

ORIGINAL ARTICLE

Habitat use and locomotion of the François' langur (*Trachypithecus francoisi*) in limestone habitats of Nonggang, China

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Abstract

We collected data on habitat use and locomotion of the François' langur (*Trachypithecus francoisi*) between August 2003 and July 2004 at Nonggang Nature Reserve, China. A total of 739 h of behavioral data were collected during this study. We tested 2 predictions: (1) that the langurs may have special patterns of habitat use and locomotion adaptive to the limestone habitat, and (2) the langurs may exhibit different patterns of habitat use and locomotion among different zones of limestone hill. Our results indicated that François' langurs spent more time in the low-risk, relatively food-poor cliff–hilltop areas. When young leaves and fruit were scarce in the dry season, the langurs increased their time in the high-risk, food-rich valley basin. François' langurs were semi-terrestrial, and leaping and climbing were their main locomotor modes. These behavioral patterns are considered to be related to characteristics of topography and vegetation in limestone habitat, such as large areas of cliff and discontinuous canopy. Our results also supported Prediction 2. The langurs confined locomotion to the main canopy and frequently adopted leaping while traveling in the hillside and valley basin. While traveling in cliff–hilltop areas, they tended to stay in the lower stratus (≤ 5 m) or move on the ground, and walking and climbing were their dominant traveling modes.

Key words: François' langur (*Trachypithecus francoisi*), habitat use, limestone habitat, locomotion

INTRODUCTION

Information on habitat use often provides evidence of behavioral adaptation in primates, and understanding terrestriality and tree stratus use are important in eluci-

dating the pattern of habitat use (Cowlshaw 1997; Li 2007). As well as morphological characteristics, such as body size and tail length (Fleagle 1998; Dunbar & Badam 2000; Bitty & McGraw 2007), ecological factors, including predation risk, habitat structure and food distribution, are considered to be important influences on habitat use, including terrestriality and tree stratus use (Cowlshaw 1997; McGraw 1998; Campbell *et al.* 2005; Lawler *et al.* 2006; Li 2007).

In addition, primates exhibit more diverse locomotor modes than any other terrestrial mammal (e.g. vertical climbing, suspensory motion and vertical leaping)

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(Chatani 2003; Garber 2007). Locomotion modes vary in species, mainly due to body size and anatomical traits (Fleagle 1998; Garber 2007). For example, leapers tend to have relatively long hindlimbs, while suspensory primates tend to elongate their forelimbs, and quadrupedal species are in between (Gebo & Chapman 1995a; Fleagle 1998). Moreover, spatiotemporal variations in the abiotic environment, such as habitat structure and food resource distribution and availability, also influence locomotion behavior (Gebo & Chapman 1995a; Lawler *et al.* 2006; Bitty & McGraw 2007), even within the same species inhabiting different types of forest (Gebo & Chapman 1995b; Garber 1998; Prates & Bicca-Marques 2008). For example, Prates & Bicca-Marques (2008) report site-specific differences in locomotion behavior of black-and-gold howlers [*Alouatta caraya* (Humboldt, 1812)], and contribute it to variations in habitat structure. Therefore, research on living primates' locomotion is important for not only understanding their adaptation to specific habitat and their adaptive radiation, but also offering insight into patterns of habitat utilization, foraging strategies and locomotor adaptations in fossil primates (Garber 2007).

The François' langur [*Trachypithecus francoisi* (Pou-sargues, 1898)] is an endangered colobine species, ranging from the Red River in Vietnam across the Chinese border as far as the Daming Hills in Guangxi and Xingyi in Guizhou (Groves 2001). They live in the habitat characterized by karst topography (Wu *et al.* 1987), which has some unique features that differentiate them from mountain forests, such as steep cliffs, which represent approximately 10–20% of the area, shortage of surface water (Huang 2002), and poor, but more diverse vegetation (Xu 1993). Therefore, the langurs may have evolved specific behavioral strategies adaptive to the drought-prone limestone habitat. Some researchers have studied François' langurs in the field. Data are available on diet (Zhou *et al.* 2006, 2009b; Huang *et al.* 2008; Hu 2011), activity pattern (Zhou *et al.* 2007b), ranging and sleeping behavior (Zhou *et al.* 2007a, 2009a, 2011). Zhou *et al.* (2010) and Xiong *et al.* (2009) provide quantitative information on the habitat use and locomotion behavior of François' langurs in Fusui Nature Reserve. They found that the langurs spent 52% of the daytime in cliff–hilltop areas. Leaping, walking and climbing were their main traveling modes, which accounted for 46.3, 34.1 and 13.4% of locomotion behavior, respectively.

