Living in forests: strata use by Indo-Chinese gray langurs (*Trachypithecus crepusculus*) and the effect of forest cover on *Trachypithecus* terrestriality

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ABSTRACT

Studies on behavioral flexibility in response to habitat differences and degradation are crucial for developing conservation strategies for endangered species. *Trachypithecus* species inhabit various habitats and display different patterns of strata use; however, the effect of habitat structure on strata use remains poorly studied. Here, we investigated strata use patterns of Indo-Chinese gray langurs (*Trachypithecus crepusculus*) in a primary evergreen forest in Mt. Wuliang, southwest China, from June 2012 to January 2016. In addition, we compared *T. crepusculus* strata use and terrestriality with five other *Trachypithecus* species from previous studies. Unlike langurs living in karst forests, our study group was typically arboreal and spent only 2.9% of time on the ground. The group showed a preference for higher strata when resting and lower strata (<20 m) when moving. The langurs primarily used time on the ground for geophagy, but otherwise avoided the ground during feeding. These strata use patterns are similar to those of limestone langurs (*T. francoisi*) when using continuous forests. At the genus level (*n*=6 species), we found a negative relationship between habitat forest cover and terrestriality. This negative relationship was also true for the five limestone langur species, implying limestone langurs increase territoriality in response to decreased forest cover. Our results document behavioral flexibility in strata use of *Trachypithecus* langurs and highlight the importance of the protection of continuous forests to promote langur conservation.

Keywords: Behavioral flexibility; Habitat degradation; Strata use; *Trachypithecus*; Indo-Chinese gray langur

INTRODUCTION

Animals demonstrate behavioral flexibility in response to habitat differences and degradation, which can help them survive and maintain an effective population size in different habitats (Galán-Acedo et al., 2019; Gordon et al., 2018; Ware et al., 2017). Studies on behavioral responses to habitat differences and degradation are crucial for understanding animal tolerance to habitat change, and for developing

conservation strategies for endangered species. For arboreal non-human primates, variances in habitat structure and resource distribution can lead to different strata-use patterns (Campbell et al., 2005; Mekonnen et al., 2018; Riley, 2008).

Asian colobines are highly arboreal species, which usually exhibit limited ground use (Bennett & Davies, 1994; Fleagle, 1998). They have evolved certain adaptations for forest living, such as long phalanges, powerful hind limbs, and ischial callosities to facilitate life and movement within trees (Kirkpatrick, 2011; McGraw & Sciulli, 2011; Oates & Davies, 1994). In addition, their diets are comprised mainly of young leaves, fruits, and seeds, which are predominantly found in the peripheral regions of forest canopies (Bennett & Davies, 1994; Kirkpatrick, 2011; Roy & Nagarajan, 2018). They also limit their ground use due to their relatively small body size, which makes them vulnerable to terrestrial predators, e.g., leopards (*Panthera pard*us), marbled cats (*Pardofelis marmorata*), and tigers (*Panthera tigris*) (Borries et al., 2014; Kirkpatrick, 2011; Srivastava et al., 1996). However, colobine species living in predator-free or unforested habitats can be highly terrestrial, as seen in provisioned groups of Hanuman langurs (*Semnopithecus entellus*) (Hrdy, 1977; Newton, 1992) and snub-nosed monkeys (*Rhinopithecus bieti* and *R. roxellana*) in open habitats (Grueter et al., 2013; Zhang et al., 2006).

The Asian colobine genus *Trachypithecus* represents a diverse lineage containing some 20 species (Mittermeier et al., 2013; Rowe & Myers, 2016). *Trachypithecus* spp. demonstrate typical arboreal morphological and ecological features, and exhibit wide variation in their use of strata and degree of terrestriality (Aggimarangsee, 2004; Hendershott, 2017; Roy & Nagarajan, 2018; Workman & Schmitt, 2012; Xiong et al., 2009; Zhou et al., 2013). For example, although they are all found in limestone habitats, Delacour's langurs (*T. delacouri*) in Van Long, Vietnam, and Cat Ba langurs (*T. poliocephalus*) on Cat Ba Island, Vietnam, spend more than 50% of their time on the ground (Hendershott et al., 2018; Workman, 2010), whereas dusky langurs (*T. obscurus*) in Khao Lommuak, Thailand, spend only 6% of their time on the ground (Aggimarangsee, 2004). Habitat quality and structure may explain the huge discrepancy in strata use found among *Trachypithecus* species (Workman & Schmitt, 2012; Xiong et al., 2009; Zhou et al., 2013). A previous study on Francois' langurs (*T. francoisi*) provided an excellent example of how such species adjust strata use patterns in response to different habitat structure. Specifically, Zhou et al. (2013) identified three habitat types used by a group of Francois' langurs, including valley with continuous forests, hillside with discontinuous canopies, and cliff-hilltop with rocky surfaces and sparse vegetation, and found that the group showed high arboreality in continuous forests and increased terrestriality in rocky areas. However, detailed studies on strata use in *Trachypithecus* species mainly come from langurs inhabiting limestone regions. Although more than half of the species in this genus inhabit non-limestone forests, their strata use patterns have rarely been studied.

