

Positional Behaviours of François' Langur (*Trachypithecus francoisi*) in the Limestone Forest of Nonggang, Guangxi, South-West China

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Keywords

Positional behaviour · Seasonal variation · François' langur · Limestone forest

Abstract

Primates' positional behaviours provide information for understanding relationships among morphology, ecology and behavioural flexibility. From September 2005 to August 2006, we collected data via instantaneous scan sampling on positional behaviours in François' langurs at Nonggang Nature Reserve, south-west China. We predicted that these langurs would use (1) leaping as the predominant locomotor mode and (2) bipedal standing more frequently in the rainy season than in the dry season. Our result showed that leaping was the dominant locomotor mode (38.38%), followed by quadrupedal walking (31.2%), vertical climbing (25.1%) and quadrupedal running (5.3%). The ground was the most frequently used stratum during movement (33.4%). Most locomotion through trees occurred on small- (48.7%) and medium-sized (47.6%) substrates. Locomotor mode, forest stratum use and substrate use during movement did not vary seasonally. When stationary, sitting was the most common posture (92.1%), followed by bipedal standing (3.7%), lying (3.5%), quadrupedal standing (0.6%), suspending (0.2%) and back-lying (<0.1%). Posture varied significantly with the season. During resting, langurs used sitting and bipedal standing more frequently in the dry season, while adopting lying more frequently in the rainy season. During feeding, sitting

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was adopted more frequently in the rainy than in the dry season, whereas bipedal standing was used more frequently in the dry season. Langurs spent more feeding time on the ground in the dry than in the rainy season. Locomotor patterns in François' langurs are likely linked to morphological and anatomical characteristics, along with the limestone forest's structure. Our result completely supported prediction 1 but not prediction 2. This study suggests that seasonal variation in positional behaviour might result from the temporal difference in spatial distribution of foods and behavioural thermoregulation strategy. We found that François' langurs adjusted positional behaviour in response to seasonality, and this behavioural flexibility allows them to survive in a variety of habitats, including limestone forests.

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Introduction

Studies of positional behaviour are relevant for understanding how animals move through their environments, access food, avoid predation and locate mates [Cant, 1992; Blanchard et al., 2015; Larson, 2018]. Because primates inhabit various environments and often face dramatic seasonal and ecological variation [Richard, 1985], positional behaviour adjustments are one way they cope with changes in food availability [Youlatos, 1998], thermoregulation demand [Dasilva, 1993] and forest structure alteration [Gebo and Chapman, 1995a]. In this regard, positional behaviour should be regarded as an important dimension of ecological adaptation [Ripley, 1967].

Primate positional behaviour is constrained by morphological and anatomical characteristics, such as body size, limb proportions and tail length [Hunt, 1992, 1994; McGraw, 1998; Wright, 2007; Prates and Bicca-Marques, 2008; Fleagle, 2013; Huang et al., 2015; Zhu et al., 2015]. In general, frequency of climbing and leaping depends on size, with smaller monkeys being more likely to leap across a gap they encounter and larger species tending to climb over or use bridging to cross a discontinuity [Fleagle and Mittermeier, 1980; Fleagle, 2013]. For example, vertical climbing in chimpanzees (*Pan troglodytes*) is significantly affected by body size, with larger males climbing less frequently than smaller males because climbing is disproportionately metabolically expensive for larger animals [Hunt, 1994]. This pattern might be because leaping completely depends on high propulsive forces generated from hind limbs, and therefore larger animals require greater forces to leap [Fleagle, 2013]. The intermembral index (IMI, length of forelimb divided by length of hind limb) helps determine primate locomotor preference [Fleagle, 2013]. In general, primates with a low IMI (longer hind limb) are skilled in leaping, those with a high IMI (longer forelimb) more frequently use arm swinging and suspension, and those with an intermediate IMI generally prefer quadrupedalism [Chatani, 2003; Huang and Li, 2005; Fleagle, 2013]. For example, brown capuchins (*Cebus apella*) have particularly short hind limbs (high IMI), and they frequently use walking and bridging when travelling. In contrast, weeper capuchins (*C. olivaceus*) have long hind limbs (low IMI), and they run, bound and leap more frequently than brown capuchins [Wright, 2007]. Additionally, tail length correlates with an animal's leaping ability [Chatani, 2003; Fleagle, 2013]. Primate species with longer tails might be able to leap further than those with shorter tails; long tails might function as balancers during leaping [Cant, 1988; Rodman,

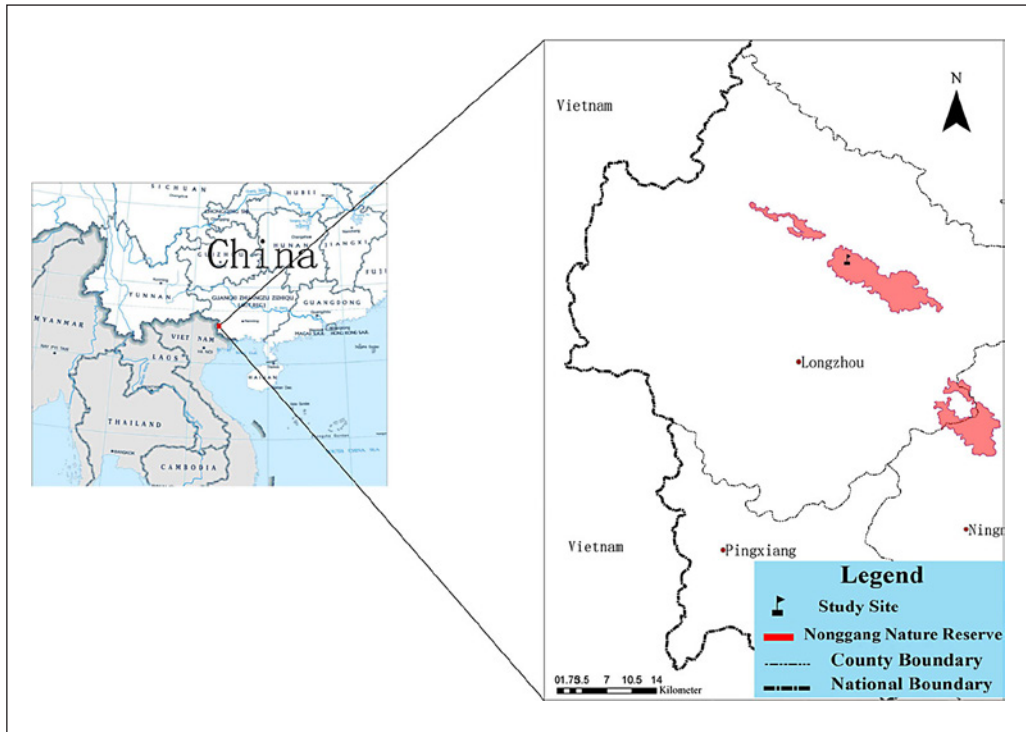
1991; Chatani, 2003; Huang et al., 2015]. Finally, larger primates use larger substrates more frequently than smaller species, apparently owing to the necessary requirement of sustaining their greater weight [Gebo and Chapman, 1995b; McGraw, 2000; Bitty and McGraw, 2007; Huang et al., 2015].

