

Letter to the editor

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Diet, food availability, and climatic factors drive ranging behavior in white-headed langurs in the limestone forests of Guangxi, southwest China

Changes in abiotic and biotic factors can affect the efficiency of biological systems in animals, forcing them to adjust their behaviors in response to daily and seasonal variations. From September 2016 to August 2017, we collected ranging behavior data on four groups of white-headed langurs (*Trachypithecus leucocephalus*) in the Guangxi Chongzuo White-Headed Langur National Nature Reserve, Guangxi, southwest China. We simultaneously analyzed how multiple ecological factors affect langur ranging behavior, which should facilitate our understanding of the potential mechanisms underlying their adaptation to limestone habitats. Results showed that langur ranging behavior was significantly affected by diet composition, food availability, and climatic factors. Specifically, moving time and daily path length increased with the increase in dietary diversity. Furthermore, moving time and daily path length were positively associated with the availability of fruit and relative humidity of the forest, and moderately associated with temperature and relative humidity of bare rock. Our study demonstrated that langurs maintain stable moving and feeding times and exhibit a short daily travel distance, likely adopting an energy-conserving behavioral strategy in response to food shortages and high temperatures in the fragmented karst forest. These results highlight the importance of food availability and temperature in shaping the ranging behavior of these karst-dwelling primates.

The living environments of most animal species are composed of complex abiotic and biotic factors (Wong & Candolin, 2015), including ambient temperature (Chatelain et al., 2013), water availability (Mandl et al., 2018), relative humidity (Li et al., 2020a), food availability (Ning et al., 2019), daylength (Hill et al., 2003), light conditions (daylight and moonlight) (Dacke et al., 2003), intraspecific/interspecific competition (Eccard & Ylönen, 2003), predation pressure

(Isbell, 1994), and social contact (McFarland et al., 2015). Furthermore, environmental factors can vary dramatically within a single year, or even on a daily scale, with inhabitants needing to cope with potentially significant changes in environmental conditions (Mandl et al., 2018). The physiology, morphology, and behavior of an animal determine its ability to adapt and respond to dramatic changes in climate through autonomic responses and behavioral thermoregulation (Hanya et al., 2007).

Food-related factors (e.g., diet and food availability) and ambient temperature are widely recognized as determinants that can constrain activity patterns in animals (Hanya, 2004; Li et al., 2020b; Ning et al., 2019). For instance, primates adjust their time budgets and ranging patterns in response to fluctuations in diet and food availability (Bach et al., 2017; Guan et al., 2018; Hanya, 2004). Ambient temperature is a major factor that affects behavioral and physiological processes, ecology, and evolution (Pörtner et al., 2006). The spatiotemporal scales of variability in habitat temperature conditions vary greatly (ranging from meters to kilometers, minutes to months) (Thompson et al., 2016; Van Schaik & Pfannes, 2005). In general, biological system efficiency can be affected by small changes in environmental factors (i.e., temperature) (Whiteman & Buschhaus, 2003), and animals must adjust their activity to adapt to these daily and seasonal variations (Hemingway & Bynum, 2005). Moreover, temperature differences among thermal microhabitats are important for understanding animal biology and ecology (Thompson et al., 2016).

By comparing various timescales (e.g., seasonal variations, daily variations, and immediate effects), we can examine the impacts of ecological factors on activity patterns (Hanya et al., 2018), thereby enhancing our understanding of how environmental factors affect animal behavior and elucidating the strategies that animals use in response to these variations. Moreover, ecological factors are often interrelated and can

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Received: 28 December 2020; Accepted: 07 May 2021; Online: 08 May 2021

Foundation items: This study was supported by the National Natural Science Foundation of China (31960106, 31870355, 31301893)

collectively influence animal behavior (Brockman & Van Schaik, 2005; Mandl et al., 2018). For example, the influence of temperature on Japanese macaque (*Macaca fuscata*) behavior is at least as important as that of food-related factors (Hanya, 2004). Therefore, when examining the effects of ecological factors on activity patterns, simultaneous analysis of multiple factors can help identify the underlying mechanisms driving primate adaptations (Mandl et al., 2018).

