Sleeping site use of the white-headed langur *Trachypithecus leucocephalus*: The role of predation risk, territorial defense, and proximity to feeding sites

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Abstract We collected data on sleeping site use from two groups of white-headed langurs *Trachypithecus leucocephalus* living in Fusui Nature Reserve, China between August 2007 and July 2008. This information was used to test several hypotheses regarding ultimate causes of sleeping site use in this primate. White-headed langurs slept either in caves (17 sites) or on a cliff ledge (one site). They used all sleeping sites repeatedly, and reused some of them on consecutive nights; three nights was the longest consecutive use of any one sleep site. We suggest that langurs use sleeping sites to make approach and attack by predators difficult, and to increase their own familiarity with a location so as to improve chances for escape. Langurs’ cryptic behaviors with an increased level of vigilance before entering sleeping sites may also help in decreasing the possibility of detection by predators.

Group 1 spent more sleeping nights in the central area of their territory than expected; in contrast, group 2 spent more sleeping nights in the periphery of their territory, which overlaps with that of another group, than expected. 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. These results suggest that territory defense and food access may play an important role in sleeping site use of white-headed langurs [Current Zoology 57 (3): 260–268, 2011].

Keywords White-headed langur; *Trachypithecus leucocephalus*; Sleeping site; Limestone habitat

Sleeping site location is crucial for the survival of animals, as these sites may provide access to necessary diurnal resources and/or protection from predation or natural elements (Lima et al., 2005). Knowledge of animal behavior in the vicinity of sleeping sites and analysis of the factors influencing their selection is important for understanding the adaptation of animals to their environment. Thus, this topic/area of research is being increasingly recognized as worthy of interest to zoologists, especially primatologists (Anderson, 1998).

Predator pressure is thought to be the major factor influencing sleeping site choice (Anderson, 1998). Primates use high trees as sleeping sites (e.g., *Colobus guereza*, von Hippel, 1998; *Hylobates lar*, Reichard, 1998; *Cebus apella*, Di Bitetti et al., 2000; *Rhinopithecus bieti*, Liu and Zhao, 2004) or spend nights on steep cliffs (e.g., *Papio hamadryas*, Sigg and Stolba, 1981; *Trachypithecus francoisi*, Zhou et al., 2009) to protect themselves against predators. Patterns observed in the use of sleeping sites may reflect strategies to minimize predation risk. Studies document that species under high predation use many different sleeping sites if they are available in order to reduce the possibility of any one location being discovered (Reichard, 1998; Franklin, 2004; Smith et al., 2007). Alternatively, some researchers suggest that reuse of sleeping sites increases the animal’s familiarity with a location, thus improve chances for escape (Struhsaker, 1967; Di Bitetti et al., 2000). By retreating to sleeping sites carefully and discreetly (e.g., by showing increased vigilance, making less noise, and moving rapidly without hesitation), prey species can also avoid predator detection (Reichard, 1998; Di Bitetti et al., 2000; Smith et al., 2007). Territory or resource (e.g., foods) defense may also influence
sleeeleeping site distribution in the home range (Anderson, 1998). One observed pattern is central clustering - pri-
imate sleeping sites often concentrate in a core area of
exclusive use (e.g., Colobus guereza, von Hippel, 1998;
Saguinus fuscicollis and S. mystax, Smith et al., 2007).
This allows superior access to exclusive resources, and
avoids intergroup conflicts. However, in other primates,
sleeping sites are located toward the periphery instead in
a zone of overlap (e.g., Saguinus mystax, Ramirez,
1989). By locating sleeping on the borders of a territory,
primates may detect neighboring groups earlier, easing
the task of range defense. A final element thought to
influence where primates sleep is proximity to food re-
sources. Some primates prefer to sleep near or in feed-
ing sites, where they can eat either immediately before
bed or first thing in the morning upon waking (e.g., Ate-
les geoffroyi, Chapman et al., 1989; Colobus guereza,
von Hippel, 1998; Saguinus fuscicollis and S. mystax,
Smith et al., 2007). This can reduce the time and ener-
getic spent searching for food. However, some primates
do not select sleeping sites on the basis of proximity to
feeding sites (e.g., Hylobates lar, Reichard, 1998).

