



Sleeping Site Use by *Trachypithecus francoisi* at Nonggang Nature Reserve, China

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Received: 27 February 2008 / Accepted: 5 December 2008 /
Published online: 27 February 2009
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Abstract We collected data on sleeping site use of the François' langur (*Trachypithecus francoisi*) between August 2003 and July 2004 at Nonggang Nature Reserve, China. We tested hypotheses regarding possible ultimate causes of sleeping site selection in light of our results. Langurs selected the ledges and caves on cliffs as sleeping sites. Of 23 identified sleeping sites, 7 were more frequently used than the others (≥ 9 times each, accounting for 64% of total observed nights). Langurs used most sleeping sites repeatedly, and reused some of them on consecutive nights; 4 consecutive nights were the longest run. We suggest that langurs choose sleeping sites to make approach and attack difficult by predators, and to increase familiarity so as to improve chances for escape. Langurs' cryptic behaviors before entering sleeping sites and the rapid movement toward sleeping sites (4 min on average) with an increased level of vigilance may help to decrease the possibility of detection by predators. Access to food appears to have a profound influence on sleeping site selection in François' langurs, as demonstrated by the langurs' tendency to select sleeping sites close to their current main feeding sites. The position of sleeping site relative to the last feeding site of the day and the first feeding site of the subsequent morning indicated a strategy closer to that of a multiple central place forager than of a central place forager. Our results do not support the influences of other factors, e.g., avoidance of parasites, seeking comfort, and range or resource defense, on sleeping site selection.

Keywords François' langur · limestone habitat · sleeping site · *Trachypithecus francoisi*

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Introduction

The choice of sleeping sites is crucial for the survival of primates, and interest in the topic has been increasing among primatologists (Anderson 1998). Researchers have proposed numerous hypotheses to explain the choice of sleeping sites in primates. The predation avoidance hypothesis asserts that primates prefer to sleep in sites inaccessible to predators, or that facilitate early detection of approaching predators (Huang *et al.* 2003; Reichard 1998; Zhang 1995). The food access hypothesis predicts that primates base their choice of sleeping site on access to food at night and after arising in the morning. They prefer to sleep near or in feeding sites (Chapman *et al.* 1989; Smith *et al.* 2007; von Hippel 1998). The parasite avoidance hypothesis asserts that primates will avoid the use of recently used sites to reduce the chance of parasitic infection (Hausfater and Meade 1982; Heymann 1995; Kowalewski and Zunino 2005). According to the comfort hypothesis, primates will seek the sleeping site that provides comfortable conditions, such as shelter from extreme weather conditions. The choice of sleeping sites is influenced by season or weather conditions, i.e., rainfall and temperature (Cui *et al.* 2006; Heymann 1995; Smith *et al.* 2007). The hypothesis that range or resource defense plays an important role—the range or source defense hypothesis—predicts that sleeping sites will concentrate in a core zone of exclusive use or a peripheral home range zone (Heymann 1995; Ramirez 1989). These factors may be interactive in influencing the choice of sleeping sites.

François' langur (*Trachypithecus francoisi*) is an endangered primate species living in a habitat characterized by limestone forests. Unlike most arboreal primates sleeping in high trees, e.g., *Colobus guereza* (von Hippel 1998), *Hylobates lar* (Reichard 1998), *Cebus apella* (Di Bitetti *et al.* 2000), *Rhinopithecus bieti* (Liu and Zhao 2004), François' langurs habitually sleep in cliff caves or on cliff ledges (Grueter and Ding 2006; Huang *et al.* 1983, 2004; Wu *et al.* 1987; Zhou *et al.* 2007). At present, quantitative information on the sleeping habits of François' langurs, from which it would be possible to deduce the determinants influencing the sleeping site selection, is still largely lacking, except for a 10-mo study at Fusui Nature Reserve by Huang *et al.* (2004) and Zhou *et al.* (2007). However, their study groups were isolated in a forest fragment encompassing a total area of ca. 25 ha, and faced with severe human disturbance. Thus, the sleeping habit of François' langurs was affected significantly by human activities.