Ecological factors, such as habitat structure, resource distribution and availability, predation risk and temperature and rainfall, also influence positional behaviour [Gebo and Chapman, 1995a; Youlatos, 2002; Huang and Li, 2005; Lawler et al., 2006; Prates and Bicca-Marques, 2008; Manduell et al., 2012; Huang et al., 2015]. Variations in positional behaviour have been linked to differences in habitat structure [Garber and Pruetz, 1995; Gebo and Chapman, 1995a; Zhou et al., 2013; Huang et al., 2015]. As documented by Gebo and Chapman [1995a], red colobus monkeys (*Colobus badius*) differ significantly in positional behaviours in different types of forests. These monkeys used quadrupedalism more commonly in secondary forest than in primary forest, whereas they leaped less frequently in secondary forest, a difference linked to higher tree continuity in primary than in secondary forest. Positional behaviours often differ among closely related species inhabiting a shared environment. For instance, Assamese macaques (*Macaca assamensis*) less frequently leap and walk than sympatric rhesus macaques (*M. mulatta*) because Assamese macaques reside on cliffs and hilltops where tall trees are scarce, while rhesus macaques predominately occupy middle-lower regions where tall trees are abundant [Huang et al., 2015].

Seasonality of food resources also determines seasonal variation in positional behaviour [Dagosto, 1995; Gebo and Chapman, 1995a; Youlatos, 1998]. Due to differences in food distribution patterns, primates adopt specific postures to reach food, based on the balance between feeding benefit and risk of falling from trees. For example, when they heavily depend on leaves during the dry season, red howler monkeys (*Alouatta seniculus*) in French Guianan primary rain forest travelled more frequently by quadrupedal walking on large supports, likely because, then, feeding on leaves with quadrupedal walking is probably energy-inexpensive and relatively stable [Youlatos, 1998]. In the wet season, howlers feed more frequently by sitting because the abundant fruits they eat then require more time for special manipulation [Youlatos, 1998].

François' langurs (*Trachypithecus francoisi*) are exclusively distributed in limestone forests in Guangxi, Guizhou and Chongqing in China, northern Vietnam and Laos [Wang et al., 1999]. Previous studies on positional behaviour in François' langurs indicated that leaping is their most common form of locomotion [Xiong et al., 2009; Zhou et al., 2013]. These langurs are able to adopt various positional behaviours to adapt to different hill zones [Zhou et al., 2013]. However, data on seasonal variations in positional behaviour and correlations with ecological factors have not been available. In this study, we first describe positional behaviours and their seasonal variations and then compare our results with reports from other karst primates to provide insights into these langurs' adaptation to limestone forests. Finally, we discuss the influence of ecological factors on langur positional behaviour by testing the following predictions:

(1) François' langurs have relatively long hind limbs (low IMI) and inhabit limestone forests characterised by vertically distributed forests and cliffs [Su et al., 1988; Pan et al., 1989; Fleagle, 2013]; thus, langurs are expected to use leaping as their predominant locomotor mode;



Color version available online

Fig. 1. Map of Nonggang Nature Reserve, Guangxi, south-west China, showing the study site and surrounding region.

(2) young tree leaves tend to be located near the periphery of tree crowns [Youlatos, 2002]. François' langurs consume more young and fewer mature leaves during the rainy months than during dry months [Huang et al., 2010]; for covering a wider (vertical) foraging area, langurs are expected to use bipedal standing more frequently in the rainy season than in the dry season.

Materials and Methods

Study Sites and Subjects

This study was conducted from September 2005 to August 2006 at the Nonggang Nature Reserve ($106^{\circ}42'28''$ – $107^{\circ}4'54''$ E, $22^{\circ}13'56''$ – $22^{\circ}33'9''$ N) in Guangxi, south-west China (Fig. 1). The reserve is covered by limestone hills with an elevation ranging from 300 to 700 m [Guangxi Forestry Department, 1993]. Vegetation is characterised by limestone seasonal rain forest, rich in trees and vines, distributed according to soil and water patterns [Su et al., 1988]. Lower elevations (including the valley floor and hillsides) feature wet soil and are covered by large trees supporting many vines and epiphytes, while higher levels (including cliffs and hilltops) consist of bare rock supporting drought-resistant plants [Su et al., 1988].

During the study period, we recorded 1,372.8 mm of rainfall. We divided the study period into a rainy season from April to September (>80 mm monthly rainfall) and a dry season from

Table 1. Definition of positional behaviour, forest strata height and substrate size in this study [in accordance with Hunt et al., 1996; Zhou et al., 2013; Huang et al., 2015]

Terms	Definitions
Maintenance activities	
Resting	The unaltered position of the langur group
Feeding	The foraging, picking, ingestion and chewing of food by the majority of individuals in the group, including the short-distance movements during the foraging period
Social grooming	Mutual grooming behaviour among individuals
Locomotor modes	
Quadrupedal walking	All four limbs contact the support in a particular sequence, and the trunk is pronograde or roughly parallel
Leaping	A gap-crossing movement in which the hind limbs are principally used as propulsors
Vertical climbing	Moving up or down a vertical or steeply inclined substrate
Quadrupedal running	Fast locomotion using asymmetrical or irregular gaits and with a period of free flight (i.e. all four limbs off the ground)
Postural modes	
Sitting	An orthograde posture in which the ischia bear a substantial portion of the body weight
Lying	Posture in which the ventral torso bears the body weight
Quadrupedal standing	Four-limbed standing on horizontal or subhorizontal supports, the elbow and knee are relatively extended, and the trunk is nearly horizontal
Bipedal standing	Standing on the hind limbs with no significant support from any other body part
Suspending	A part of the body hangs on the support, including hind limb suspension
Back-lying	Posture in which the back or side of the torso bears the body weight
Forest strata height	
Ground	On the bare rock
Low	Height of strata ≤ 5 m
Lower-middle	Height of >5 m, ≤ 10 m
Upper-middle	Height of >10 m, ≤ 15 m
Upper	Height of >15 m
Substrate size	
Small	Substrate diameter of ≤ 2 cm
Medium	Substrate diameter of >2 cm, ≤ 10 cm
Large	Substrate diameter of >10 cm

October to March (<80 mm monthly rainfall) [Huang et al., 2007]. We selected a group of François' langurs that ranged nearest our temporary camp. The study group included 1 adult male, 5 adult females and 3 infants/juveniles.

