituated to observers before data collection began. It varied from 12 individuals (4 adult males, 5 adult females, and 3 immatures) at the start of the study to 10 individuals by the end, owing to the disappearance of an adult female and her infant.

Ecological Sampling

To estimate the potential food availability, we opportunistically placed 13 50-m-long, 10-m-wide belt transects, including 4 in the valley floors and 9 on the slopes, in the main study area, at the beginning of detailed behavioral data collection. We determined the locations of the vegetation transects by the vegetation types per Shu *et al.* (1988), and the transects covered most of the vegetation types in the main study area. Within the transects, we tagged all trees of ≥5 cm diameter-at-breast height (DBH) and checked them by visual inspection for the presence of young leaves, fruits, and flowers each month from August 2003 to July 2004. In total, we examined 312 trees from 30 families at monthly intervals, and Zhou *et al.* (2006) described monthly phenology changes.

Behavioral Data Collection

From August 2003 to July 2004, we spent a mean of 10 d each month following the focal group. On each day, we observed subjects via binoculars (10×60) at a distance of 10–200 m. We collected no datum in July 2004 because many places were flooded and follows were almost impossible, so we used only 11 mo of data for analysis. Further, it was not possible to conduct full-day consecutive behavior samples on many observation days because the subjects always hid in the dense vegetation in midday or moved to places where observers could not follow. We collected a total of 739 h of behavioral data.

During full-day follows, we began data collection at 0600 h and ended it when the subjects entered the sleeping site. We also collected behavior data during partial-day follows, which began when we first encountered the subjects. We used instantaneous scan sampling in behavioral data collection (Altmann 1974), with 15-min intervals. During each time interval, we limited scan sampling to the first 5 min. We recorded the activities of all individuals that came into view, and sampled each individual only once. We tried to collect as many different individuals as possible during a scan by changing observing positions. Whenever possible, we recorded the age-sex class of a scanned individual. We divided the ages of sampled individuals into 3 classes according to color of fur and body size: infant, juvenile, and adult. We identified sex by the color of fur in the circumgenital area: black for males and white for females. When the study group was out of view during the scanning time of a given interval,

we interrupted scan sampling until the beginning of the next scan. We obtained a total of 12,186 individual activity records from 2962 scan samples, with an average of 4.11±2.32 individuals per scan.

We noted an observation of each scanned individual during a scan as a behavioral record, which we assigned to one of the following activity categories:

Resting	not involved in change of location, either sitting or lying down in the branches of trees or on rocks; includes scanning the environment, e.g., vigilance, and autogrooming.
Moving	any movement in walking, running, jumping, or climbing posture that results in change of location; excludes that movement taking place during feeding.
Feeding	reaching for and manipulating a food item with hands or mouth, bringing it into the mouth and chewing; includes the movement occurring during feeding.
Grooming	referred only to allogrooming.
Playing	includes social playing and solitary playing, involving running, climbing or jumping with or without one another, or mock fighting.
Other	includes other social behavior, such as mating and fighting with hostility; and some rare behavior, such as drinking water and vocalizing.

Data Analysis

We calculated time budgets per Clutton-Brock (1977a). 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 of individuals recorded in a scan. We treated each scan budget as an independent data point and used it in subsequent analyses, which can reduce potential biases introduced by scan sampling technique (Clutton-Brock 1977a). To avoid potential biases introduced by unequally distributed samples in different months or at different times of the day, we first calculated hourly time budgets by averaging scan budgets in an hour. We averaged the hourly budgets in a month to construct monthly time budgets. We obtained the annual time budget of the group by averaging monthly budgets. We calculated the average percentage of time allocated to each of 3 main activities —resting, moving, and feeding— in hourly classes from 0600 to 1900 h to express the diurnal activity patterns. We expressed the time budgets of different age-sex classes as the averages of monthly relative frequencies with which they engaged in various activities.

We used only the hours comprising 4 scan samples in calculating time budgets. The results given here thus derived from 2696 scans. We used Spearman rank correlation tests to assess the relationship between activity budgets and diets, as well as food availability. In keeping with Poulsen *et al.* (2001), we normalized the percentage of time spent on resting, moving, and feeding during each hour by arcsine transformation, and tested for differences among hours of the day via 1-way ANOVA. We used the Mann-Whitney *U* test to compare monthly average of time

budgets and activity patterns from the 5 rainy season mo vs. the 6 dry season mo (Dytham 1999). All tests are 2-tailed, and we applied a .05 or a .01 significance level for the data condition reached.