We here provide detailed information on sleeping habits of 1 François' langur group at Nonggang Nature Reserve. We collected data on the pattern of sleeping site use, the characteristics of sleeping sites, and behavior before and while entering sleeping sites. We also recorded the locations of sleeping sites within the home range relative to range boundary and to feeding sites. We contrast our results with those predicted by the aforementioned hypotheses, and discuss the functional value of the behavior in light of our results.

Methods

We conducted the study between August 2003 and July 2004 at Nonggang Nature Reserve (106°42'–107°4'E, 22°13'–22°33'N), Guangxi Province, South China. The

reserve consists of 3 areas: Nonggang (5426 ha), Longhu (1034 ha), and Longshan (3949 ha), which are separated by farmlands and villages (Fig. 1). Our research site is in the northwestern portion of Nonggang, and the main study area is *ca.* 200 ha. The limestone hills consist of dense rocky hills and flat lands, with altitudes ranging from 300 m to 700 m above sea level (Deng 1988). The habitat is characterized as limestone seasonal rain forest (Shu *et al.* 1988). Small-scale agriculture occurs around reserve boundaries, but the structure and composition of forests are undisturbed by human activities. There are still many emergent trees >30 m high. During the study period, total precipitation in the study area was 977 ml, with a marked rainy season between April and September (Zhou *et al.* 2006).

Two groups of langurs inhabited the study area. Group 1 consisted of 12 individuals (4 adult males, 5 adult females, and 3 immatures) at the start of our study, but had been reduced to 10 individuals by the end due to the disappearance of an adult female and her infant. Group 2 consisted of 7 adults and 3 immatures. Because of temporal and logistic constraints, we could not determine the sex ratio of group 2. Group 1 ranged nearest to our camp, and we were able to track it closely for detailed behavioral data collection; thus it was our focal group.

A sleeping site is any place in which animals spend the night. For François' langurs, sleeping sites can be easily identified by the deep brown deposits of langur excrements below them. Each day, we followed the focal group when they left sleeping site at dawn until they remained resting at night in the sleeping site. We also

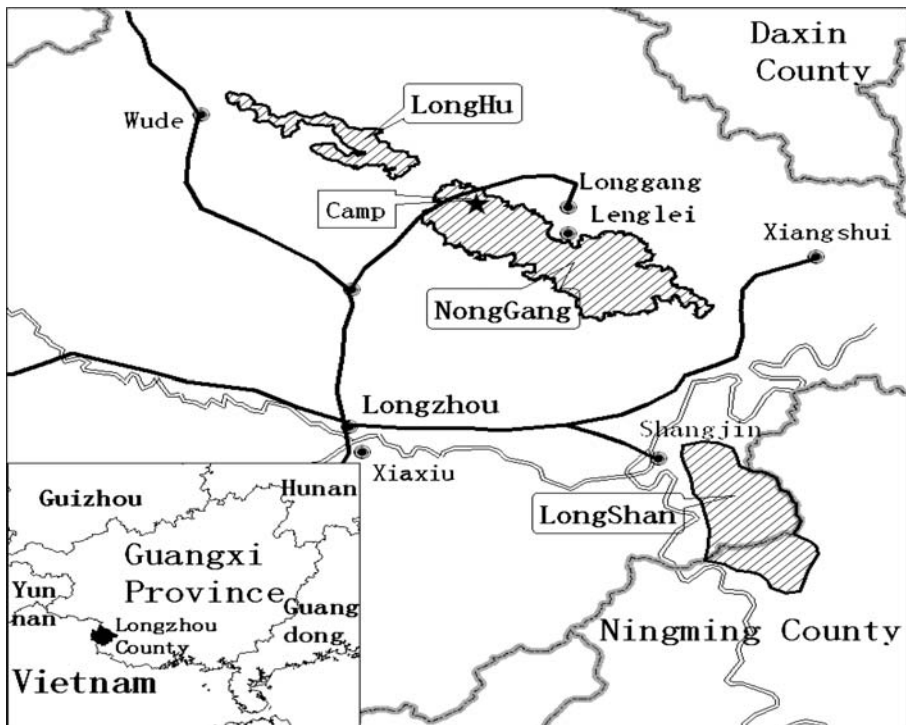


Fig. 1 Map of Nonggang Nature Reserve showing the study site and surrounding area.