Data Collection and Analysis

We observed the François' langur group with binoculars and collected data via the instantaneous scan sampling method, using 5-min scans at 10-min intervals [Altmann, 1974]. We scanned these langurs from left to right or in a clockwise sweep to avoid potential bias toward given individuals or age-sex categories. We recorded the behaviour of as many as possible during scanning, with no individual sampled twice. During each scan, we identified the predominant behaviour of the sampled individual after observing it for 5 s. We observed the group for a total

of 149 days (7–22 days/month) from September 2005 to August 2006 and collected data on maintenance activity, positional behaviour, forest strata heights and substrate size. Full-day observations began at 06:00 h and ended when the langurs entered their sleeping sites. We also collected behavioural data during partial-day observations, which began whenever the group was first encountered and ended either when they became unobservable for >30 min or entered a sleeping site. During the study period, we collected 8,168 records from 3,051 scans.

During scanning, maintenance activity (resting, feeding and social grooming) and positional behaviour were recorded for each individual. Due to long distances and inaccessibility of most hill zones for observers, langurs were not individually identified. Following a pilot study, we divided positional behaviours into four locomotor modes (quadrupedal walking, leaping, vertical climbing and quadrupedal running) and six postural modes (sitting, lying, quadrupedal standing, bipedal standing, suspending and back-lying). Locomotor and postural modes were defined as in Hunt et al. [1996]. During scanning, we also catalogued forest strata used by langurs into five classes (ground, low, lower-middle, upper-middle and upper) based on definitions of forest strata for sympatric primates in Huang et al. [2015]. The size of the substrate supporting the individual was based on visually estimated diameter and divided into three classes (small, medium and large), also in accordance with Huang et al. [2015]. Definitions of activities, locomotor and postural modes, forest strata height and substrate size are shown in Table 1.

Behavioural records were collected from adult males and females only and the data were pooled for statistical analyses. We expressed monthly percentages for locomotor mode, posture, stratum and substrate based on monthly total samples for each specific behaviour. Each scan was treated as an independent sample. Annual and seasonal percentages were obtained by averaging relative monthly values. Following Huang et al. [2017] and Kurihara and Hanya [2015], we built generalised linear mixed models to explain locomotion, posture, stratum and substrate use by the langurs and then examined seasonal variations. For this purpose, we set seasons as fixed factors and sample sizes as random factors in the models. Furthermore, we examined differences between models with and without the factor “season,” using ANOVA to detect influences of “season” on each dependent variable. “Season” was regarded as a factor that significantly shaped the model’s goodness of fit when the p value was <0.05. To improve linearity, all variables were arcsine square root transformed, except for sample sizes. We ran all tests in R 3.3.2, with statistical significance set at 0.05.

Results

Locomotion, Stratum and Substrate Use

Leaping was the most frequent locomotor mode for François’ langurs ($38.4 \pm 6.9\%$ of annual records), followed by quadrupedal walking ($31.2 \pm 15.3\%$), vertical climbing ($25.1 \pm 11.2\%$) and quadrupedal running ($5.3 \pm 2.5\%$) ($\chi^2 = 42.664$, $df = 3$, $p < 0.001$). There was no significant difference in locomotor modes between rainy and dry seasons (quadrupedal walking: $\chi^2 = 0.618$, $df = 1$, $p = 0.432$; leaping: $\chi^2 = 3.093$, $df = 1$, $p = 0.079$; vertical climbing: $\chi^2 = 0.005$, $df = 1$, $p = 0.943$; quadrupedal running: $\chi^2 = 0.141$, $df = 1$, $p = 0.708$) (Fig. 2).

Langurs most frequently used the ground as the stratum while moving, accounting for $33.4 \pm 8.6\%$ of records, followed by lower-middle ($26.4 \pm 9.0\%$), upper-middle ($25.0 \pm 8.6\%$), upper ($8.7 \pm 8.1\%$) and low ($6.7 \pm 4.4\%$) strata, respectively ($\chi^2 = 60.804$, $df = 4$, $p < 0.001$). We did not detect marked seasonal variation in use of forest strata during movement (ground: $\chi^2 = 1.639$, $df = 1$, $p = 0.200$; low: $\chi^2 = 0.501$, $df = 1$, $p = 0.479$; lower-middle: $\chi^2 = 0.034$, $df = 1$, $p = 0.854$; upper-middle: $\chi^2 = 1.206$, $df = 1$, $p = 0.272$; upper: $\chi^2 = 0.037$, $df = 1$, $p = 0.847$) (Fig. 2).

When langurs travelled through trees, most locomotion occurred on small- ($48.7 \pm 10.2\%$) and medium-sized ($47.6 \pm 9.5\%$) substrates, with little occurring on

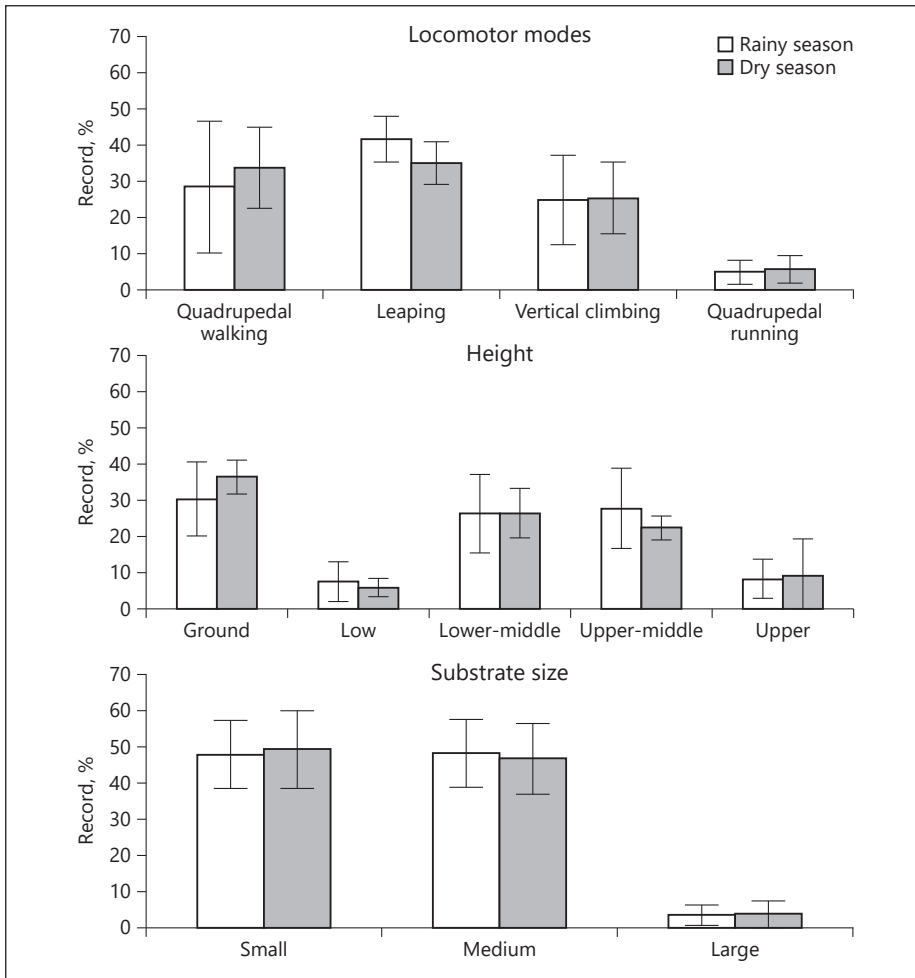


Fig. 2. Frequencies of each locomotor mode, forest stratum and substrate size used during moving by François' langur at Nonggang Nature Reserve from September 2005 to August 2006.