In this paper, we present quantitative data on the habitat use and locomotion behavior of François' langurs at

Nonggang Nature Reserve, and test the following hypotheses: (1) the langurs may have special patterns of habitat use and locomotion adaptive to the limestone habitat, and (2) the langurs may exhibit different patterns of locomotion and habitat use among different zones of limestone hill.

MATERIALS AND METHODS

Study site and langur groups

Nonggang Nature Reserve is located in the southwest of Guangxi, China (106°42'–107°4'E, 22°13'–22°33'N) and consists of 3 areas, Nonggang (5426 ha), Longhu (1034 ha) and Longshan (3949 ha), which are separated by farmlands and villages (Guangxi Forestry Department 1993). The reserve is dominated by rocky hills and flat lands, with altitudes ranging from 300 to 700 m above sea level (Den 1988). In terms of vegetation, this reserve is limestone seasonal rain forest. Small-scale agriculture occurs around reserve boundaries, but the forest in the reserve is under limited anthropogenic pressure. There are significant changes at different zones of limestone hills because of the differences in temperature, humidity and soil available to plants. The lower levels of hills (including valley floor and hillside) are wet and rich in soil, and are covered in large trees with rich vines and epiphytes. The common tree species are *Deutzianthus tonkinensis*, *Dracontomelon dao*, *Cinnamomum burmannii*, *Burretiodendron hsienmu* and *Cephalomappa sinensis*. The higher levels (including cliffs and hilltops) consist of bare rocks. These areas are covered drought-resistant trees, such as *Sinosideroxylon pedunculatum*, *Tirpitzia ovoidea*, *Pittosporum puchrum* and *Leptodermis affinis* (Shu *et al.* 1988; Fan *et al.* 2011). During the study period (August 2003–July 2004), annual precipitation was 977 mm. There was a distinct rainy season between April and September, with >50 mm monthly rainfall, and a dry season in the remainder of the year, with <50 mm monthly rainfall (Zhou *et al.* 2006).

Our field research was carried out in northwestern Nonggang. The size of the main study area is approximately 200 ha. Two langur groups inhabited the study area. Our focal group (group 1) had been semi-habituated to observers before data collection began. Group 1 consisted of 12 individuals (4 adult males, 5 adult females and 3 juveniles) at the start of our study, but had been reduced to 10 individuals by the end, owing to the

disappearance of an adult female and her infant. Group 2 was rarely observed to enter the home range of group 1, and we did not collect data from this group during the study period.

Ecological sampling

We conducted vegetation surveys in the main study area at the onset of behavioral data collection. We used a stratified random sampling method for the placement of vegetation plots. A total of 13 plots (50 × 10 m) were placed in the main study area, including 4 at the valley basins and 9 on the hillsides. The plots covered most of the vegetation types described by Shu *et al.* (1988). Within the plots, all trees of ≥5 cm diameter at breast height were tagged. A limit of 5 cm was used because pilot observation showed that most foraging by langurs occurred in trees of this size and larger. We checked all tagged trees ($n = 312$) by visual inspection at monthly intervals for the presence of young leaves, fruit and flowers, and used the data to calculate a tree index, expressed simply as the percentage of trees bearing the plant parts of interest, checked each month regardless of the size of the canopy (Zhou *et al.* 2006).

Data collection

We undertook behavioral observations of group 1 for 126 days in August 2003–June 2004 (7–8 days each month). No data were collected in July 2004 because many places were flooded, preventing us from locating the group; therefore, only 11 months of data were used for analysis in the present study. During full-day observation, data collection began at 06.00 hours and ended when the monkeys entered the night sleeping site. We also collected behavioral data during partial-day observation, which began when the langurs were first encountered. A total of 739 h of behavioral data were collected during this study.

We recorded the locations of langur groups in different vertical zones of the hills every 30 min to analyze vertical habitat use. We visually divided hills into 3 zones: valley basin, hillside and cliff–hilltop. The zones only indicate relative differences in height and gradient. Information on locomotion behavior, vertical ranging and patterns of support utilization was collected using an instantaneous scan sampling method (Altmann 1974) with 15 min intervals. The scans lasted 5 min, followed by 10 min of inactivity until the next scan began. To avoid sampling bias toward certain individuals or a particular age–sex class, we collected behavioral records on as many different individuals as possible dur-

ing a scan to include all individuals in the focus group but sampled no individual more than once. As some individuals hid in dense vegetation, we could sample only a fraction of the group during most scans (mean = 4.2, SD = 2.29, range = 1 to 10).