Results

General Pattern of Activity Budget

François' langurs spent on average 51.5% of the day time resting (Table I). Feeding and moving accounted on average for 23.1% and 17.3% of monthly activity budgets, respectively. The langurs spent little time on social activities in the daytime, averaging 2% for grooming and 5.5% for playing. Other activities only contributed on average to .6% of monthly time budgets. The percentage of time spent on resting and social activities, e.g., grooming, is probably underestimated because the subjects often hid in the dense vegetation and out of view from observers during the middle of the day, especially in summer, when they were possibly resting or conducting social activities.

Only feeding showed significantly variation according to season (Table II). Considering that all grooming occured during resting periods, we combined grooming time with resting time, and found significant seasonal variation (Mann-Whitney U test $Z=-2.191$, $p=.028$). There are also significant and negative correlations between feeding time and resting time + grooming time ($r_s=-.827$, $n=11$, $p=.002$). Thus, the langurs spent more time feeding in the dry season than in the rainy season. Accordingly, they reduced resting + grooming time.

Table I Monthly and annual time budgets of François' langurs represented as a percentage of time spent on each activity category in the Nonggang Nature Reserve between August 2003 and June 2004

Month	Resting	Moving	Feeding	Grooming	Playing	Others	No. of scans
Aug. 2003	51.6	16.3	22.5	2.8	5.7	1.1	132
Sept. 2003	49.5	17.8	2.0	3.3	8.0	1.5	336
Oct. 2003	5.1	18.6	21.7	2.2	6.9	.3	332
Nov. 2003	5.6	19.0	23.6	1.6	4.6	.8	268
Dec. 2003	45.2	17.8	28.3	1.9	6.9	.1	312
Jan. 2004	54.8	12.3	27.2	.5	3.8	1.4	140
Feb. 2004	48.1	18.1	27.8	1.6	4.4	.2	352
Mar. 2004	43.7	18.7	29.9	1.7	5.6	.4	376
Apr. 2004	59.8	15.3	16.8	1.9	5.8	.6	188
May 2004	53.4	19.0	19.9	1.0	6.6	.0	160
June 2004	59.9	16.9	17.0	3.6	2.0	.7	100
Mean	51.5	17.3	23.1	2.0	5.5	.6	
SD	5.22	2.01	4.60	.92	1.71	.53	

Table II Seasonal variations in time budgets of François' langurs for various activity categories in the Nonggang Nature Reserve between rainy season and dry season

Season	Resting	Moving	Feeding	Playing	Grooming
Rainy season n=5	54.8	17.0	19.2	5.6	2.5
Dry season n=6	48.7	17.4	26.4	5.4	1.6
Mann-Whitney test	Z=−1.826, p=.068	K=−.913, p=.361	K=−2.556, p=.009	K=−.548, p=.584	K=−1.461, p=.144

The figures are the monthly averages of the percentage of records for different activity categories per season.

Diurnal Activity Pattern

The percentage of time allocated to resting, moving, and feeding in different hours of the day showed significant variations (1-way ANOVA Test F=5.597, df=13,131, p<.001 for resting; F=4.073, df=13,131, p<.001 for moving; F=2.960, df=13,131, p=.001). There was a morning feeding peak, with a reduction in feeding time through midday, after which there was a general trend for greater feeding until the end of the evening (Fig. 2). Similarly, moving was much more common in the morning and afternoon relative to midday. Consequently, resting activity reached highest level in the middle of the day, which lasted for 4–5 h, in response to the reduction of feeding and moving time. In summer, langurs often hid in the forest and caves during midday resting time, which became more marked on sunny days than on cloudy ones. But in winter, they often sat or lay on the bare rocks for a long resting at noon.