collected data during partial-day follows, which began when we first encountered the monkeys. During the study period, we successfully followed the focal group to their sleeping sites during 148 nights. We marked the locations of sleeping sites on a 1:10,000 scale map. We recorded sleeping site location on a cliff, which is defined as the height relative to the top edge of hillside. We divided the height visually into 3 equal levels: low, middle, and top, because the cliff is difficult to reach and measure. The level indicates only relative differences in height. When possible, we recorded the time that langurs entered sleeping site and the presleeping activities after the last feeding bout *ad libitum* (Altmann 1974). We also noted the duration between the time of the first and last group member entering sleeping sites during 15 nights.

To assess the spatial distribution of sleeping sites in langurs' home range, we superimposed a grid of 0.25-ha quadrats (50×50 m) over the topographical map of the main study area. We estimated the range size in terms of the total number of different quadrats used by langurs during the study period. We also marked the locations of group feeding bouts in the gridded map to assess the influence of location of feeding sites on sleeping site selection. We scored a bout of group feeding when most members of a group were feeding simultaneously for >20 min. We recorded a total of 382 group feeding bouts during the study period. We represented the intensities of quadrats used for group feeding as the percentage of group feeding bout records in each quadrat among total group feeding bout records.

We used χ^2 tests to determine whether langurs showed a preference for the sleeping site use according to their expected use based on the frequency in each sleeping site. We also used χ^2 tests to determine whether there was a different number of sleeping sites than expected in the peripheral or core zones based on the relative sizes of these areas compared to overall home range size. We used Mann-Whitney *U* tests to examine whether there were significant differences in rainfall and maximum and minimum temperatures when each type of sleeping site was used, whether langurs spent a different number of nights in sleeping sites distributed in the peripheral zone and the core zone of the home range, and whether there was a significant difference between the distances from sleeping site to the last group feeding site and to the first group feeding site in the subsequent morning. To examine the possibility that langurs may adopt a central place foraging (CPF) strategy in which animals return to a central place, or multiple central place foraging (MCPF) strategy in which animals choose between one of a number of limited central places (Chapman *et al.* 1989), we estimated the linear distances between the last group feeding site and the observed sleeping site, the nearest sleeping site used, and the central sleeping site and compared the via paired *t*-tests. Following Smith *et al.* (2007), the central place in a CPF strategy was indicated by the arithmetic mean of the coordinates of all sleeping sites used.

Results

Use of Sleeping Sites

We recorded a total of 23 different sleeping sites, all of which were located on cliffs. However, the number of new sleeping sites continued to increase during the study

period (Fig. 2), suggesting that there are still usable sleeping sites available to langurs in their home range.

Of 23 sleeping sites, the langurs used 7 sleeping sites during 96 nights (≥ 9 times each), accounting for 64% of total observed nights. Langurs used 50% of the sleeping sites only 2–3 times, and only 1 was used once (Table I). We compared the observed frequencies of sleeping sites use to the frequencies expected by chance, as calculated using the total number of sleeping sites and the total number of observed nights. There is a significant difference between observed and expected frequencies ($\chi^2=118.08$, $df=22$, $p<0.001$), indicating that langurs showed preference in sleeping site use. Over 146 d when we followed the group on consecutive nights, the group used the same sleeping site as on the previous night during 69 d (47%). Four consecutive nights was the longest run for which a sleeping site was reused, which occurred on 3 occasions. Although most sleeping sites were used repeatedly during the study period, there was a marked difference in the time of reuse of sleeping sites. For example, sleeping site 1 was used most frequently, and langurs returned to it after 6.7 d ($SD=5.2$) on average, varying from 1 d to 15 d.