In this research, we investigated the patterns of strata use by Indo-Chinese gray langurs (*Trachypithecus crepusculus*) based on direct observations in a non-limestone habitat dominated by primary evergreen broadleaf forests at Mt. Wuliang, Yunnan, China (Fan et al., 2015; Jiang et al., 1994; Yu, 2004). Based on data from previous research, we also examined the impact of habitat differences on terrestriality in *Trachypithecus* species by exploring the relationship between the degree of terrestriality and habitat forest cover in six species for which comparative data were available. According to the morphological and ecological traits relevant to arboreality in *Trachypithecus* langurs, we made the following two predictions: Prediction (1): *T. crepusculus* langurs that inhabit a continuous forest will avoid using the ground or lower strata of the forest; and Prediction (2): habitat forest cover will be negatively correlated with terrestriality across the genus. In addition, we compared strata use patterns between our study group and a group of *T. francoisi* langurs inhabiting different habitat types (Zhou et al., 2013) (Prediction 3: the study group will show a similar pattern to *T. francoisi* in continuous forest).

MATERIALS AND METHODS

Study area

We conducted research at Dazhaizi on the western slopes of Mt. Wuliang, Jingdong County, Yunnan Province, China (Fan et al., 2015). Between 1 700 m to 2 700 m a.s.l., vegetation consists mainly of primary semi-humid evergreen broadleaf forests and mid-mountain humid evergreen broadleaf forests (Fan et al., 2009), which are typical habitat for langurs in Mt. Wuliang. The annual air temperature in the area is 16.1–18.3 °C and annual precipitation is >1 500 mm on average (Fan & Jiang, 2008; Fan et al., 2007; Guan, 2013). Air temperature changes seasonally, with the lowest monthly mean temperature (~10 °C) found in December and January and highest (~20 °C) found in June, July, and August. Rainfall also changes seasonally, with more than 80% of annual precipitation occurring in the wet season (May to October) and little rainfall occurring in the remaining dry season months (Fan & Jiang, 2008; Guan, 2013).

Three species of primate, including Indo-Chinese gray langurs, western black crested gibbons (*Nomascus concolor*), and stump-tailed macaques (*Macaca arctoides*), live in the study area (Fan et al., 2008). Large raptor predators, including hawk eagles (*Nisaetus cirrhatus*) and black eagles (*Ictinaetus malaiensis*), are regularly encountered. Terrestrial predators, such as yellow-throated martens (*Martes flavigula*) are common, whereas leopards (*Panthera pardus* and *Neofelis nebulosa*) are rarely reported (Fan et al., 2015; Jiang et al., 1994; Liu, 2017; Yu, 2004). Local people graze cows and goats and collect forest products such as mushrooms and herbal medicines (Fan, 2007). Illegal hunting and logging have not been recorded in the study area since 2003 because of the long-term study and conservation of the western black crested gibbons (Hu et al., 2018).

Study animals

Trachypithecus crepusculus is listed as a National Class I

Protected Species under Chinese Wildlife Conservation Law (Fan & Ma, 2018). There are no current population estimates of *T. crepusculus* in China; however, a recent survey indicated that approximately 2 000 Indo-Chinese gray langurs reside at Mt. Wuliang (Ma et al., 2015). Its conservation status has not yet been assessed by the IUCN because it was not considered a separate species until recently (He et al., 2012; Mittermeier et al., 2013; Rowe & Myers, 2016).