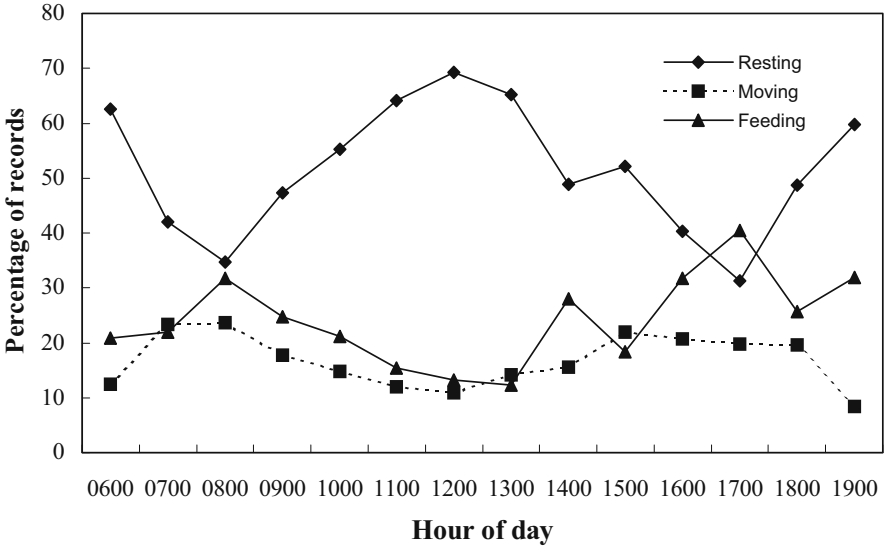

Fig. 2 Whole-year diurnal cycle of general activities of François' langurs in the Nonggang Nature Reserve between August 2003 and June 2004.

The schedule of activity showed slight seasonal changes: in the dry season, the feeding peak was delayed by 1 h in the morning and occurred 1 h earlier in the afternoon, than in the rainy season (Fig. 3). In addition to shifting the schedule of activities, François' langurs appeared to change the proportion of time devoted to main activities in different hours of the day according to season. With one exception (resting, 1800–1900 h), seasonal variations occured only in the diurnal distribution of time for feeding (Table III). They appeared to increase feeding time both in the morning (0800–0900 h) and afternoon (1700–1800 h), which results in 2 significant feeding peaks in the diurnal activity patterns in the dry season, whereas there was only 1 significant feeding peak in the rainy season.