Previous studies suggest that the sleeping site use of
the white-headed langur Trachypithecus leucocephalus,
a critically endangered primate species in the world en-
demic to China (Huang et al., 2002) is mainly influ-
enced by predator pressure (Huang et al., 2003). How-
ever, this does not preclude the influence of other fac-
tors, such as territory or resource defense or proximity
to food resources, on sleeping site selection. Here, we
present data intended to help resolve the role of two
other considerations in white-headed langurs’ choice of
sleeping site: (1) If selection of sleeping sites is affected
by range or resource defense, we may observe behavior
consistent either with monopolizing resources and
avoiding contact with hostile groups (concentration in a
central area) or early detection of rival neighbors (con-
centration on the periphery where territories overlap).
(2) If selection of sleeping site is affected by location of
food resources, it may be expected that they prefer to
sleep near to feeding sites.

1 Materials and Methods

1.1 Study site and animal

This study was conducted between August 2007 and
July 2008 at Fusui Nature Reserve, Guangxi province,
China (22°24′51″– 22°36′20″N and 107°23′–107°41′43″E,
Fig. 1), which was founded in 1981 for protecting the
white-headed langur and the Français’ langur
Trachypithecus francoisi. This reserve covers 80 km²,
and consists of limestone hills, with altitude ranging
from 400 m to 600 m above sea level. The predominant
forest type is limestone seasonal rainforest (Guangxi
Forestry Department, 1993). It has been degraded by
human activities such as firewood collection and planta-
tion construction (Huang, 2002). The main potential
predators in the reserve are crested serpent eagles Spi-
lornis cheela, which are large enough to catch infant
langurs (Li, 2000). Rainfall was seasonal with a distinct
rainy season between April and September, and annual
precipitation during the study period (August 2007–July
2008) was 1035 mm.

Fig. 1  Map of Fusui Nature Reserve
Our study site is located in the central part of Fusui Nature Reserve. We focus on two neighboring groups of the white-headed langur who ranged nearest to our camp. Group 1 consisted of 14 individuals (one adult male, eight adult females, two juvenile and three infants) at beginning of the study, and increasing 18 individuals by the end after four births. Group 2 contained 11 individuals (one adult male, five adult females, three juveniles and two infants) throughout the study period.

1.2 Data collection and analysis

The groups were followed from sleeping site to subsequent sleeping site for 93 days (Group 1: \( n = 54 \); Group 2: \( n = 39 \)). We also followed groups for part of the day on other occasions, averaging 4.04 hours of observation on those days (range = 2.5 to 9, \( SD = 2.29 \)). Additional sleeping site records without systematic tracking were collected by an experienced field assistant who followed study groups independently. Because of differences in difficulty of tracking each group, we followed the study groups to their sleeping sites 127 nights (5–20 nights each month) for group 1, and 88 nights (5–11 nights each month) for group 2. We marked the locations of sleeping sites on a 1:10,000 scale topographical map. We also recorded sleeping site position on the cliff, which is defined as the height relative to the top edge of hillside. The height was visually divided into three equal levels (low, middle, and top) following Zhou et al. (2009). Conditions permitting, we recorded the entry time and behavior while entering the sleeping site of each individual in a group ad libitum (Altmann, 1974).

To assess the spatial distribution of sleeping sites in whit-headed langurs’ home range, we superimposed a grid of 0.25-ha quadrats (50 m × 50 m) over the map of the main study area. We use a 0.25-ha quadrat size because the group members rarely spread over an axis of >50 m. In order to determine the influence of feeding sites on the choice of sleeping sites, we marked the locations of group feeding bouts in the gridded map. Following Zhou et al. (2009), we scored a bout of group feeding when more than half adult individuals of a group were feeding simultaneously for >20 min. During the study period, we recorded a total of 397 group feeding site records in each quadrat among total group feeding bout records.

In order to examine whether there was preference for sleeping primarily in either the peripheral or overlap areas, we used Chi-square tests for goodness-of-fit with the expected values in the peripheral (or overlap) and central (or core) areas based on the relative sizes of these areas compared to overall home range size. The home range size was estimated as the total number of different 0.25-ha quadrats used by langurs during the study period. The home range periphery was limited within 50 m from the edge of the home range, with the remainder of home range was central area.