We recorded the behavior of each individual seen during each scan. In behavioral sampling, the following information was collected: (i) locomotor maintenance activity (traveling or foraging); (ii) locomotor modes: walking, running, leaping and climbing; (iii) forest strata: ground, lower (≤5 m), middle (≤5 m, ≤10 m), middle+ (>10 m, ≤15 m) and upper canopy (>15 m); (iv) substrate size (based on visually estimated diameter): small (≤2 cm), medium (>2 cm, ≤10 cm), and large (>10 cm); and (v) substrate orientation (relative to true horizontal): horizontal (0–10°), moderate (10–45°), steep (45–80°) and vertical (80–90°). The locomotor modes were defined as follows. Walking: moving quadrupedally on moderate substrate slanting less than 45°, with 3 or 4 limbs contacting the substrate in 1 sequence. Running: like walking, but faster and with a period of free flight in gait. Leaping: the hindlimbs propel an animal across a gap. Climbing: moving up or down a vertical or steeply inclined substrate.

Data analysis

Habitat use was expressed as the proportion of time the group spent in different zones of limestone hill, calculated as the percentage of records the group used each zone among monthly total location records. Annual pattern of habitat use was obtained by averaging the monthly percentages. The Kruskal–Wallis H -test was used to examine whether there were significant differences in use intensity of different zones. We also used the χ^2 -test to determine whether langurs showed a preference in vertical habitat use according to their expected use based on the availability of each zone in the home range. To estimate the availability of each zone in the 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 proportion of each zone in the home range as the percentage of quadrats dominated by each zone among the total number of quadrats. The Mann–Whitney U -test was used to examine whether there were significant seasonal differences in use intensity of different zones. We also used the Spearman correlation test to assess the relationship between vertical habitat use and food availability. All tests above are 2-tailed, with a significance level of 0.05.

Table 1 Home range habitat availability and overall and monthly habitat use by the focus François' langur group at Nonggang Nature Reserve

Habitat	Cliff–hilltop	Hillside	Valley basin
Available ha home range	30.5	30.0	8.5
% of home range size	43.5	44.2	12.3
Overall % habitat use	58.1	38.9	2.9
August % habitat use	79.0 [†]	21.1	0.0
September % habitat use	57.1 [†]	42.9	0.0
October % habitat use	52.1 [†]	46.3	1.5
November % habitat use	57.5 [†]	38.6	4.0
December % habitat use	31.7	63.8 [†]	4.6
January % habitat use	40.4	51.4 [†]	8.3
February % habitat use	47.6 [†]	47.2	5.2
March % habitat use	56.5 [†]	35.9	7.7
April % habitat use	75.7 [†]	23.4	0.9
May % habitat use	73.2 [†]	26.8	0.0
June % habitat use	68.9 [†]	31.1	0.0

[†]Monthly dominant habitats.

In this study, we excluded records for dependent juveniles from analysis because they did not move independently. We compared locomotor behaviors (including locomotor modes, forest strata and substrate size and orientation) among different zones of limestone hills using the χ^2 -test, with a significance level of 0.05. We also compared interclass differences in locomotor behaviors using the binomial test post hoc of 2 proportions, with a protected level of significance of 0.025 (= 0.05/2 tests, Prates & Bicca-Marques 2008). All tests were performed using SPSS 13.0 for Windows.

RESULTS

Patterns of habitat use

In the home range of the study group, cliffs–hilltops, hillsides and valley basins accounted for 43.5, 44.2 and 12.3% of the total area, respectively (Table 1). There was significant difference in the use of different zones of the limestone hill ($H = 24.907$, $n = 2$, $P < 0.05$). The cliffs–hilltops and hillside accounted for 58.1 and 38.9%, respectively, of the total of location records, whereas valley basin accounted for only 2.9%. A comparison of the overall pattern of relative habitat use with

that of habitat availabilities within the langurs' home range showed that langurs spent more time than expected in cliff–hilltop areas, and less time than expected in the hillside, but they were not significantly different (cliff-top: $\chi^2 = 1.896$, $df = 1$, $P = 0.168$; hillside: $\chi^2 = 0.249$, $df = 1$, $P = 0.618$), whereas they used the valley basin significantly less than expected ($\chi^2 = 5.798$, $df = 1$, $P = 0.016$).