large substrates ($3.7 \pm 3.2\%$) ($\chi^2 = 72.243$, $df = 2$, $p < 0.001$). Substrate use showed no significant seasonal variation during locomotion (small: $\chi^2 = 0.002$, $df = 1$, $p = 0.962$; medium: $\chi^2 = 0.017$, $df = 1$, $p = 0.896$; large: $\chi^2 = 0.014$, $df = 1$, $p = 0.907$) (Fig. 2).

Posture, Stratum and Substrate Use

Overall, sitting was the most common posture for langurs ($92.1 \pm 2.1\%$ of records), followed by bipedal standing ($3.7 \pm 2.4\%$), lying ($3.5 \pm 1.6\%$), quadrupedal standing ($0.6 \pm 0.6\%$), suspending ($0.2 \pm 0.2\%$) and back-lying ($<0.1 \pm 0.1\%$) ($\chi^2 = 450.98$, $df = 5$, $p < 0.001$). Seasonal variations occurred in bipedal standing (Fig. 3). Bipedal standing was more frequently used in the dry season than in the rainy season ($\chi^2 = 4.348$, $df = 1$, $p = 0.037$). There were no seasonal differences in sitting ($\chi^2 = 0.459$, $df = 1$, $p = 0.498$),

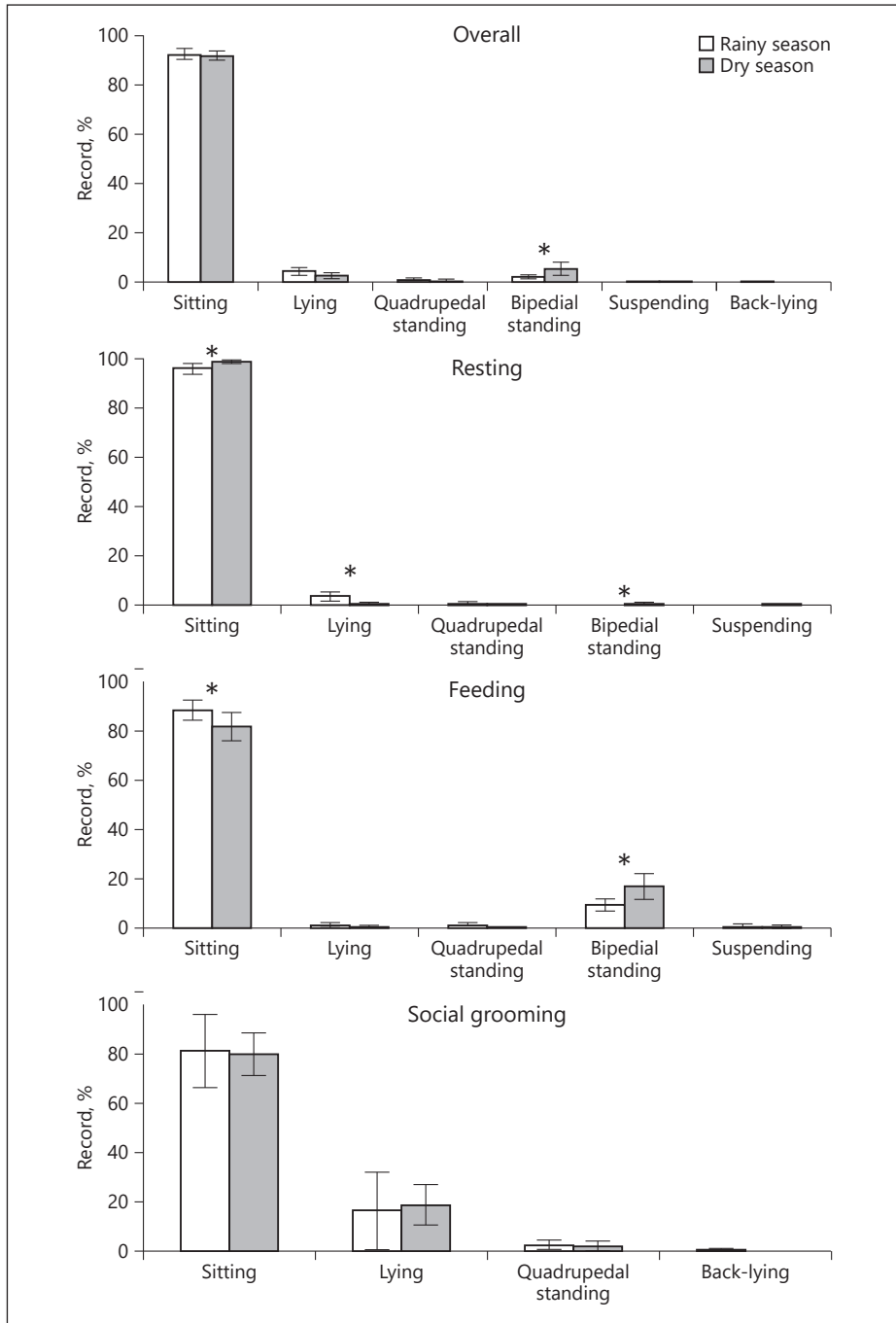


Fig. 3. Frequencies of posture during overall activity, resting, feeding and social grooming by François' langur at Nonggang Nature Reserve from September 2005 to August 2006. Asterisks represent statistically significant differences between the dry and rainy seasons.

lying ($\chi^2 = 2.915$, $df = 1$, $p = 0.088$), quadrupedal standing ($\chi^2 = 2.430$, $df = 1$, $p = 0.119$), suspending ($\chi^2 = 0.242$, $df = 1$, $p = 0.623$) and back-lying ($\chi^2 = 0.000$, $df = 1$, $p = 1$).