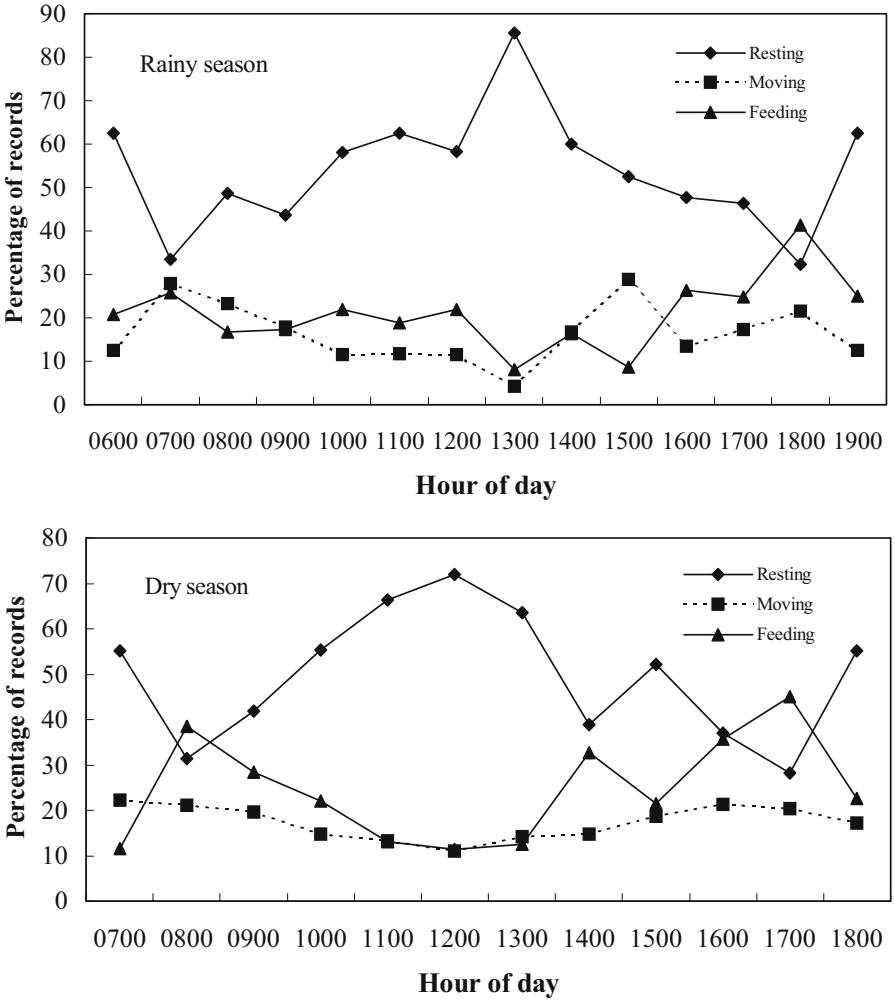

Fig. 3 Seasonal variations in diurnal cycle of general activities of François' langurs in the Nonggang Nature Reserve between the rainy and dry seasons.

Table III Seasonal variations in diurnal cycles of general activities via Mann-Whitney *U* test between rainy and dry seasons

Time of day	No. of scans		Resting		Moving		Feeding	
	Dry season	Rainy season	*Z*	*P*	*Z*	*P*	*Z*	*P*
0700–0800	72	76	−1.984	.056	−.94	.421	−1.984	.056
0800–0900	200	88	−2.008	.052	−.183	.931	−2.739	.004*
0900–1000	188	100	−.73	.537	−.183	.931	−2.008	.052
1000–1100	188	100	−.365	.792	−.73	.537	−1.461	.177
1100–1200	168	92	−.548	.662	−1.461	.177	−.183	.931
1200–1300	140	68	−1.095	.329	−.274	.792	.000	1.000
1300–1400	128	68	−1.83	.082	−1.775	.082	−.921	.429
1400–1500	144	64	−1.164	.126	−.183	.931	−2.008	.052
1500–1600	136	52	−.213	.914	−1.919	.067	−1.706	.114
1600–1700	140	72	−1.461	.177	−1.738	.082	−1.278	.247
1700–1800	160	60	−1.826	.082	−.548	.662	−2.191	.030*
1800–1900	108	60	−2.191	.030*	−1.006	.329	−1.826	.082

Intragroup Differences in Activity Budget

Of 12,186 activity records, there are 10,300 records of adults and 1886 of immatures. The great differences occurred in the time budgets of adults and immatures, including infants and juveniles (Fig. 4): adults allocated proportionately much more time to resting, feeding and grooming (Mann-Whitney *U* test $Z=-3.576$, $p<.001$ for resting; $Z=-2.693$, $p=.006$ for feeding; $Z=-2.96$, $p=.002$ for grooming); immatures spent much more time playing ($Z=-3.576$, $p<.001$). There is no significant difference between adults and immatures in the percentage of time spent moving ($Z=-1.193$, $p=.258$).

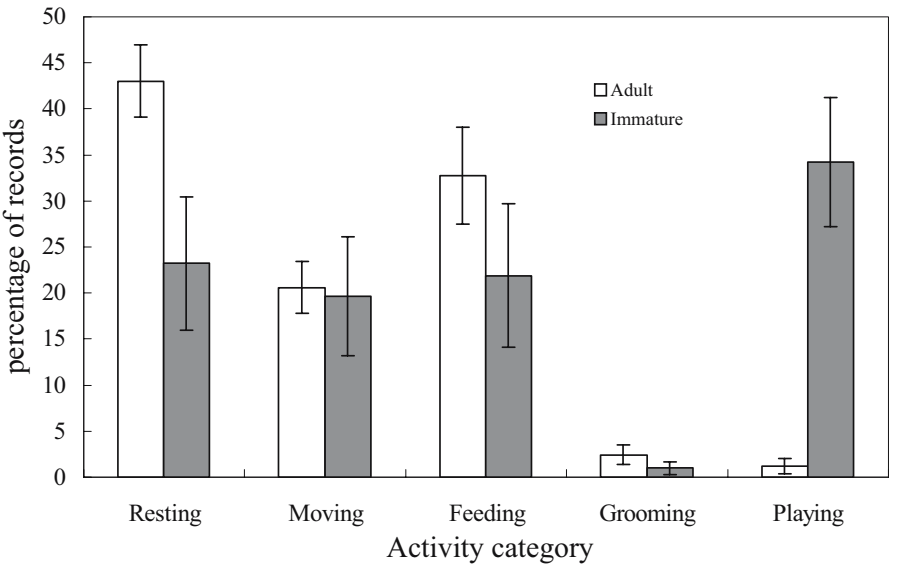

Fig. 4 Comparison of time budgets (mean ± SE) between adults and immatures, based on data collected from August 2003 to June 2004.