We studied a group of Indo-Chinese gray langurs inhabiting the evergreen broadleaf forests in the Dazhaizi area and collected data over 27 months during two periods (June 2012 to August 2013 and February 2015 to January 2016). As the only group of *T. crepusculus* in China, the study group has been monitored since 2008, including research on its activity budgets, dietary patterns, and population dynamics (Fan et al., 2015). The number of individuals in the study group increased from 70–80 in 2012 to more than 120 in 2014. In March 2014, the group split into two, with approximately 70–80 and 50 individuals in group A and group B, respectively (Fan et al., 2015). After group fission, we collected data on group A, which consisted of a similar number of individuals as the original group.

Data collection
We followed the study group for more than 5 d on average per month (mean: 5.6±1.9 days, range: 2–11 days per month; *n*=27 months). Once the group split into subgroups, we followed the largest subgroup. We estimated the group center and recorded it every half hour using a GPS device (Garmin eTrex20). We observed langurs at less than 20 m, except when they were on inaccessible cliffsides. We collected behavioral data using instantaneous scan sampling at 10 min intervals (Altmann, 1974). Each scan lasted for a maximum duration of 3 min, during which time we recorded the age-sex class, behavior, and stratum of each visible individual. We classified the target langurs into five age-sex classes: i.e., adult male, adult female, adult female with clinging infant, juvenile, and infant. We estimated the age classes by body size and identified sex of adult langurs by external genitalia. We classified langur behaviors into six categories: i.e., (1)

resting: inactive including self-grooming; (2) feeding: catching, swallowing, or chewing food; (3) traveling: moving including walking, climbing, running, and leaping; (4) geophagy: licking the surface of a rock for mineral matter; (5) social behaviors: grooming and playing; and (6) other, rare activities such as fighting, copulating, and drinking water. We estimated strata use as the height of langurs from the ground, divided into seven categories: i.e., ground; 1–5 m; 6–10 m; 11–15 m; 16–20 m; 21–25 m; and >25 m. Two research assistants estimated the heights of langurs during the study. During previous habitat surveys, they participated in the measurements of >4 500 trees using laser range finders and could accurately estimate tree heights to each category.

We collected terrestriality data of five *Trachypithecus* species from previous literature that provided the proportion of time spent by langurs on the ground (Table 1). In the paper reporting strata use of Francois' langurs in different habitats, the results were shown as a figure (Zhou et al., 2013). We used image digitizing software Engauge Digitizer (v4.1) to obtain values from this figure.

We graphed the maximum convex polygon of the home range of our study group using group location data collected every half hour (Fan et al., 2015). We obtained GPS coordinates or research site maps from studies on comparative *Trachypithecus* species. For each langur species, we digitized and georeferenced their range in ArcMap (v10.0), and randomly selected 100 points within the range. We then derived forest cover from 30 m×30 m grids where the selected points were located using Global Forest Change 2000–2017 (https://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.5.html) and calculated the average value of these points to represent forest cover of each site.

Data analysis
To test Prediction 1, we calculated the percentage of records across all behaviors in each stratum monthly and obtained a mean value from the monthly value to represent the strata use pattern of the group over the whole study period. We then determined differences in record proportions among strata. Specifically, we calculated the percentage of behavioral

Table 1 Habitat characteristics and terrestriality of six *Trachypithecus* species

Species	Forest cover (%)	Terrestriality (%)	Habitat	Location	Method for collecting behavior data	Sample size	References
T. crepusculus	78.00	2.9	Evergreen broadleaf forest	Dazhaizi, China	10 min scan	43 347 records, 2–11 d/mon, 24 mon	This study
T. obscurus	73.00	6.0	Limestone	Khao Lommuak, Thailand	15 min scan	14 341 records, 5–20 d/mon, 12 mon	Aggimarangsee, 2004
T. leucocephalus	68.15	30.0	Limestone	Fusui, China	10 min scan	10 570 records	Huang et al., 2002; Xiong et al., 2009
T. francoisi	59.48	39.2	Limestone	Fusui, China	10 min scan	7 030 records	Xiong et al., 2009
T. poliocephalus	58.34	54.0	Limestone	Cat Ba Island, Vietnam	10 min scan	549 h, 180 d, 12 mon	Hendershott et al., 2018
T. delacouri	41.40	79.0	Limestone	Van Long, Vietnam	Focal animal	13 976 bouts, 372 h, 203 d, 12 mon	Workman, 2010; Workman & Schmitt, 2012

records in different forest strata for different age-sex classes and tested differences using the Kruskal-Wallis test. We used the Mann-Whitney U test to examine differences in strata use between wet and dry seasons. We also calculated the percentage of records for each behavior type in every stratum and examined the variation in the proportion of each behavior type in different forest strata using the Kruskal-Wallis test.