Two different foraging strategies have been suggested with respect to the sleeping site selection in animals when proximity to food is consideration. One is the central place foraging (CPF) strategy in which animals return to a central place to sleep (e.g., Tamias striatus, Giraldeau and Kramer, 1982). Another is the multiple central place foraging (MCPF) strategy in which animals choose one of a number of limited central places for sleeping, usually close to their last feeding sites (e.g., Ateles geoffroyi, Chapman et al., 1989). To examine the possibility that white-headed langurs display either a CPF strategy, or MCPF strategy, we estimated the linear distances between the last group feeding site and the observed sleeping site, the nearest sleeping site used, and the central place and compared them via paired t-tests. Following Smith et al. (2007), the central place in a CPF strategy is expressed as the arithmetic mean of the coordinates of all sleeping sites used. We estimated the linear distances from sleeping site to the last group feeding site of the day and to the first group feeding site of the following morning and used Wilcoxon signed-rank tests to examine the difference.

2 Results

2.1 Characteristics of sleeping sites

The sleeping sites of white-headed langurs were easily identified by the deep brown deposits of langur excrements below them. During the study period, we recorded a total of 18 different sleeping sites used by the two study groups, 17 of which were caves in contrast to only 1 ledge. During the study period, langurs spent 213 nights (99%) in caves and only two nights (1%) on the ledge. Most sleeping sites were located at middle or top levels of cliffs (Table 1).

2.2 Use of sleeping sites

Of 18 recorded sleeping sites, nine were used by each group. There was no overlap between the two groups’ sleeping sites. The relationship between the cumulative use of sleeping sites and the number of observation days is in Fig. 2. The curve reached a clear plateau after 60 d
Table 1  Frequency of the different types of sleeping sites and their intensity of use by white-headed langurs

<table>
<thead>
<tr>
<th>Code</th>
<th>Group1</th>
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<th>Group2</th>
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<tr>
<td></td>
<td>Form</td>
<td>Level</td>
<td>Total frequency</td>
<td>% (F)</td>
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<tr>
<td>1</td>
<td>C</td>
<td>M</td>
<td>31</td>
<td>24.4 % (F)</td>
</tr>
<tr>
<td>2</td>
<td>C</td>
<td>T</td>
<td>29</td>
<td>22.8 % (F)</td>
</tr>
<tr>
<td>3</td>
<td>C</td>
<td>M</td>
<td>20</td>
<td>15.7 % (F)</td>
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<tr>
<td>4</td>
<td>C</td>
<td>L</td>
<td>15</td>
<td>11.8 % (F)</td>
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<tr>
<td>5</td>
<td>C</td>
<td>M</td>
<td>10</td>
<td>7.9 % (F)</td>
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<tr>
<td>6</td>
<td>C</td>
<td>T</td>
<td>9</td>
<td>7.1 % (F)</td>
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<tr>
<td>7</td>
<td>C</td>
<td>L</td>
<td>6</td>
<td>4.7 % (F)</td>
</tr>
<tr>
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<td>C</td>
<td>M</td>
<td>5</td>
<td>3.9 % (F)</td>
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<tr>
<td>9</td>
<td>L</td>
<td>T</td>
<td>2</td>
<td>1.6 % (F)</td>
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C: cave; L: ledge. L: low; M: middle; T: top. % (F): percentage of total frequency.

Fig. 2  Cumulative relationship between the number of different sleeping used sites by white-headed langurs and the number of days langurs were followed to sleeping sites of data collection for group 1 and 40 d for group 2, suggesting that these were accurate estimates of total sleeping site use.

All sleeping sites were reused more than once (Table 1). In order to examine consecutive reuse of sleeping sites, we excluded the first night in a continuous block of observation nights, which resulted in a total of 76 nights for group 1 and 49 for group 2. In total, consecutive reuse occurred on 14 occasions for group 1, and 9 for group 2. Three consecutive nights was the longest run for sleeping site reuse, which occurred on 1 occasion for group 2. Although all sleeping sites were used repeatedly, there was a difference in the frequency ofreuse. For example, sleeping site Code 1 was used most frequently by group 1 (n=31, Table 1), and langurs returned to it after 8.8 d (SD=5.8) on average, varying from one to 21 days.