The white-headed langur (*T. leucocephalus*) is a highly endangered, karst-endemic primate species (Huang, 2002), with the current wild population consisting of only 1 100 individuals (Konstant et al., 2003; Huang et al., 2018). The species inhabits the karst limestone forests of southwest China (Huang, 2002), which show significant seasonal variations in rainfall, food availability, and ambient temperature, as well as dramatic fluctuations in temperature over the 24-h cycle (Huang, 2002; Huang et al., 2015; Li et al., 2020a). In addition, intensive human disturbance has led to severe habitat degradation and fragmentation (Huang et al., 2008), resulting in changes in resource availability, thermal conditions, and water conditions (Aristizabal et al., 2018; Tuff et al., 2016). Therefore, white-headed langurs face considerable challenges regarding environmental fluctuations and degradation, with their behavioral patterns influenced accordingly (Huang et al., 2008; Tuff et al., 2016). Previous studies have found that habitat quality (Li & Rogers, 2005), group size (Zhang et al., 2020), water resources (Zhou et al., 2011), sleeping sites (Zhou et al., 2011), and forest fragmentation (Huang et al., 2017) are important factors affecting the ranging patterns of white-headed langurs. To date, however, these factors have been considered separately or limited to descriptive analysis only.

Here, we examined the effects of diet composition, food availability, and climatic factors (i.e., rainfall, temperature, humidity, and daylength) on the ranging behavior of four groups of white-headed langurs. We collected activity pattern data, i.e., activity budget, daily path length, and diet, from September 2016 to August 2017. Over the study period, we completed 216 full-day observations (G-DS: 52 d, G-ZWY: 52 d, G-LZ: 55 d, and G-NN 57 d) and obtained a total of 9 761 scans (G-DS: 2 251, G-ZWY: 2 250, G-LZ: 2 542, and G-NN: 2 718). Furthermore, resource availability and climatic factors varied across the year, showing significant seasonal variation (Table 1; Figure 1; Supplementary Materials and Methods). The availability of young leaves and fruits in the rainy season was higher than that in the dry season, but there was no significant seasonal difference in the availability of mature leaves and flowers. In general, temperature and relative humidity were higher in the rainy season than in the dry season, except for the humidity of bare rock.

Results showed that the white-headed langurs were highly folivorous (Table 1). The major food was young leaves, followed by mature leaves, fruits, other parts, and flowers. There were seasonal differences in young leaf composition ($U=519.000$, $n=48$, $P<0.001$), mature leaf composition ($U=51.000$, $n=48$, $P<0.001$), and other parts ($U=181.000$, $n=48$, $P=0.027$). The consumption of flowers and fruits and the dietary diversity index did not differ significantly between the dry and rainy seasons.

The langurs spent most of their daily activity time resting, followed by feeding, moving, grooming, playing, and other activity (Table 1). Langurs spent more time resting ($U=122.500$, $n=48$, $P=0.001$), less time grooming ($U=553.000$, $n=48$, $P<0.001$), and more time on other activities ($U=151.000$, $n=48$, $P=0.004$) during the dry season compared to the rainy season (Table 1). However, there were no significant seasonal changes in time spent feeding, moving, or playing. The average daily path length was 437.1 ± 89.3 m (216 d), ranging from 213.3 m to 703.0 m, but with no significant seasonal variation.

The ranging behavior of the white-headed langurs was significantly affected by dietary composition (Supplementary Tables S1, S2). Resting time increased with the consumption of mature leaves ($\beta=0.132$, $W_{ip}=0.37$), but decreased with an increase in the dietary diversity index ($\beta=-1.326$, $W_{ip}=0.96$). Moving time increased with an increase in the dietary diversity index ($\beta=2.472$, $W_{ip}=0.98$); however, there was no significant correlation between dietary composition and feeding time. Furthermore, daily path length increased with an increase in the dietary diversity index ($\beta=1.123$, $W_{ip}=0.99$).