Characteristics of Sleeping Sites

We identified 2 categories of sleeping sites: ledge and cave. Of 23 sleeping sites, 17 were ledges and 6 were caves. During the study period, langurs spent 59 nights (40% of 148 observed nights) in caves and 89 nights (60%) on ledges (Table I). However, we compared the frequencies that langurs used both categories of sleeping sites to the expected frequencies based on the number of sites in each category and the total number of observed nights, and found that langurs spent more nights in caves and fewer nights on ledges than expected ($\chi^2=13.926$, $df=1$, $p<0.001$), indicating their preference for sleeping in caves.

In the dry season, langurs spent significantly more nights on ledges than in caves ($\chi^2=5.261$, $df=1$, $p=0.021$), but there is no significant difference in the rainy season ($\chi^2=1.143$, $df=1$, $p=0.285$). We then compared the rainfall, and maximum and minimum temperatures when each type of sleeping site was used, and documented no significant differences in any of the variables examined ($Z=-1.530$, $n_1=59$, $n_2=89$,

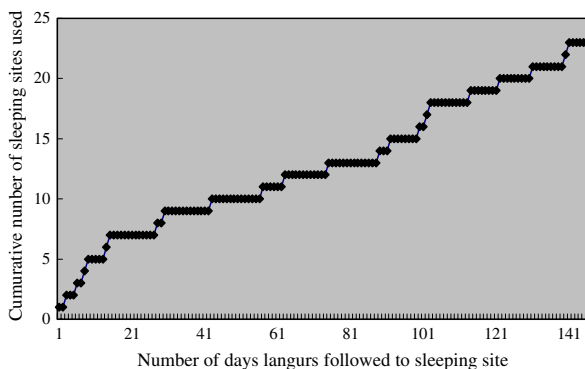


Fig. 2 Cumulative relationship between the number of different sleeping sites used by François' langurs and the number of days we followed langurs to sleeping sites.

Table 1 Frequency of the different types of sleeping sites and intensity of use by François' langurs

Code	Form	Level	Dry season	Rainy season	Total frequency	% (F)
1	C	L	15	7	22	14.9
2	L	M	4	3	7	4.7
3	L	T	11		11	7.4
4	L	L	8	6	14	9.5
5	L	T	3	5	8	5.4
6	L	T	3		3	2.0
7	L	M	1	2	3	2.0
8	C	M	3		3	2.0
9	L	M	7	4	11	7.4
10	C	T	9		9	6.0
11	C	T	2	1	3	2.0
12	L	L	1		1	0.7
13	L	T	2		2	1.4
14	L	T	2	1	3	2.0
15	L	M	9		9	6.0
16	L	M	2		2	1.4
17	C	L	6	14	20	13.5
18	L	M	3	1	4	2.7
19	L	L	1	1	2	1.4
20	L	M		5	5	3.4
21	C	L		2	2	1.4
22	L	T		2	2	1.4
23	L	T		2	2	1.4

Form: C = cave; L = ledge. Level: L = low; M = middle; T = top. % (F) = percentage of total frequency

$p=0.126$ for rainfall; $Z=-0.463$, $p=0.643$ for maximum temperature; $Z=-0.595$, $p=0.552$ for maximum temperature).

Seventy-four percent of the sleeping sites were located at middle or top levels of cliffs (Table 1). However, there is no significant difference in the frequencies of langurs' use among various levels of cliffs at which they slept ($\chi^2=4.149$, $df=2$, $p=0.123$; Fig. 3). We then compared the observed frequencies of langurs' use of various levels of cliffs to the expected frequencies based on the number of sleeping sites distributed at various levels of cliffs. Langurs spent more nights at the low level and fewer nights at the middle and top levels than expected ($\chi^2=17.913$, $df=2$, $p<0.001$), indicating a preference for low-level cliffs.