The monthly percentage of habitat use showed that langurs used hillside and valley basin more frequently in the dry season than in the rainy season (hillside: $Z = -2.373$, $n_1 = 5$, $n_2 = 6$, $P = 0.018$; valley basin: $Z = -2.803$, $P = 0.005$). Accordingly, they decreased cliff–hilltop time ($Z = -2.556$, $P = 0.011$). To analyze whether the seasonal variations in vertical habitat use are caused by the changes in ecological conditions, we tested the relationships between the time spent on different zones of the limestone hill and the availability of foods. Vertical habitat use was affected significantly by the seasonal changes in the availability of foods. When the availability of young leaves and fruits declined, langurs increased the use of hillside (young leaf: $r_s = -0.855$, $n = 11$, $P = 0.001$; fruit: $r_s = -0.0786$, $P = 0.004$) and valley basin (young leaf: $r_s = -0.893$, $P < 0.05$), and decreased the use of cliff–hilltop (young leaf: $r_s = 0.845$, $P = 0.001$).

Locomotion

Leaping is the most common locomotor mode ($n = 729$ moving records, 43.3%), followed by climbing ($n = 429$, 25.5%), walking ($n = 335$, 19.9%) and running ($n = 189$, 11.2%). The use of locomotor modes varied among different zones of limestone hill ($\chi^2 = 64.914$, $df = 6$, $P < 0.05$; Fig. 1). Walking was more frequently observed in cliff-hilltop areas than in the valley basin, while running was less frequent. Langurs leaped more frequently in the valley basin and hillside than in cliff-hilltop areas. Climbing was more often observed in cliff-hilltop areas than in the hillside. Langurs were rarely observed climbing in the valley basin.

Figure 1 Percentage of moving records engaged in each locomotor mode among different zones of limestone hill. Within each histogram (locomotor mode), letters indicate group classes; the same letter above a subset of bars denotes lack of statistical difference, whereas different letters represent statistically different classes ($P < 0.025$) according to the binomial test.

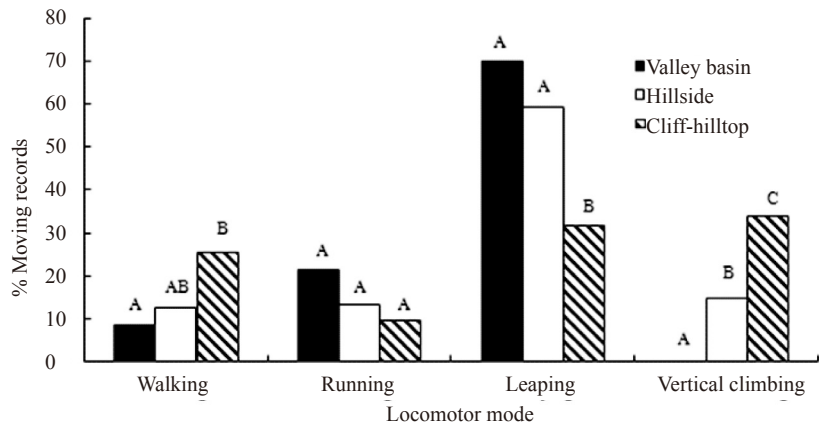
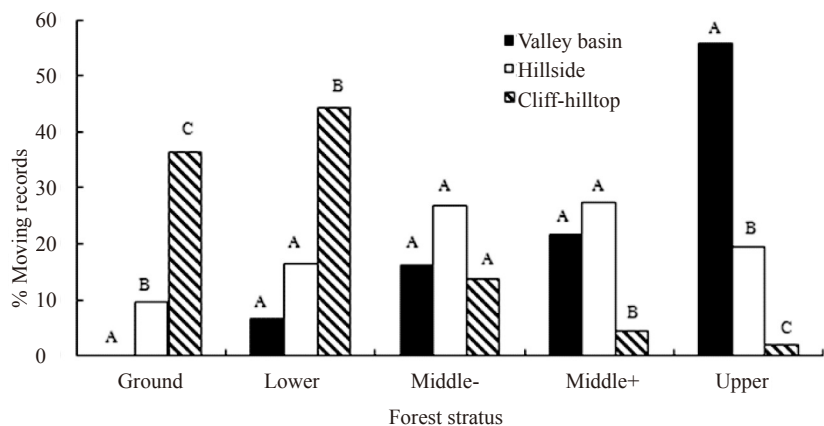


Figure 2 Percentage of moving records for each forest stratus among different zones of limestone hill. Within each histogram (forest stratus), letters indicate group classes; the same letter above a subset of bars denotes lack of statistical difference, whereas different letters represent statistically different classes ($P < 0.025$) according to the binomial test.