2.3 Spatial distribution of sleeping sites

The total home range size was 23.8 ha for group 1, and 33.8 for group 2. A number of sleeping sites were located in the home range periphery (group 1: n=5; group 2: n=7, Fig. 3). The home range periphery accounted for 68.4% (group 1) and 77.5% (group 2) of the range areas. There were neither more nor less sleeping sites in the peripheral and central areas than expected values based on the relative sizes of these areas compared to overall home range size (group 1: $\chi^2 = 0.500, df = 1, P = 0.480$; group 2: $\chi^2 = 0.000, df = 1, P = 1.000$). We also compared the number of nights spent in the peripheral and central areas between observed values and expected ones. Group 1 spent significantly more nights in the central area and few nights in the peripheral area than expected ($\chi^2 = 64.376, df = 1, P < 0.001$). Conversely, Group 2 spent more nights in the peripheral area and few nights in the central area than expected, but the difference is not strictly significant ($\chi^2 = 3.171, df = 1, P = 0.075$).

The two study groups were separated by a road and sugarcane plantations and never entered one another’s home range. Thus, we used overlap with other groups in the area. Group 1 shared 3.8 ha at the northwestern edge of its range with another unstudied harem group, accounting for 16% of group 1’s range. 15.8-ha of group 2’s home range (47%) overlapped with that of an all-male group (Fig. 3). Some sleeping sites were located in the overlap area (group 1: n=2; group 2: n=6). There were no more or less sleeping sites in the overlap area than expected value based on the relative size of this area compared to total home range size (group 1: $\chi^2 = 1.125, df = 1, P = 0.288$; group 2: $\chi^2 = 1.800, df = 1, P = 0.180$). We also compared the number of nights spent in the overlap area between observed values and expected ones. Group 1 spent few nights in the overlap area than expected ($\chi^2 = 3.798, df = 1, P = 0.051$).
Conversely, Group 2 spent significantly more nights in the overlap area than expected ($\chi^2 = 41.100$, $df = 1$, $P < 0.001$).

The frequently used sleeping sites tended to be located either within or adjacent to the most frequently used quadrats for group feeding (Fig. 4). Based on full-day follows (group 1: $n = 54$; group 2: $n = 39$), langurs slept in the same quadrat or neighboring quadrat as the last group feeding site during 38 nights (70%) for group 1, and 17 nights (44%) for group 2. A comparison of 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) revealed that all differences were significant (group 1, observed vs. MCPF: $t = 3.022$, $df = 53$, $P = 0.004$; observed vs. CPF: $t = -7.032$, $df = 53$, $P < 0.001$; group 2, observed vs. MCPF: $t = 3.134$, $df = 38$, $P = 0.004$; observed vs. CPF: $t = -4.938$, $df = 38$, $P < 0.001$). 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 central sleeping site (group 1: $t = -4.607$, $df = 53$, $P < 0.001$; group 2: $t = -7.032$, $df = 38$, $P < 0.001$; Fig. 5), indicating that langurs tended to adopt a strategy closer to that of multiple center places foragers than central place foragers.
We identified the sleeping site used the previous night and noted the first group feeding bout next morning in 46 cases for group 1 and 30 cases for group 2. Langurs fed in the same quadrat as the sleeping site the previous night or in the neighboring quadrat in 26 cases (57%) for group 1, and 17 cases (58%) for group 2. Wilcoxon signed-rank tests indicated no significant difference between the distances from sleeping site to the last group feeding site of the day and to the first group feeding site of the next day for the two study groups (group 1: 68 ± 63 m vs. 88± 51 m, Z = −1.299, n = 20, P = 0.194; group 2: 85 ± 47 m vs. 80± 82 m, Z = −0.680, n = 10, P = 0.496).

2.4 Behavior before entering sleeping sites

When the last group feeding site was far from the sleeping site, langurs moved rapidly to the sleep site after feeding. When langurs fed near the sleeping site, they usually hid in the dense vegetation afterward. Langurs entered the sleeping site between 1806 and 1945 h when it was dark. Entering time occurred earlier

Fig. 4  Distribution of feeding activity and sleeping sites of the study groups in different 50 m × 50 m quadrats in total home range

The numbers in the figure indicate the locations of sleeping sites and the frequency of use.
The 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 white-headed langurs in winter-spring than in summer-autumn, which in part reflects seasonal difference in length of the photoperiod. When langurs moved along the cliff to the sleeping sites, they kept quiet and usually climbed cliff single-file. This process was sometimes interspersed by short pauses, during which langurs scanned the environment.