To test Prediction 2, we applied simple linear regression to analyze the relationship between habitat forest cover and proportion of terrestrial activities in *Trachypithecus* species. We set the confidence interval to 95%. To exclude the effect of habitat type on terrestriality, we reperformed this analysis after excluding *T. crepusculus* from the dataset and focused on five limestone species, i.e., *T. obscurus*, *T. leucocephalus*, *T. francoisi*, *T. poliocephalus*, and *T. delacouri*. To test Prediction 3, we compared strata use patterns between our study group and a group of Francois' langurs inhabiting different habitats (Zhou et al., 2013) using the cross-tab X^2 test. All statistical analyses were performed using IBM SPSS Statistics 21.0. All data collection protocols complied with the current laws of China.

RESULTS

Strata use by Indo-Chinese gray langurs
In total, we conducted 7 091 scans and collected 44 459 behavioral records (record=record of one individual in a scan) with 6.3 langurs on average during each scan (mean: 6.3±3.3, range: 1–21 langurs). To avoid errors caused by small sample size, we only used data from months in which more than 500 behavioral records were collected. Thus, we excluded datasets from July 2013, May 2015, and August 2015 (242–488 records per month) in all analyses. Consequently, we analyzed 43 347 records from 24 months (12 months in wet season and 12 months in dry season; 1 806.1±131.2 records per month, ranging from 541 to 2 327). We found no significant age-sex differences in strata use patterns (Kruskal-Wallis test: ground, X^2=8.831, df=4, P=0.065; 0–5 m, X^2=0.820, df=4, P=0.936; 5–10 m, X^2=1.392, df=4, P=0.846; 10–15 m, X^2=4.757, df=4, P=0.313; 15–20 m, X^2=0.846, df=4, P=0.932; 20–25 m, X^2=0.451, df=4, P=0.978; >25 m, X^2=1.368, df=4, P=0.850). We also found no significant differences in strata use between the wet and dry seasons (Mann-Whitney U test: ground, U=57.000, P=0.410; 1–5 m, U=41.000, P=0.078; 6–10 m, U=74.000, P=0.932; 11–15 m, U=82.000, P=0.590; 16–20 m, U=76.000, P=0.843; 21–25 m, U=90.000, P=0.319; >25 m, U=80.500, P=0.630).

The study group did not use strata evenly (Figure 1, Kruskal-Wallis test: X^2=95.220, df=6, P<0.01). They spent 97.1% of their time in trees and only 2.9% of time on the ground. When in trees, they used the 11–15 m and 16–20 m strata more often than the ≤10 m and >20 m strata (Figure 1).

Based on all behavioral records, resting accounted for 40.4%, feeding accounted for 22.5%, traveling accounted for 33.0%, social behaviors accounted for 2.7%, and geophagy accounted for 1.4%. The langurs also engaged in different

behaviors when using different strata (Kruskal-Wallis test: resting, X^2=51.247, df=6, P<0.01; feeding, X^2=60.61, df=6, P<0.01; traveling, X^2=21.322, df=6, P<0.01; social behavior, X^2=27.358, df=6, P<0.01; geophagy, X^2=110.289, df=6, P<0.01). When on the ground, the langurs mainly engaged in geophagy (32.5%), travelling (40.7%), and resting (20.4%), and rarely in feeding (2.6%) and social behavior (1.4%) (Figure 2). Occasionally, the langurs exhibited geophagy on cliffs with their body supported by trees, but this behavior was recorded rarely (0.00%–0.07% for each tree stratum). In the 1–5 m, 6–10 m, 11–15 m, and 16–20 m strata, the langurs spent, on average, 37.2% of time resting (range: 33.1%–40.5%), 37.0% traveling (range: 33.1%–40.5%), 22.5% feeding (range: 20.6%–26.0%), and 3.0% on social behaviors
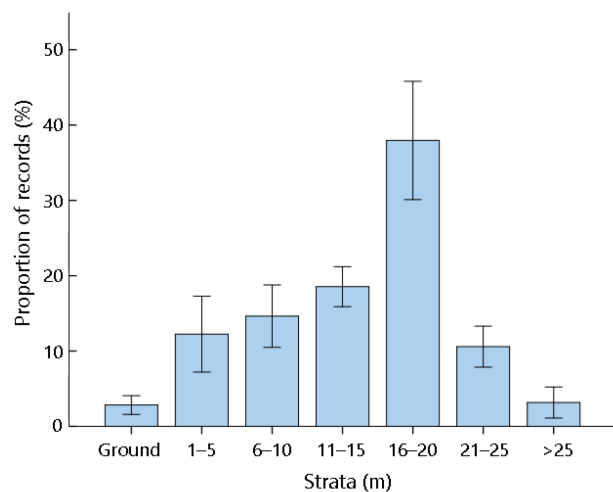