Spatial Distribution of Sleeping Sites

The home range size used by the focal group was 69.3 ha (Fig. 4). More than 50% sleeping sites ($n=13$) were ≤ 100 m of the range boundary. This peripheral region accounted for 64.6% of the range area. We compared the number of sleeping sites in the peripheral and core zones between observed values and expected ones based on

frequently are all distributed in the quadrats or neighboring quadrats used frequently for group feeding (Fig. 4). We then examined the location of sleeping sites with respect to the location of the last feeding bout before langurs entered sleeping sites. Over 74 d when we observed the last group feeding bouts, the focal group slept in the same quadrat as the last group feeding site or in the neighboring quadrats during 37 nights (50%).

We then compared the distances between the last group feeding site and the observed sleeping site to that between the last group feeding site and the nearest sleeping site (MCPF), as well as to that between the last group feeding site and the central sleeping site (CPF). All differences are significant (paired *t*-tests, observed vs. MCPF: $t=5.438$, $df=73$, $p<0.001$; observed vs. CPF: $t=-12.490$, $df=73$, $p<0.001$). However, differences between the distances from the last group feeding site to the observed sleeping site and to the nearest sleeping site are significantly smaller than that between distances from the last group feeding site to the observed sleeping site and to the mean sleeping site ($t=-12.913$, $df=73$, $p<0.001$; (Fig. 5), indicating that langurs may adopt a strategy closer to that of multiple center places foragers than central place foragers.

We also examined the location of sleeping site with respect to the location of the first group feeding bout after leaving sleeping site next morning. In 48 cases in which we identified the sleeping sites used the previous night and noted the first group feeding bouts next morning, the focal group fed in the same quadrat as the sleeping site the previous night or in the neighboring quadrat in 30 cases (63%). We compared the mean distances between the sleeping site and the last group feeding site of the day to the mean distance between sleeping site and the first group feeding sites the next morning. There is no significant difference between both distances (80.4 ± 42.1 m vs. 79.2 ± 63.4 m; Mann-Whitney *U* test $Z=-0.969$, $n_1=74$, $n_2=48$, $p=0.333$).

Behavior Before Entering Sleeping Sites

After the last group feeding bout of the day, langurs traveled rapidly along underforest to the sleeping site, and spent prolonged period, usually >30 min, resting nearby the sleeping site. They usually hid in the dense vegetation. Langurs entered the sleeping site between 1820 and 1950 h, which occurred earlier in winter-spring

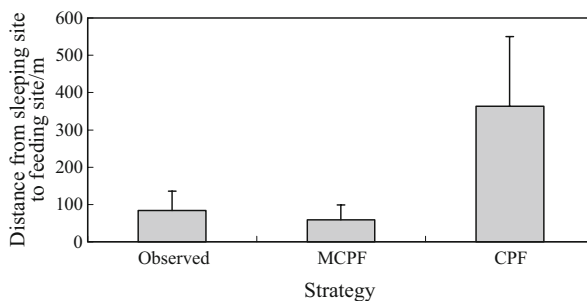


Fig. 5 Mean distance between the last feeding site of the day and the observed sleeping site, the nearest sleeping site (multiple central place foraging, MCPF), and the central sleeping site (central place foraging, CPF) in the focal group of François' langurs.

than in summer-autumn. Differences in the time of entering sleeping site according to season were likely in part a consequence of the different length of the photoperiod. In this process, langurs moved quietly along cliffs to the sleeping ledges or caves one by one, often using single-file cliff climbing locomotion. The travel lasted on average 4 min (ranging 3–6 min, $n=15$ sequences), and was often interspersed by short pauses, during which langurs scanned the environment. Because of poor light, we could not determine the identity of individual entering sleeping site for most cases. In a few cases in which we could identify the individuals, adult females with independent infant usually entered sleeping site first, closely followed by other adult females, and finally adult males.