Diets and Activity Budget

Fiber-rich food made up the largest proportion of the diet of the François' langur, but their diets showed significant seasonal changes (Zhou *et al.* 2006). To evaluate the influence of diet on activity budgets, we examined the relationship between the monthly proportion of food items and the monthly percentage of time spent on various activity categories. Time spent feeding correlated negatively with the consumption of young leaves (Spearman rank correlation coefficient r_s=−.727, n=11, p=.011) and flowers (r_s=−.679, n=11, p=.022), and significantly positively correlated with the consumption of seeds (r_s=.82, n=11, p=.002) and other (r_s=.665, n=11, p=.025). The monthly dietary diversity, calculated as the Shannon-Weaver Diversity Index, ranged from 1.49 to 2.87 and peaked at the end of dry season (Zhou *et al.* 2006). There is a significant and positive correlation between dietary diversity and feeding time (r_s=.745, n=11, p=.008).

Ecological Influences on Activity Budget

To analyze whether the seasonal variations in activity budgets are caused by the changes of ecological conditions, we tested the relationships between the time spent on various activity categories and the availability of foods (Table IV). Only feeding and grooming were affected significantly by the seasonal changes in the availability of foods. When the availability of young leaves and fruits declined in the dry season, langurs increased feeding time and reduced grooming time.

Discussion

Diurnal Activity Pattern

The diurnal activity patterns of François' langurs in the Nonggang Nature Reserve showed a resting peak in the midday, with 2 feeding peaks in the morning and afternoon, which is in accordance with reports for some colobines. For example, white-headed langurs had morning and afternoon feeding peaks, with a long period

Table IV Spearman rank correlation coefficients between activity categories and the availability of foods[a]

Activity category	Tree index		
	Young leaf	Fruit	Flower
Resting	.345	.346	−.032
Moving	.045	−.077	.443
Feeding	−.700*	−.715*	.027
Grooming	.309	.752**	−.461
Playing	.318	.428	−.151

[a] N=11 for all cells, all tests are 2-tailed.
*Correlation is significant at the .05 level.
**Correlation is significant at the .01 level.

of resting at midday (Huang *et al.* 2003). Other species also have similar daily activity patterns for feeding and resting (*Cercopithecus mitis*, Lawes and Piper 1992; *Colobus guereza*, Oates 1977; *C. vellerosus*, Teichroeb *et al.* 2003; *Piliocolobus badius*, Marsh 1981; *Trachypithecus pileatus*, Stanford 1991; *Pan troglodytes*, Doran 1997). In some primates, e.g., *Alouatta villosa*, *Callicebus torquatus*, *Lophocebus albigena*, *Cercopithecus mitis* and *Piliocolobus badius*, there is also another feeding peak in the midday (Clutton-Brock 1977b; Lawes and Piper 1992). However, some large-bodied, terrestrial species, e.g., *Macaca nigra*, *Papio anubis*, *P. cynocephalus*, show less marked feeding peaks in diurnal activity patterns (Harding 1976; O'Brien and Kinnaird 1997; Post 1981).

The activity pattern of morning and afternoon feeding peaks, with midday resting peak may represent an adaptation to temperature variation (Clutton-Brock 1977b; Hill 1999; Huang *et al.* 2003). We found that langurs often stayed hidden in the forest or caves, where it is cooler than outside, at noon in summer, and had a long rest for 4–5 h. Thus, midday resting peak in diurnal activity pattern of François' langurs may be an adaptation strategy to avoid the hot noon temperature and sunlight. However, it was not always the case, because langurs also sat or lay on the bare rocks for a long rest at noon on winter sunny days, as well as sunbathing. Researchers have reported the phenomenon among other primates, which they considered a thermoregulatory strategy in response to low ambient temperature (Fashing 2001; Huang *et al.* 2003; Oates 1977). In addition to an adaptation to temperature changes, the long midday resting of François' langurs possibly aids fibrous food digestion after morning feeding peak.