Locomotion and strata use

Langurs conducted 46.7% of locomotion on the ground, and 53.3% in the trees. They moved on the ground more frequently in cliff-hilltop areas than in the hillside, and were rarely observed to come down to the ground in the valley basin (Fig. 2). Though langurs tended to stay in the lower and middle canopy heights while traveling (50.9% in middle canopy heights and 38.4% in lower canopy heights), there were significant differences in the use of forest strata among different zones of limestone hill ($\chi^2 = 114.710$, $df = 6$, $P < 0.05$; Fig. 2). Langurs preferred using the lower canopy heights while traveling in cliff-hilltop areas than in other zones of lime-

stone hills. They used the middle canopy heights more frequently while traveling in the hillside and valley basin than in cliff–hilltop areas. Langurs spent more time traveling in the upper canopy heights in the valley basin than in other zones of limestone hills.

Locomotion and substrate use

Although langurs relied primarily upon medium-sized branches while traveling (71.7%), frequencies of branch size utilization were significantly different among different zones of limestone hill ($\chi^2 = 30.392$, $df = 4$, $P < 0.05$; Fig. 3). Langurs used small-sized branches more frequently in the valley basin than in the hillside and cliff–hilltop areas, whereas were rarely observed to use large-sized branches in the valley basin. Langurs frequently used moderately inclined supports while traveling (40%). However, there were significant differences in the use of substrate orientation among different zones of limestone hill ($\chi^2 = 102.235$, $df = 6$, $P < 0.05$; Fig. 4).

Langurs used moderately inclined supports more frequently while traveling in the valley basin than in other zones of limestone hills. They used a greater percentage of horizontal supports while traveling in the hillside. The use of steeply inclined and vertical supports was rare in the valley basin.

DISCUSSION

Habitat use

Food availability and predation risk are thought to be the major factors influencing habitat use in primates (Cowlshaw 1997; Enstam & Isbell 2004). In this study, François' langurs used cliff–hilltop areas more frequently than expected, as previously reported for this species (Zhou *et al.* 2010), and used the hillside and valley basin less frequently. Compared to the hillside and valley basin, the cliff–hilltop area is a low-risk relatively food-

Figure 3 Percentage of moving records for each substrate size among different zones of limestone hill. Within each histogram (substrate size), letters indicate group classes; the same letter above a subset of bars denotes lack of statistical difference, whereas different letters represent statistically different classes ($P < 0.025$) according to the binomial test.

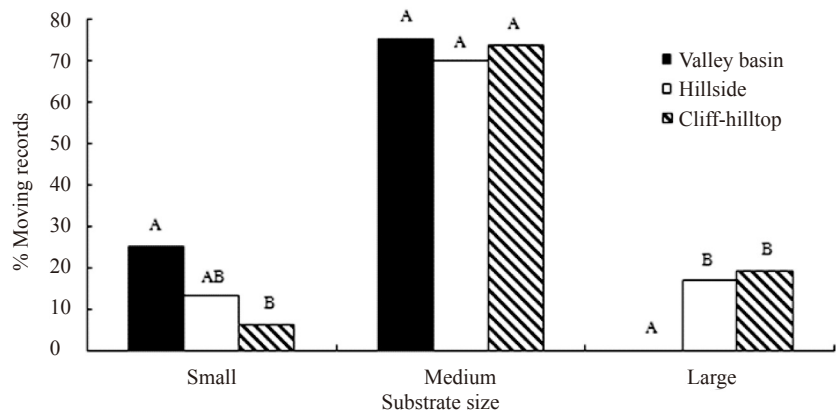
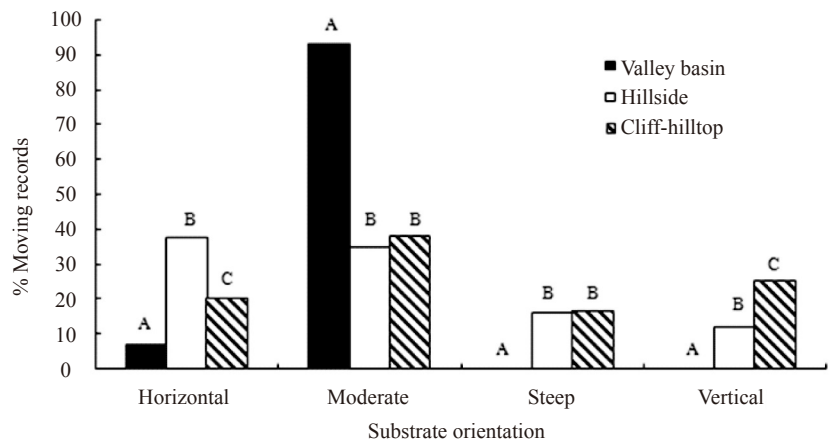