Langurs used seasonal variations in postures during various activities (Fig. 3). During resting, langurs used sitting and bipedal standing more frequently in the dry than in the rainy season (sitting: $\chi^2 = 5.152$, $df = 1$, $p = 0.023$; bipedal standing: $\chi^2 = 5.223$, $df = 1$, $p = 0.022$), whereas they adopted a lying posture more frequently in the rainy than in the dry season ($\chi^2 = 7.706$, $df = 1$, $p = 0.006$). Seasonal variations in other resting postures were not detected (quadrupedal standing: $\chi^2 = 1.352$, $df = 1$, $p = 0.245$; suspending: $\chi^2 = 1.144$, $df = 1$, $p = 0.285$). During feeding, sitting was adopted more frequently in the rainy than in the dry season ($\chi^2 = 4.255$, $df = 1$, $p = 0.039$), whereas bipedal standing was used more frequently in the dry than in the rainy season ($\chi^2 = 5.857$, $df = 1$, $p = 0.016$). Other feeding postures showed no significant seasonal differences (lying: $\chi^2 = 0.878$, $df = 1$, $p = 0.349$; quadrupedal standing: $\chi^2 = 2.277$, $df = 1$, $p = 0.131$; suspending: $\chi^2 = 0.000$, $df = 1$, $p = 0.985$). Moreover, frequency of social grooming postures did not differ between the two seasons (sitting: $\chi^2 = 0.047$, $df = 1$, $p = 0.829$; lying: $\chi^2 = 0.111$, $df = 1$, $p = 0.739$; quadrupedal standing: $\chi^2 = 0.217$, $df = 1$, $p = 0.642$; back-lying: $\chi^2 = 0.000$, $df = 1$, $p = 1$).

With respect to forest stratum use while stationary, langurs spent the most time on the ground ($28.1 \pm 12.3\%$), followed by lower-middle ($21.0 \pm 5.2\%$), low ($20.0 \pm 12.0\%$), upper-middle ($19.2 \pm 6.5\%$) and upper strata ($11.7 \pm 10.1\%$) ($\chi^2 = 15.415$, $df = 4$, $p = 0.004$). Frequencies of forest stratum use between the two seasons differed significantly (Fig. 4). Langurs spent much more time on the ground in the dry than in the rainy season ($\chi^2 = 6.038$, $df = 1$, $p = 0.014$). No seasonal variations were observed in use of other forest strata (low: $\chi^2 = 3.825$, $df = 1$, $p = 0.051$; lower-middle: $\chi^2 = 0.070$, $df = 1$, $p = 0.791$; upper-middle: $\chi^2 = 0.091$, $df = 1$, $p = 0.764$; upper: $\chi^2 = 0.011$, $df = 1$, $p = 0.918$).

Seasonal variations in the forest stratum use pattern differed during various activities (Fig. 4). Resting showed marked seasonal variation. Langurs devoted significantly more time to the ground in the dry than in the rainy season ($\chi^2 = 3.875$, $df = 1$, $p = 0.049$). However, other forest stratum use while resting showed no obvious seasonal variation (low: $\chi^2 = 3.621$, $df = 1$, $p = 0.057$; lower-middle: $\chi^2 = 0.238$, $df = 1$, $p = 0.626$; upper-middle: $\chi^2 = 0.237$, $df = 1$, $p = 0.627$; upper: $\chi^2 = 0.028$, $df = 1$, $p = 0.868$). During feeding, langurs spent more time on the ground in the dry than in the rainy season ($\chi^2 = 7.742$, $df = 1$, $p = 0.005$). However, use of other strata while feeding showed no significant seasonal variation (low: $\chi^2 = 1.504$, $df = 1$, $p = 0.220$; lower-middle: $\chi^2 = 0.319$, $df = 1$, $p = 0.572$; upper-middle: $\chi^2 = 0.004$, $df = 1$, $p = 0.948$; upper: $\chi^2 = 0.102$, $df = 1$, $p = 0.749$). The frequency of social grooming while on the ground in the dry season was significantly higher than that in the rainy season ($\chi^2 = 19.882$, $df = 1$, $p < 0.001$), whereas social grooming on the low and lower-middle stratum in the rainy season occurred more frequently than in the dry season (low: $\chi^2 = 4.964$, $df = 1$, $p = 0.026$; lower-middle: $\chi^2 = 4.986$, $df = 1$, $p = 0.026$). Grooming frequency while on other strata did not vary markedly (upper-middle: $\chi^2 = 2.483$, $df = 1$, $p = 0.115$; upper: $\chi^2 = 1.240$, $df = 1$, $p = 0.265$).

While active in trees, langurs spent more than 97% of their time on small- and medium-sized substrates (39.4 ± 13.4 and $57.9 \pm 12.7\%$ of annual records, respectively) ($\chi^2 = 61.407$, $df = 2$, $p < 0.001$). Use of large substrates while stationary accounted for $2.7 \pm 2.9\%$ of records. Overall, there was no significant seasonal variation in substrate size use (small: $\chi^2 = 1.240$, $df = 1$, $p = 0.776$; medium: $\chi^2 = 0.906$, $df = 1$, $p = 0.341$; large: $\chi^2 = 0.005$, $df = 1$, $p = 0.941$) nor during resting (small: $\chi^2 = 0.699$,