3 Discussion

3.1 Predation avoidance

In accordance with Huang et al. (2003) study, white-headed langurs used caves and cliff ledges as sleeping sites, most of which were located at middle or top levels of cliffs, which may provide effective physical barriers to potential (terrestrial) predators, as well as facilitate early detection of approaching predators (Huang et al., 2003). They reused several sleeping sites, which can increase familiarity with the area and improving chances for escape, although it may also cue predators due to build-up of odor (Franklin, 2004; Reichard, 1998). Cryptic behaviors with an increased level of vigilance before entering sleeping sites may also help in decreasing the possibility of detection by predators. These results support predator pressure as the major factor for sleeping site selection in white-headed langurs.

Although predator pressure is the primary influence in the choice of sleeping sites, it is not mutually exclusive with other considerations, such as physical comfort. Caves are not only natural shelters from rain and wind, 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). Barrett et al. (2004) documented improved thermoregulation as an important factor determining cave use by chacma baboons Papio hamadryas ursinus. Thus, cave use by white-headed langurs may also be related to improved thermoregulation. However, more information is required on the influence of microclimatic differences on thermoregulation and metabolism in this species.

3.2 Range or resource defense

As expected, group 1 spent more sleeping nights in the central area of exclusive use than expected, even though a number of sleeping sites were located in the home range periphery. This has also been reported in studies of other territorial primates (e.g. Saguinus fuscicollis and S. mystax, Smith et al., 2007; Colobus guereza, von Hippel, 1998; Hylobates pileatus, Phoonjampa et al., 2010), and seems to indicate that exclusive access plays primary role in determining the selection of sleeping site. In white-headed langurs, harem groups have rather fixed home ranges with exclusive defended areas which the males use to attract more females (Li and Rogers, 2005). Thus, sleeping in the core area of the territory allows langurs more easily defend important food resources. Early detection and defense against intruders may not be hampered by this strategy because of relatively short travel distances from the central sleeping sites to the home range border (Smith et al., 2007). Moreover, sleeping in the central area can potentially avoid boundary disputes when in or near to the sleeping site. This is important given that territorial aggression in white-headed langurs can be lethal on rare occasions (Li and Rogers, 2005).

Contrary to group 1, group 2 spent more sleeping nights in the periphery of the territory than expected. This variation may be related to the invasion of an all-male group into the home range of group2. In white-headed langurs, extra-group males try to gain access to established groups of females by attacking and attempting to defeat the harem males. Thus, harem males must defend mates as well as territories (Li, 2000). Thus, sleeping in the periphery of the overlap area can help the male of group 2 detect the all-male group early and chase them out of his territory.

3.3 Proximity to the food resources

Our results support the prediction that proximity to food resources plays an important role in determining the pattern of sleeping site use in white-headed langurs. All sleeping sites were used repeatedly, with 44% – 70% of sleeping sites situated close to the last group feeding site of the day. This is similar to that observed for François’ langurs (50%), a close phylogenetic
relative living in a similar habitat (Zhou et al., 2009). Reusing several sleeping sites close to their last feeding sites may indicate that white-headed langurs are multiple central place foraging. The result from the 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 suggests that white-headed langurs tended to adopt a strategy closer to that of multiple center places foragers than central place foragers. Chapman et al. (1989) found that repeatedly using several sleeping sites close to their current feeding areas (MCPF strategy) can reduce overall travel costs. MCPF strategy has been reported for in platyrrhines (e.g., *Ateles geoffroyi*, Chapman et al., 1989; *Saguinus midas*, Day and Elwood, 1999; *S. fuscicolli* and *S.mystax*, Smith et al., 2007), Asian and African colobines (e.g., *Trachypithecus francoisi*, Zhou et al., 2009; *Colobus guereza*, von Hippel, 1998), and hyllobatids (*Hylabates pileatus*, Phoonjampa et al., 2010).

Primates may also select sleeping site close to the first feeding site of the next morning (Chapman et al., 1989; Day and Elwood, 1999). In this study, 57-58% sleeping sites were situated close to the first group feeding site next morning, which is similar to that observed for François’ langurs (63%, Zhou et al., 2009). We documented no significant difference between the distances from sleeping site to the last feeding site of the day and to the first feeding site of the following morning. This indicates that sleeping site selection may not only minimize travel costs to sleeping sites from the last feeding sites, but can also minimize travel costs the following day.

In conclusion, predator pressure appears to influence on sleeping habit of white-headed langurs. However, territory defence and access to food may also play important role in the choice of sleeping sites.

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