Figure 4 Percentage of moving records for each substrate orientation among different zones of limestone hill. Within each histogram (substrate orientation), letters indicate group classes; the same letter above a subset of bars denotes lack of statistical difference, whereas different letters represent statistically different classes ($P < 0.025$) according to the binomial test.



poor habitat (Huang & Li 2005; Li & Rogers 2005). Thus, François' langurs may have preferred cliff–hilltop areas for greater safety from terrestrial predators rather than advantage in food acquisition. Humans are likely the primary predators of François' langurs, and more than 1500 langurs were hunted for medicinal wine in the 1980s in Daxi and Longzhou County (including Nonggang Nature Reserve), Guangxi (Wu *et al.* 1987). We suggest that past hunting pressure from humans may have resulted in the choice of locating in cliff–hilltop areas, and this habit has persisted, even though hunting has been eradicated.

With reduced young leaf and fruit availability in the dry season, the langurs were forced to use the high-risk, food-rich valley basin. Exploitation of the seeds of *Pithecellobium clypearia*, an important supplementary food in the dry season (Zhou *et al.* 2006), appeared to have major influence on the time spent in the valley basin. However, even staying in the valley basin, the langurs tended to forage and rest in the safer upper stratus, and rarely came down to the ground. This indicates that trade-offs between foraging and predation risk may determine habitat use of François' langurs in limestone habitat.

Locomotion

Leaping was the dominant locomotor mode of François' langurs at Nonggang Nature Reserve (43.3% of locomotor behavior, this study and Fusui Nature Reserve (46.4%, Xiong *et al.* 2009). This is probably related to characteristics of vegetation in limestone habitat. In the hillsides of limestone hills, most trees are vertically distributed and canopies are not continuous (Fan *et al.* 2011). Therefore, in a discontinuous canopy, one would expect relatively more leaping from a small-bodied primate such as the François' langur, as there are relatively more gaps to leap across (Fleagle 1998). There are relative continuous canopies in the valley basin at Nonggang Nature Reserve. However, in these areas, the most important food trees, *P. clypearia*, are emergent trees characterized by large, smooth trunks with no midtrunk branches (Zhou *et al.* 2006). During the study period, we never observed langurs climbing up these trees. To reach these trees, langurs leaped from neighboring trees in the discontinuous canopy, making long-distance leaps from a stationary position. Thus, much of the leaping in the valley basin may be related to the exploitation of these food resources. In addition, langurs tended to travel in the middle canopy. These areas are structurally complex and few options are available for uninter-

rupted, horizontal travel, given the high density of lianas and vines. Short-distance leaping is proven to be an effective way of traveling in these habitats (Lawler *et al.* 2006).

The white-headed langur (*T. leucocephalus* Tan, 1955), a close phylogenetic relative living in a similar habitat, exhibited a similar repertoire, and leaping accounted for 47.3% of the overall locomotor profile (Xiong *et al.* 2009). This indicates behavioral convergence of leaping behavior of François' langurs and white-headed langurs. However, leaping represents only 6% of overall locomotion behavior in another limestone langur, the Delacour's langur (*T. delacouri* Osgood, 1932) at Van Long Natue Reserve (Workman & Schmitt 2012). This variation is probably related to the difference in habitat quality. Compared to Nonggang and Fusui Nature Reserve, Van Long Natue Reserve is a more degraded habitat, with a preponderance of climbers and stunted trees, and 40% of the main study area is exposed rock. Because there is no understory, there is no discontinuity of substrates, but rather a type of substrate (rock), leading to greater amounts of quadrupedalism (Workman & Schmitt 2012).