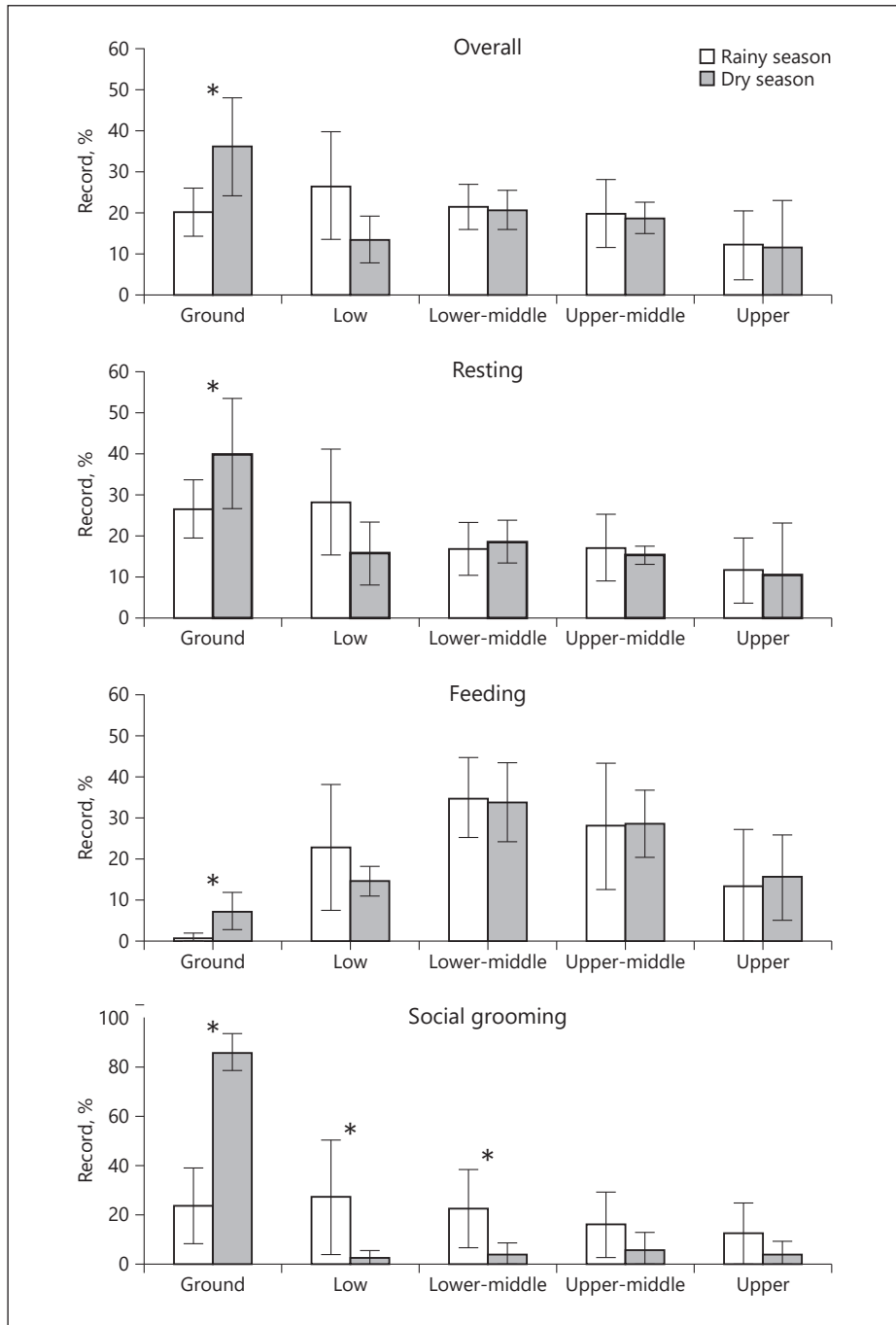


Fig. 4. Frequencies of forest strata used during overall activity, resting, feeding and social grooming by François' langur at Nonggang Nature Reserve from September 2005 to August 2006. Asterisks represent statistically significant differences between the dry and rainy seasons.

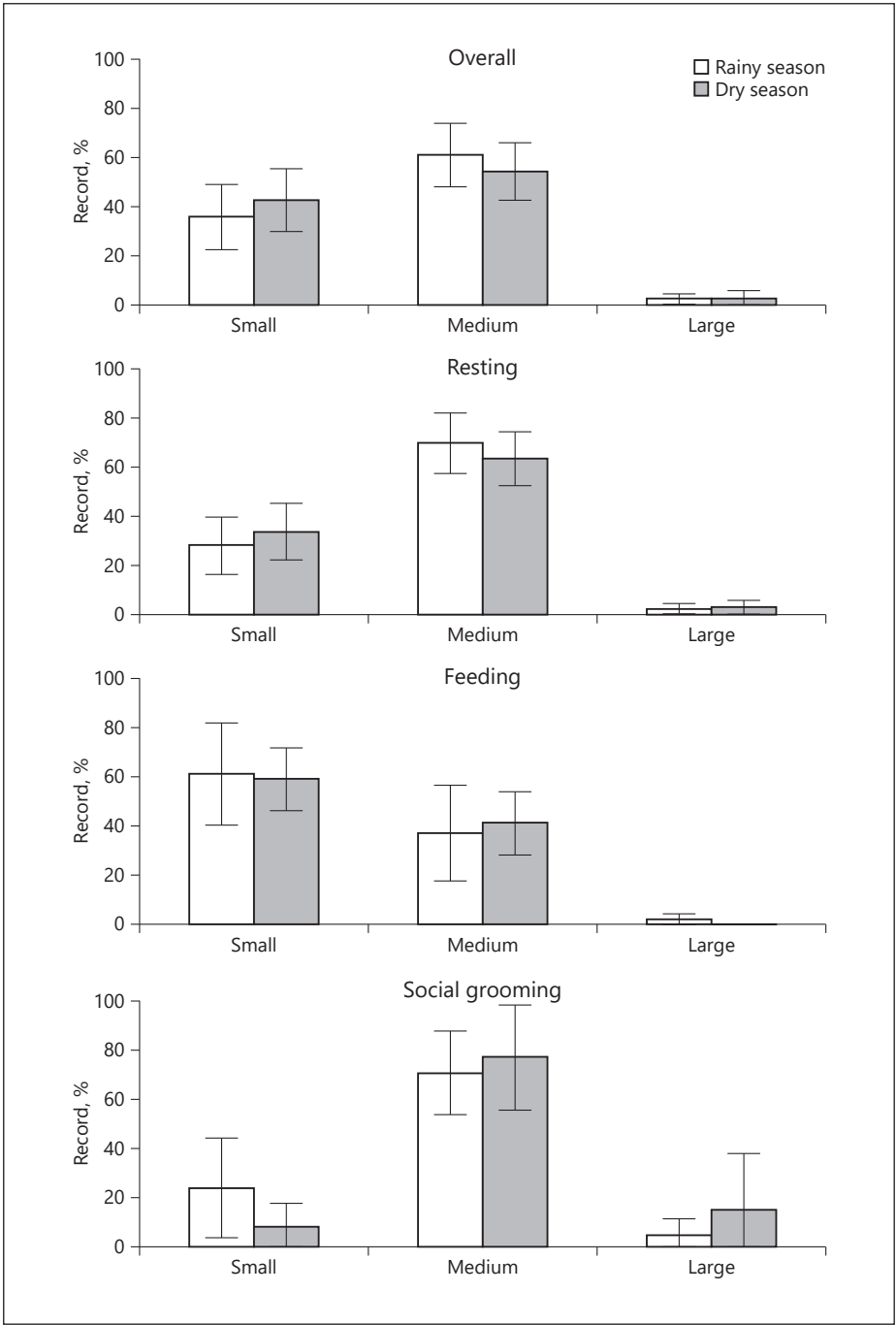


Fig. 5. Frequencies of substrate size used during overall activity, resting, feeding and social grooming by François' langur at Nonggang Nature Reserve from September 2005 to August 2006.

df = 1, $p = 0.403$; medium: $\chi^2 = 0.868$, df = 1, $p = 0.352$; large: $\chi^2 = 0.174$, df = 1, $p = 0.677$), feeding (small: $\chi^2 = 0.055$, df = 1, $p = 0.814$; medium: $\chi^2 = 0.177$, df = 1, $p = 0.674$; large: $\chi^2 = 3.147$, df = 1, $p = 0.076$) or social grooming (small: $\chi^2 = 3.225$, df = 1, $p = 0.725$; medium: $\chi^2 = 0.182$, df = 1, $p = 0.670$; large: $\chi^2 = 0.676$, df = 1, $p = 0.411$) (Fig. 5).