Figure 1 Monthly mean forest strata use by a group of *Trachypithecus crepusculus* in Mt. Wuliang over 24 months
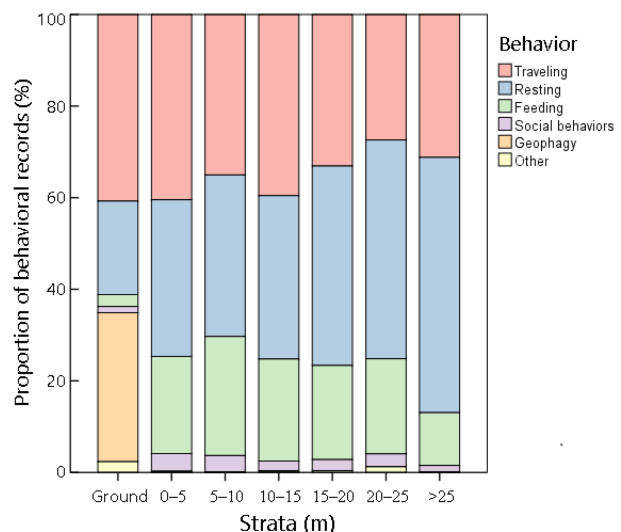Error bars indicate 95% confidence intervals.

Figure 2 Strata use patterns in a group of *T. crepusculus* in Mt. Wuliang over 24 months when engaged in different activities

(range: 2.2%–3.9%). When they used tree strata >20 m, they spent more time resting (47.8% in stratum 21–25 m; 55.7% in stratum >25 m) and less time traveling (27.4% in stratum 21–25 m; 31.2% in stratum >25 m) and feeding (20.8% in stratum 21–25 m; 11.5% in stratum >25 m) (Figure 2).

Effect of forest cover on terrestriality in *Trachypithecus*

Forest cover for the six *Trachypithecus* species habitats varied from 41.4% (*T. delacouri*) to 78.0% (*T. crepusculus*), and terrestriality varied from 2.9% (*T. crepusculus*) to 79.0% (*T. delacouri*) (Table 1). We found a significant negative correlation between forest cover and terrestriality for these species (simple linear regression: Beta=–2.172, R^2=0.955, P=0.001; Figure 3). This correlation was still significant for the five limestone species (simple linear regression: Beta=–2.177, R^2=0.936, P=0.007).

Previous results showed that *T. francoisi* prefer to use higher strata and avoid using ground when they are in continuous forests in valleys, similar to the strata use pattern found in our study group (cross-tab X^2 test: X^2=5.395, df=4, P=0.249; Figure 4). In addition, *T. francoisi* use ground more frequently in both hillside (cross-tab X^2 test: X^2=23.378, df=4, P<0.01) and cliff-hilltop habitats (cross-tab X^2 test: X^2=102.320, df=4, P<0.01) compared to our study group (Figure 4).