The diurnal activity patterns of François' langurs showed significant seasonal variations: 2 feeding peaks occurred in the dry season, while there was only 1 feeding peak in the rainy season, which may relate to seasonal variations in food sources and temperature. However, activity peaks may have been obscured by lumped data from different days because the diurnal activity patterns varied considerably between days (Clutton-Brock 1974, 1977b; Post 1981). Thus, morning feeding peak in the rainy season may, in fact, be more common than originally supposed.

Activity Budget and Seasonal Variation

The overall time budget of François' langurs follows the typical pattern of leaf-eating colobines: a large proportion of time spent resting (Table V). This pattern seems to be related to their fiber-rich foliage diet (Clutton-Brock and Harvey 1977; Dasilva 1992). For example, white-headed langurs in Fusui spent 52% of daytime resting, and leaves constituted 88% of their annual diet (Li and Rogers 2004). In our study, resting accounted for 51.5% of the daytime, and leaves contributed to 53% of their annual diet (Zhou *et al.* 2006), whereas frugivorous or insectivorous species spend much less time resting. For example, fruits accounted for 76% of the annual diet of woolly monkeys (*Lagothrix lagotricha poeppigii*), and resting occupied only 23% of their daytime (Di Fiore and Rodman 2001). Compared to fruits and insects, leaves are abundant and evenly distributed food resources but poor in nutrition and energy, so less time is needed for foraging, and long resting times provide more time for digestion of fibrous food and save energy (Clutton-Brock 1977b; Richard 1985; Waterman and Kool 1994).

Table V Activity budgets of colobine species

Species	Resting	Moving	Feeding	Other	References
Trachypithecus francoisi	52	17	23	8	This study
T. leucocephalus	52	15	13	20	Li and Rogers 2004
Presbytis pileatus	40	18	35	7	Stanford 1991
P. thomasi	59	8	32	?	Stanford 1991
P. ayguta	63	5	29	3	Stanford 1991
Colobus polykomos	55	12	31	2	Dasilva 1992
C. guereza	57	5	20	11	Oates 1977
	44	24	26	5	Bocian 1997
	63	3	23	11	Fashing 2001
C. satanas	54	4	23	10	Mckey and Waterman 1982
C. angolensis	52	19	22	5	Bocian 1997
C. vellerosus	59	15	24	3	Teichroeb *et al.* 2003
Piliocolobus badius	35	9	47	8	Struhsaker 1975
	47	13	25	15	Marsh 1981
	51	13	25	10	Starin 1991

Values are percentage of time or records spent in the given activity.

To maintain a certain daily energy intake, primates will adjust their activity budgets in response to changing ecological conditions. When food resources are scarce, they would make 3 possible adjustments: 1) increase the total time for subsistence, 2) increase feeding time, 3) increase resting time or reduce the time allocated to high-cost behaviors such as moving so as to minimize energy expenditure (Schoener 1971). Our results indicate significant seasonal variations in the time budgets of the François' langur in the Nonggang Nature Reserve, and documented that they were related to seasonal changes in diet or food availability and rainfall. In typical colobine diets, young leaves and fruits account for a large proportion, and are preferred foods (Li and Rogers 2004; Oates 1994; Yeager and Kool 2000). In our study, young leaves and fruits constituted 56% of the langurs annual diet. When the preferred foods were scarce in the dry season (Zhou *et al.* 2006), François' langurs increased feeding time and reduced time spent on resting and social activities. Further, they consumed seeds, an alternative high-quality food with rich fats and starch (Richard 1985), in large quantities, and use more different species as foods when preferred foods are scarce. Thus, François' langurs might adopt the second adjustment, i.e., maximizing energy intake, when few preferred resources are available in the dry season. Similar results also come from some other studies of colobine. For example, white-headed langurs in Fusui increased feeding time and reduced resting time in winter when young leaves and fruits were scarce (Huang *et al.* 2003). In contrast, some colobine species spent more time resting and less time feeding in response to poor ecological circumstances, e.g., *Colobus polykomos* (Dasilva 1992), *C. satanas* (Mckey and Waterman 1982), and *Rhinopithecus bieti* (Ding and Zhao 2004). In summary, François' langur in the Nonggang Nature Reserve have similar activity budgets to those of other colobines, with a large proportion of time allocated to resting and more feeding time when foods are scarce.

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