Predation Risk

We witnessed no predation for the François' langur. However, there are still some potential predators at Nonggang. The clouded leopard (*Neofelis nebulosa*) is a potential predator. According to interviews with local people, this large felid still occurs at the reserve, but appears to be uncommon. During the study period, we did not detect any signs of the presence of this species. Other potential predators occurring at Nonggang probably include a few smaller cat species such as Asian golden cat (*Felis temminckii*) and leopard cat (*Felis bangalensis*). These cats are probably a threat only to immatures. In addition, François' langurs at Nonggang may be at risk from predation by avian raptors such as crested serpent eagles (*Spilornis cheela*) and mountain hawk eagles (*Spizaetus nipalensis*), which are large enough to catch infant langurs. We observed crested serpent eagles more than once hovering above resting sites of the focal group. Each time, the langurs became very vigilant, and infants always stayed with their mothers.

Discussion

Predation Avoidance Hypothesis

Predator pressure is a major factor influencing on sleeping habits of primates (Anderson 1998). François' langurs at Nonggang may face predator pressure from terrestrial and aerial direction. A potential terrestrial predator seems to be the clouded leopard. Rabinowitz *et al.* (1987) reported these medium-sized cats hunt arboreal Hose's leaf monkeys (*Presbytis hosei*). Although clouded leopards at Nonggang seem to be extremely scarce, we believe that past predation threat from the clouded leopard may have been slightly higher because the species were probably more common previously. At present, François' langurs at Nonggang are likely more at risk from predation by aerial raptors, such as crested serpent eagles and mountain hawk eagles. Researchers previously suggested that these eagles are likely predators of young individuals of many Asian primates, e.g., *Hylobates lar* (Reichard 1998) and *Trachypithecus leucocephalus* (Li 2000).

To reduce the chance of being captured, the prey should choose sleeping sites as safe as possible from predation. In limestone habitat, there are many natural ledges and caves on cliffs, which are always far away from the flat ground and can hardly

be reached by terrestrial carnivores. Therefore, choosing such sleeping sites can reduce the possibility of predation (Huang *et al.* 2003, 2004). Many studies have also documented that primates use ledges or caves on cliffs as sleeping sites to protect themselves against predators (Hamilton 1982; Huang *et al.* 2003; Sigg and Stolba 1981).

Previous researchers indicated that, to reduce the chance of detection by predators, primates used many sleeping sites, and changed their sleeping sites frequently (Franklin 2004; Smith *et al.* 2007). Our results document a similar strategy adopted by François' langurs. Although langurs did not avoid frequently reusing the same sleeping site, even though it may cue in predators due to build-up of odor (Franklin 2004; Reichard 1998), Di Bitetti *et al.* (2000) and Struhsaker (1967) also suggested reuse of the same sleeping site as a strategy to reduce predation risk by increasing familiarity and improving chances for escape. In addition, their cryptic behaviors before entering sleeping sites, such as the rapid movement toward sleeping sites with an increased level of vigilance, may also help in decreasing the possibility of detection by predators.

Food Access Hypothesis

Access to food resources may also be a factor influencing sleeping site selection in François' langurs. In our study, langurs used most sleeping sites repeatedly, and 50% of the sleeping sites were situated close to the last group feeding site of the day. A comparison of the observed distances between the last group feeding site and the observed sleeping site with distances predicting for MCPF strategy and CPF strategy documented that the strategy langurs adopted was closer to that of multiple central place foragers than of central place foragers. As Chapman *et al.* (1989) documented, repeatedly using several sleeping sites close to their current feeding area (MCPF strategy) could reduce overall travel costs. Researchers have reported a similar strategy from another François' langur group in a fragmented forest (Zhou *et al.* 2007) and other primates, e.g., *Papio hamadryas* (Sigg and Stolba 1981), *Macaca nemestrina* (Caldecott 1986), *Ateles geoffroyi* (Chapman *et al.* 1989), *Saguinus midas* (Day and Elwood 1999), and *Saguinus fuscicollis* and *Saguinus mystax* (Smith *et al.* 2007).