DISCUSSION

Strata use patterns in Indo-Chinese gray langurs

Arboreality is an adaptive feature in *Trachypithecus* based on their morphological, anatomical, and ecological traits (McGraw & Sciulli, 2011; Oates & Davies, 1994; Roy & Nagarajan, 2018). In our study area with continuous forest, we predicted
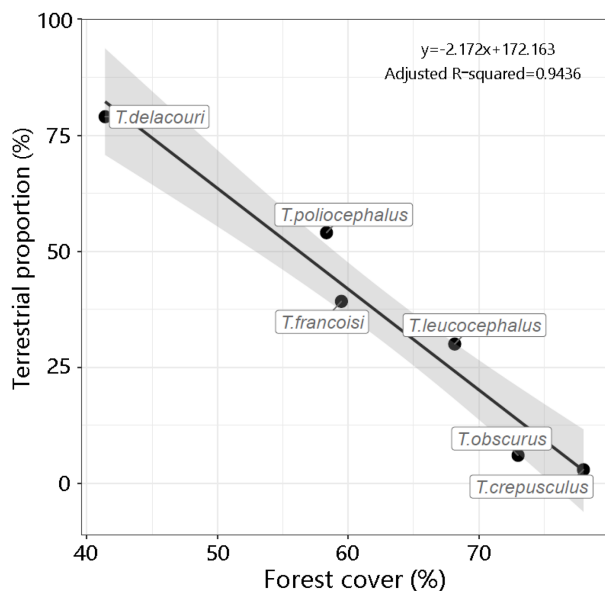

Figure 3 Relationship between terrestriality and habitat forest cover for six species of *Trachypithecus*
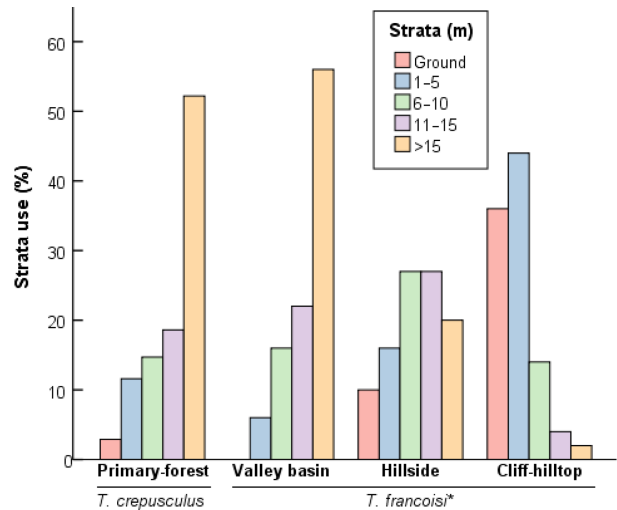

Figure 4 Forest layer use by *T. crepusculus* and *T. francoisi* when traveling.
* indicates data collected from Zhou et al. (2013).

that langurs would avoid using the ground. Consistent with this prediction, the study group were found to be highly arboreal, spending only 2.9% of their time on the ground. The langurs spent most of their time (56.5%) in the strata between 10 m and 20 m, which is likely a response to the specific forest structure of the study site. Previous study on habitat structure (Tian et al., 2007) indicated that trees with a height of 10–20 m are more abundant in the study area, hence providing more substrates in this stratum for langurs.

Our study group preferred to rest in the higher forest strata. As resting is a behavioral state with high security requirements (Fruth & McGrew, 1998), the tendency of langurs to avoid resting at low strata could result from the potential, or perceived, risk of predation by terrestrial predators. Pressure from aerial predators is likely to be low at our study site. Although aerial predators such as hawk eagles and black eagles were present and approached langurs occasionally, langurs rarely escaped to lower strata and normally responded with alarm calls, prompting adults to hold infants in their arms. However, because predation on langurs is rarely reported in the literature, we could not compare the differential predation pressures exerted by aerial and terrestrial predators.

Although *Trachypithecus* species are well known for their ability to digest leaves, they prefer young leaves, fruits, and seeds when these food resources are abundant (Fan et al., 2015; Ma et al., 2017). Distribution of these preferred food resources plays an important role in strata use by *Trachypithecus* species. Our study group tended to use higher strata during feeding, which was likely due to young leaves, fruits, and seeds being more abundant in canopies. Similar patterns have been reported from studies on Delacour's langurs (Workman & Schmitt, 2012) and Cat Ba langurs (Hendershott, 2017), which show high terrestriality in their degraded habitats and higher strata use during feeding. Research on *T. phayrei* on Mt. Gaoligong found they consume

many fruits and seeds (over 80% in monthly diet) in September and October, but descend to the ground to search for fallen seeds in January when their main foods (fruits, seeds, buds and young leaves) are limited in the canopy (Ma et al., 2017). In our study group, fruits and seeds accounted for 32.1% of the annual diet, and the proportion of fruits and seeds in the monthly diet reached over 70% in September and October (Fan et al., 2015). However, our study group did not descend to the ground to search for fallen seeds. Future studies should be conducted to elucidate the relationship between canopy use by langurs and local phenology and food distribution.