Discussion/Conclusion

Leaping, quadrupedal walking and vertical climbing were predominant locomotor modes for François' langurs in the limestone forest. Thus, prediction 1 that langurs would use leaping as the predominant locomotor mode was supported. The langurs spent less time on the ground than in trees, where the majority of locomotion occurred on small- and medium-sized substrates. This pattern was similar to previous reports [Xiong et al., 2009; Zhou et al., 2013]. François' langurs used leaping as the most frequent locomotor mode, and this could be attributed to the species' morphological and anatomical characteristics (Table 2). In general, an animal's leaping ability depends on body size and the propulsive force of its hind limbs [Fleagle, 2013]. François' langurs have a small body size and low IMI [Pan et al., 1989], possibly contributing to their leaping skills [Fleagle, 2013]. Moreover, they have a long tail [Pan et al., 1989] that might enhance their leaping ability through balance during long-distance jumping [Chatani, 2003; Fleagle, 2013]. Similar patterns have been observed in locomotor modes of sympatric primates [Huang and Li, 2005; Xiong et al., 2009; Zhou et al., 2013].

The high frequency of leaping and vertical climbing could also be correlated to the limestone forests' structure. Trees are vertically distributed in the limestone forest but are not contiguous in most areas, obliging primates to cross gaps while moving [Fan et al., 2011]. Thus, leaping could be an effective locomotion for langurs, especially when travelling downward on hillsides. Moreover, limestone forests are characterised by large areas of vertical cliffs covered by sparse vegetation [Su et al., 1988]. The langurs in this study very frequently used the bottom of hillsides as feeding sites and the cliffs as resting sites [Zhou et al., 2013]. Climbing is a common locomotor mode when travelling upward on cliffs, as documented for other karst-dwelling primates [Huang and Li, 2005; Xiong et al., 2009; Workman and Schmitt, 2012; Zhou et al., 2013] (Table 2). Furthermore, langurs are known to use cliff ledges and caves as sleeping sites [Zhou et al., 2009], and climbing along cliffs is the only way to reach them. Climbing might also minimise path length and thus save energy [Huang et al., 2015]. Like François' langurs, sympatric Assamese macaques also spend much of their time on cliffs and choose ledges and caves as sleeping sites [Zhou et al., 2014], and climbing is their most common locomotor mode [Huang et al., 2015].

However, common locomotor modes for karst-living langurs vary dramatically (Table 2). For instance, Delacour's langurs (*Trachypithecus delacouri*), a karst-endemic primate in Vietnam, move predominantly by quadrupedal walking [Workman and Schmitt, 2012]. François' langurs in this study leaped more frequently than Delacour's langurs (38.4 vs 7.5%). This difference could be accounted for by the great difference between forest structures in Vietnam and south-western Guangxi, China. Vegetation is sparse and stunted in the forest where Delacour's langurs live, and trees capable of supporting the langurs' weight are less numerous, while rocks are more common in that karst environment [Workman and Schmitt, 2012]. In fact, more than 80% of the Dela-

Table 2. Comparison of locomotor modes of several colobines

	Study site ^a	Method ^b	IMI	Body mass		Locomotion, %				Strata, %		Substrate, %			Reference
				male	female	quadrupedalism	leaping	climbing	others	ground	trees	small	medium	large	
<i>Trachypithecus francoisi</i>	1	S	83 ^c	8.0 ^d	7.8 ^d	36.5	38.4	25.1	0	33.4	66.7	48.7	47.6	3.7	This study
	1	S	–	–	–	31.1	43.3	25.5	0	46.7	53.3	–	71.7	–	Zhou et al., 2013
	1	S	–	7.1	6.7	34.1	46.3	13.4	6.2	64.8 ^e	35.2	–	–	–	Xiong et al., 2009
<i>T. leucocephalus</i>	1	S	–	8.8	7.8	30.6	47.3	19.7	2.4	50.3 ^f	49.7	–	–	–	Xiong et al., 2009
	1	F	76	8.8	7.8	50.3	12.6	37.1	0	70.9	–	–	–	–	Huang and Li, 2005
<i>T. delacouri</i>	2	F	77 ^g	8.6	7.8	63.8 ^h	7.5 ^h	26.3 ^h	2.5 ^h	79 ⁱ	21 ⁱ	–	–	–	Workman and Schmitt, 2012
<i>T. obscurus</i>	3	F	83 ^c	7.9 ^c	6.4 ^c	50.6	40.2	9.2	0	Arboreal	–	–	–	–	Fleagle, 1980
<i>Presbytis melalophos</i>	3	F	78 ^c	6.6 ^c	6.1 ^c	20.7	67.5	8.4	3.4	Arboreal	–	–	–	–	Fleagle, 1980
<i>P. potenziani</i>	4	S	–	–	–	71.6 ^j	23.2 ^j	2.6 ^j	2.6 ^j	Arboreal	–	–	–	–	Fuentes, 1996
<i>Colobus badius</i>	5	F	87	8.3	8.2	37	25	32	6	Arboreal	18	68	14	–	Gebo and Chapman, 1995b
<i>C. guereza</i>	5	F	79	10.1	8.0	41	38	15	6	Arboreal	16	62	22	–	Gebo and Chapman, 1995b

^a Study site: 1 – Southwest China, limestone forest; 2 – Northern Vietnam, limestone forest; 3 – Peninsular Malaysia, non-limestone forest; 4 – Pagai Islands, Indonesia, non-limestone forest; 5 – Western Uganda, non-limestone forest. ^b Method: S – Scanning sampling; F – Focal animal sampling. ^c Cited from Pan et al., 1989. ^d Cited from Fleagle, 2013. ^e Including proportion for both substrates (34.4%). ^f Including proportion for both substrates (22.3%). ^g Cited from Workman and Covert, 2005. ^h Mean value for all age/sex classes. ⁱ Summing of locomotion and posture. ^j Obtained from the observation records. –, Data were not available.

cour's langurs' activity occurred on bare rock [Workman and Schmitt, 2012], whereas only one-third of François' langurs' activity was devoted to rocky ground. According to studies on karst-endemic langurs living in well-protected forests, François' langurs prefer the upper-middle stratum in trees for their daily activity rather than the ground [this study; Xiong et al., 2009]. Abundance of trees and forest structure likely explain the lower proportion of leaping and the higher proportions of quadrupedalism in our records. We admit that differences in data collection among studies might introduce error but comparisons are still worthwhile, especially as large sample sizes probably describe most of the behaviour of a given species [Youlatos, 2002]. This study describes positional behaviour characteristics of François' langurs on the basis of a single-family group, likely leading to tempering of the conclusion by the sample's small size. However, the current paper undoubtedly provides a general pattern of the positional behaviour of François' langurs.