Smith *et al.* (2007) suggested that animals may decide where to sleep based on where they plan to feed the subsequent day. In our study, >50% of feeding activities occurred in locations close to the previous night's sleeping sites. The distances from a sleeping site to the first group feeding site in the subsequent morning were not significantly different from that to the last group feeding site the previous night, indicating that sleeping site use may similarly be influenced by a need to minimize travel costs on the subsequent day. We also documented that langurs tended to sleep at low-level cliffs, which may reduce the distance of travel to feeding sites. However, it cannot be ruled out that other factors, such as differences in the microclimate of caves and ledges or other site-specific features, may also influence the langurs' choice.

Parasite Avoidance Hypothesis

Contrary to the prediction from the parasite avoidance hypothesis that primates should avoid recently used sleeping sites to reduce the possibility of parasitic

infection from contact with accumulated feces below sleeping sites (Hausfater and Meade 1982; Heymann 1995; Kowalewski and Zunino 2005), our results show that François' langurs did not avoid sleeping in the same site for several consecutive nights, indicating that avoidance of parasites did not play a significant role in the choice of sleeping sites. In accordance with the study of Zhou *et al.* (2007) at Fusui Nature Reserve, François' langurs also reused the same sleeping site for ≤ 5 consecutive nights. Huang *et al.* (2003) also documented that white-headed langurs in the same reserve usually reused the same sleeping cave for 2–4 nights in a row. In addition, langurs never defecate in caves or on ledges, and their feces all fall to the ground below sleeping caves and ledges. These behaviors may well be adaptive in terms of avoiding parasitic infection.

Comfort Hypothesis

We found no strong support for the comfort hypothesis. Compared to the ledges, caves are not only natural shelters from rain, but also cooler in summer (3–6°C lower inside than outside of the cave), and warmer in winter (2–4°C higher inside than outside; Huang 2002). Although our results indicate that François' langurs showed a preference for sleeping in caves, they still spent more nights on ledges. Even in the rainy season, langurs did not spend more nights in caves. Moreover, there were no significant differences in rainfall and temperature on days when each type was used, which is contrary to the prediction of the comfort hypothesis that the choice of sleeping sites will be influenced by season or weather conditions.

Range or Source Defense Hypothesis

To defend range or resource, animal sleeping sites often concentrate in a core zone of exclusive use or a peripheral home range zone. However, our results revealed no preference for each zone in terms of the number of sleeping sites and sleeping nights. This is in line with findings for golden-handed tamarins (*Saguinus midas midas*; Day and Elwood 1999) and white-handed gibbons (*Hylobates lar*; Reichard 1998). Moreover, we recorded no aggression between neighboring groups. Thus, our preliminary observations suggest that range or resource defense does not influence the choice of sleeping sites in François' langurs. However, it is worth noting that the absence of recording intergroup aggression may be due to the nonhabituated status of neighboring group 2, which may be frightened by the presence of observers. Thus, further studies on habituated groups must be conducted to reach a conclusive interpretation.

In summary, caves and ledges on cliffs provide safe sleeping places for François' langurs living in limestone habitats. Langurs seem to have developed strategies to reduce predation risk, such as exhibiting cryptic behavior before entering sleeping sites and increasing vigilance while entering sleeping sites. Although predator pressure appears to influence on the sleeping habit of langurs, our results also document the influence of food access. To maximize economic foraging, langurs tended to select sleeping sites closer to current perhaps feeding sites to reduce travel costs. Thus, the strategy of sleeping site use in François' langurs at Nonggang may reflect an optimization between safety and resource access.

Acknowledgments This project was financially supported by CAS Innovative Research International Partnership Project (CXTDS2005–4), CAS 100 Talent Programme, National Nature Science Foundation of China (No. 30830020, 30560023, 30860050), the Ecology PhD Construction Fund of Guangxi (XKY2006ZD01), and Project of Creative Team from Colleges and Universities in Guangxi. We thank H-S. Huang, S-Y. Liu, X. Wang, and J-Y. Bai for assistance in the field. The Guangxi Forestry Bureau and Nonggang Nature Reserve Administration Bureau provided enormous assistance for this project. We thank Mr. Cyril C. Grüter for language editing of this paper.

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