The availability of substrates can affect how arboreal primates select travel routes. For example, African colobines travel more frequently in the mid-layers where arboreal substrates are more available (McGraw, 1996). In this study, langurs used the strata above 20 m less often than lower strata when traveling. As trees taller than 20 m were less abundant in our study area (Tian et al., 2007), study subjects may have been limited in their ability to travel in strata above 20 m due to the lack of continuous travel paths.

Geophagy is a widely reported behavior in primates and is explained by its potential function for detoxification and as a mineral supplement (Pebsworth et al., 2019). Indo-Chinese gray langurs have shown home-range expansion in order to visit saltlick locations (Pages et al., 2005), indicating the importance of geophagy for this species. At Mt. Wuliang, geophagy was the main factor attracting Indo-Chinese gray langurs to the ground. Our study group spent a considerable proportion (31.2%) of their terrestrial time engaged in licking rocks. This result highlights the importance of geophagy sites as essential resources for *T. crepusculus*. Although the specific nutritional or mineral benefits langurs gain from terrestrial geophagy remain unclear and deserve research, future conservation strategies for the endangered Indo-Chinese gray langur should take geophagy sites into consideration.

Effect of forest cover on terrestriality in *Trachypithecus*

At the species level in *Trachypithecus*, we found a significantly negative relationship between the degree of terrestriality and proportion of forest cover in habitats. This relationship was also significant when focusing on the five limestone species. Francois' langurs living in limestone forests are highly arboreal when visiting continuous forests, but increase the degree of terrestriality when they use cliff-hilltop areas with fewer trees (Zhou et al., 2013). These results support the inference that the high degree of terrestriality in limestone langurs is an adaptation to the absence of more optimal arboreal substrates (Huang & Li, 2005; Workman & Schmitt, 2012; Zhou et al., 2013). However, we need to note that canopy cover is a rough index of habitat quality and other habitat characteristics such as tree diversity, abundance, and height could also affect strata use patterns. Further studies on habitat structure and resource distribution in different langur habitats are needed in the future.

In addition to terrestriality, limestone langurs are also differentiated from non-limestone langurs in other behaviors. For example, limestone langurs use cliff caves and ledges as sleeping sites, whereas non-limestone langur species sleep among the tree canopies (Hendershott, 2017; Huang et al., 2003; Workman, 2010; Zhou et al., 2009). Limestone langurs normally live in small groups of less than 20 individuals and consume less than 10% of fruits and seeds in their annual diet (Li & Rogers, 2006; Workman, 2010), whereas Phayre's langurs and Indo-Chinese gray langurs in non-limestone evergreen forests live in larger groups of more than 40 individuals (Ma et al., 2015, 2017), and consume more fruits and seeds in their annual diet (*T. crepusculus*: 32.1%, Fan et al., 2015; *T. phayrei*: 40.9%, Ma et al., 2017). Future comparative studies are needed to test whether these features are species-specific natures or behavioral adaptations to low-quality habitats.

Overall, our results demonstrate how *Trachypithecus* langurs flexibly use their habitat in response to habitat differences and degradation. This behavioral flexibility enables them to survive in diverse habitats including evergreen forests and limestone hills degraded to differing degrees. Together with other studies, our results highlight the importance of continuous forests for *Trachypithecus* langurs. Although limestone hills provide shelter for several *Trachypithecus* species, limestone langurs tend to forage in and compete for continuous forest patches, which produce more food resources (Li & Rogers, 2005; Zhou et al., 2013). To effectively protect critically endangered limestone langurs, such as Cat Ba, white-headed, Delacour's, and Francois' langurs, conservation efforts should not be limited to their limestone hill habitats, but should also include the lowland forests in valleys around these hills, which require protection from intense human disturbance (Chapman, 2018; Huang et al., 2002).

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

P.F.F, C.M., and W.C. conceived and designed this study. C.M., W.G.X, W.C., and P.F.F performed the study. C.M., L.Z., and L.Y. analyzed the data. C.M., P.R.T., and P.F.F wrote the paper. All authors read and approved the final version of the manuscript.

for providing support for this study. We thank the editors and reviewers of Zoological Research for their valuable comments.

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