As in other primates [Cant, 1988; Gebo, 1992; McGraw, 2000; Chatani, 2003; Prates and Bicca-Marques, 2008; Grueter et al., 2013; Huang et al., 2015; Zhu et al., 2015; Mekonnen et al., 2018], and particularly in colobines, sitting was the most frequently used stationary posture for François' langurs in the limestone forest in this study (Table 3). However, sitting frequency varied seasonally. During resting, langurs sat more frequently, but lay down less frequently in the dry season. This could be cor-

Table 3. Comparison of posture of several colobines

	Study site ^a	Method ^b	Posture, %						Strata, %		Substrate (%)			References
			sitting	lying	reclining	standing	others	ground	trees	small	medium	large		
<i>Trachypithecus francoisi</i>	1	S	92.1	3.5	<0.1	4.3	0.2	28.1	71.9	39.4	57.9	2.7	this study	
<i>Trachypithecus delacouri</i>	2	F	95	2	–	3	<1	79 ^c	21 ^c	–	–	–	Workman and Schmitt, 2012	
<i>Trachypithecus obscurus</i>	3	F	76 ^d	22 ^d	–	–	2 ^d	–	arboreal	–	–	–	Fleagle, 1980	
<i>Presbytis melalophos</i>	3	F	94 ^d	5 ^d	–	–	1 ^d	–	arboreal	–	–	–	Fleagle, 1980	
<i>Colobus angolensis palliatus</i>	4	T	91 ^c	5 ^c	2.7 ^c	0.8 ^c	0.5 ^c	–	–	8.7 ^d	58.8 ^d	23.4 ^d	Dunham, 2015	
<i>Colobus badius</i>	5	F	93	–	5	2	0	0	100	20	67	13	Gebo and Chapman, 1995b	
<i>Colobus guereza</i>	5	F	78	–	21	1	0	0	100	16	59	25	Gebo and Chapman, 1995b	

^a Study site: 1 – Southwest China, limestone forest; 2 – Northern Vietnam, limestone forest; 3 – Peninsular Malaysia, non-limestone forest; 4 – South coastal Kenya, non-limestone forest; 5 – Western Uganda, non-limestone forest. ^b Method: S, scan sampling; F, focal animal sampling; T, instantaneous time point sampling. ^c Summing of locomotion and posture. ^d Data from sitting posture. ^e Mean value for all age/sex classes; –, data were not available.

related to behavioural thermoregulation and heat stress avoidance. Studies have shown that body posture adjustment might assist body temperature regulation [Stelzner and Hausfater, 1986; Bicca-Marques and Calegario-Marques, 1998]. Thus, behavioural thermoregulation might play an important role in an animal's adaptation to the environment [Campos and Fedigan, 2009]. For example, white-faced capuchins (*Cebus capucinus*) usually dissipate heat by extending their tongues and stretching (lying or back-lying) on branches during high temperatures [Campos and Fedigan, 2009]. At our study site, temperatures in the dry season are lower than in the rainy season [Huang et al., 2007]. Moreover, the limestone forests are composed of carbonatite matrix, causing the bare rock surface to have lower temperatures during the dry season and higher temperatures during the rainy season than those of the tree canopy [Larson et al., 2000; Huang, 2002]. François' langurs are able to relax completely and stretch themselves to extend their contact with substrate surfaces, thus contributing to heat radiation in high temperature conditions during rainy seasons, as documented by Campos and Fedigan [2009]. During dry months, sitting together in huddles to conserve energy could be an effective adaptation for lowering temperatures. In fact, behavioural thermoregulation occurs in sympatric primates, including white-headed langurs (*Trachypithecus leucocephalus*) and Assamese macaques, which sun-bathe in winter and rest in the shade or in caves in summer [Huang, 2002; Zhou et al., 2014]. A detailed study on thermoregulation in François' langurs is needed.

This study revealed significant seasonal variation in the frequency of sitting and bipedal standing. Langurs more commonly used bipedal standing to feed but used sitting less frequently in the dry season than in the rainy season, completely contradicting prediction 2. This pattern could be due to differences in dietary composition and distribution of food resources. François' langurs in this study were almost exclusively folivores, preferring to eat young leaves and fruits while using mature leaves as fallback food (see dietary composition in Huang et al. [2010]). Compared to leaves, fruits tend

to occur on smaller twigs located near the periphery of tree crowns [Fleagle, 1984; McGraw, 1998; Youlatos, 2002]. Primates can cover a wider foraging area by bipedal standing while they feed on fruits [Huang et al., 2015]. In the dry season, the study group used the seed of *Pithecellobium clypearia* as fallback food, accounting for 8.6% of their diet [Huang et al., 2010]. During the rainy season, François' langurs consumed more leaves, which were more evenly and abundantly distributed in tree crowns, probably allowing the langurs to harvest them while sitting. The seeds of *P. clypearia* were limited and gradually declined in availability according to harvesting duration, causing the langurs to use bipedal standing to reach seeds borne on less accessible twigs. A similar posture is also used by sympatric macaques [Huang et al., 2015].

François' langurs used the ground as a substrate more frequently in the dry season, likely due to seasonal variation in diet. During dry months, the study group consumed more mature leaves [Huang et al., 2010]. In some cases, they could reach food without difficulty by sitting on the ground because of the vegetation's vertical distribution. In particular, *Ficus nervosa*, a species which provided most of the mature leaves [Huang et al., 2010], was commonly used when sitting on rock. Similarly, variations in use of forest strata were found during the study period. The langurs used the ground less frequently but were more focused on low and lower-middle strata during the rainy season when social grooming occurred. This could be related to behavioural thermoregulation. To avoid high temperatures and sunshine at noon during summer, François' langurs usually rested in the tree canopy, whereas in winter, to conserve energy, they often huddled together on the rock to bask and groom each other [Huang et al., 2007; Zhou et al., 2007]. In hot summer sunshine, the temperature is lower in tree crowns than on bare rock [Huang, 2002]. Social grooming mostly occurred for long periods around noon and could account for increased ground use in winter and decreased use of low and lower-middle strata.

In summary, leaping was the dominant locomotor mode for these François' langurs, and the ground was the stratum most frequently used during movement. Locomotor mode, forest stratum and substrate use during movement did not vary seasonally, but posture varied significantly by season. François' langurs' positional behaviours are likely linked to morphological and anatomical characteristics including body size and length of limbs, as well as by the limestone forest's structure. François' langurs inhabiting limestone forests display locomotor modes distinct from those of colobines living in non-limestone forests, despite similarities in body mass and IMI among forest environments. Seasonal variation in positional behaviour might be accounted for by temporal difference in the spatial distribution of preferred/fallback foods and behavioural thermoregulation strategy. These results highlight that primate locomotor behaviour, while constrained to some degree by morphology, is also flexible to local ecological conditions and also to seasonal changes within a particular locality.

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Statement of Ethics

The authors have no ethical conflicts to disclose.

Disclosure Statement

The authors have no conflicts of interest to declare.

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Author Contributions

H.C.M. designed the research. H.Z.H. and W.H. collected data. C.T. wrote the manuscript. H.Z.H revised the manuscript.

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