Climbing was the next most frequent locomotor mode of François' langurs at Nonggang (25.3% of locomotor behavior), which is similar to other limestone *Trachypithecus* species (e.g. 19.7% of white-headed langurs' locomotor behavior, Xiong *et al.* 2009; 26% of Delacour's langurs' locomotor behavior, Workman & Schmitt 2012). Why these limestone langurs frequently adopted climbing is probably related to characteristics of topography in limestone habitat. A large area of cliff is unique to the limestone habitat (Huang 2002), and climbing was the predominant mode of traveling on the cliffs. Furthermore, langurs selected the ledges and caves on cliffs as sleeping sites, which provide effective physical barriers to terrestrial predators (Huang & Li, 2005; Zhou *et al.* 2009a). Climbing along cliffs is the only way to reach these sites.

Strata and substrate use

François' langurs at Nonggang used arboreal (53.3%) and terrestrial supports (46.7%) for traveling. A similar pattern was also found in the study of François' langurs (61% in trees, 39% on rocks) at Fusui (Xiong *et al.* 2009), as well as in other limestone *Trachypithecus* species, such as white-headed langurs (70% in trees, 30% on rocks) at Fusui (Xiong *et al.* 2009) and Delacour's langurs (20% in trees, 80% on rock) at Van Long Natue Reserve (Workman & Schmitt 2012). Moreover, they

spent much time resting on rocks (Huang *et al.* 2003; Zhou 2005). It is clear that these limestone langurs can be classified as semi-terrestrial species in the genus *Trachypitecus*. This is in contrast to non-limestone *Trachypitecus* species, which are usually considered to be arboreal species (e.g. *T. vetulus* [Erxleben, 1777], Napier 1985; *T. cristatus* [Raffles, 1821], Brotoisworo & Dirgayusa 1991; *T. pileatus* [Blyth, 1843], Standford 1991; and *T. johnii* [Fischer, 1829], Fleage 1998). As discussed above, the limestone langur's semi-terrestrial habit is explained by their adaptation to cliff-hilltop areas, characterized by steep cliff-rocky surfaces and less vegetation (Huang & Li 2005; Xiong *et al.* 2009; Workman & Schmitt 2012).

In this study, we documented marked variations in the use of forest strata when François' langurs traveled among different zones of limestone hill. These variations are probably due to food resource distribution and predation risk. Leaves contributed to 53% of the annual diet of François' langurs (Zhou *et al.* 2006), and tend to be more ubiquitously distributed than fruits and seeds (Richard 1985). It is easy for langurs to access leaves from every forest strata. When traveling in the hillside and valley basin, langurs tended to stay in the middle stratus to protect themselves against potential aerial predators, such as crested serpent eagles (*Spilornis cheela*, Latham, 1790) and mountain hawk eagles (*Spizaetus nipalensis*, Hodgson, 1836), which are large enough to catch infant langurs (Zhou *et al.* 2009a). Besides predation risk, more upper stratus use while traveling in the valley basin might be related to the exploitation of the seeds of *P. clypearia*. These seeds are usually distributed in upper tree stratus. However, other factors cannot be ruled out, such as difference in vegetation height and structure, which result in langurs using stratus differently among different zones of limestone hills. For example, the trees on the cliff-top are small and low (Li & Rogers 2005); therefore, the langurs used lower stratus more frequently in this habitat.

Differences in support use during locomotion appear to be as much a function of species-specific behavioral characteristics as they are of body size (McGraw 2000). The François' langur has a medium body size, and use medium-sized branches most frequently while traveling. This pattern also reflects François' langur's frequent use of the middle stratus, where large, horizontal supports are most abundant (Q. Zhou, pers. observ.). However, there was significant difference in support use of François' langurs among different zones of limestone

hills. Langurs used small-sized branches more frequently in the valley basin than in the hillside and cliff-hilltop areas. As discussed above, langurs used the valley basin mainly for exploitation of the seeds of *P. clypearia*, which are usually found suspended among the peripheral twigs of the upper tree stratus (Q. Zhou, pers. observ.). Thus, high small-size branch use is probably related to foraging for preferred food items in the periphery of tree crowns, which are characterized by high densities of small supports.

In summary, François' langurs seem to have developed behavioral adaptation to their limestone habitat, demonstrated through their preference for cliff-hilltop areas, their semi-terrestrial habit and their high rates of leaping and climbing.

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