Food availability and climatic factors significantly affected the ranging behavior of the white-headed langurs (Supplementary Tables S3, S4). Results showed that resting time was positively associated with the availability of mature leaves ($\beta=0.719$, $W_{ip}=0.59$). Moving time was positively associated with the availability of fruit ($\beta=0.394$, $W_{ip}=0.69$), and moderately associated with the availability of mature leaves ($\beta=-0.908$, $W_{ip}=0.54$) and daylength ($\beta=-2.922$, $W_{ip}=0.61$). Grooming time was positively associated with daylength ($\beta=8.075$, $W_{ip}=0.83$). However, there were no significant correlations between these ecological factors and feeding, playing, and other activity time. Daily path length was positively associated with the availability of fruit ($\beta=0.144$, $W_{ip}=0.55$) and moderately associated with the mean highest temperature of bare rock ($\beta=-0.738$, $W_{ip}=0.43$).

Results from hourly data analysis (Supplementary Tables S5, S6) showed that moving time was positively associated with hourly relative humidity of the forest ($\beta=0.577$, $W_{ip}=0.98$), and moderately associated with hourly relative humidity of rock ($\beta=-0.432$, $W_{ip}=0.59$). Feeding time was positively associated with hourly relative humidity of the forest ($\beta=0.402$, $W_{ip}=0.66$). Daily path length was positively associated with hourly relative humidity of the forest ($\beta=0.220$, $W_{ip}=0.92$), and moderately associated with the mean temperature of bare rock ($\beta=-0.967$, $W_{ip}=0.87$) and hourly relative humidity of rock ($\beta=-0.260$, $W_{ip}=0.76$).

The white-headed langurs adapted to their seasonal habitats by adjusting their ranging behavior. They spent more time resting and less time moving and feeding, similar to the results reported in Huang (2002) and Zhou et al. (2013). This behavior is consistent with typical folivorous primates, who spend most of their time resting (Eustace et al., 2015; Hendershott et al., 2016; Zhou et al., 2007). Studies have shown that resting time is determined by diet, as leaf-eating animals need a long resting time to ferment and digest their food (Korstjens et al., 2010; Van Soest, 1994). Feeding and moving times of the white-headed langurs were relatively stable throughout the year, and their daily travel distance was

Table 1 Ranging behavior and dietary composition of white-headed langurs, and food availability and climatic factors during study period

Group	Season	Time budgets (% of total activity time, mean±SD)						Daily path length (m)
		Resting	Moving	Feeding	Grooming	Playing	Other	
G-DS	Annual	46.3±7.4	19.7±3.6	23.9±4.5	9.1±3.8	0.9±0.9	0.1±0.1	455.6±43.8
G-ZWY	Annual	41.2±7.1	21.5±4.7	23.8±4.0	7.7±3.9	5.5±2.3	0.3±0.3	499.1±105.7
G-LZ	Annual	51.6±7.4	15.0±3.9	24.5±3.9	8.4±3.1	0.1±0.4	0.4±0.6	430.4±78.0
G-NN	Annual	49.8±8.3	15.8±4.4	25.4±3.2	8.7±3.1	0.1±0.1	0.2±0.2	363.1±61.4
Mean	Annual	47.2±8.3	18.0±4.9	24.4±3.9	8.5±3.4	1.7±2.7	0.3±0.4	437.1±89.3
	Dry	51.0±8.8	17.5±5.9	24.2±4.7	5.8±2.2	1.1±2.0	0.4±0.5	434.9±100.2
	Rainy	43.4±5.8	18.5±3.6	24.6±2.8	11.2±1.9	2.2±3.3	0.1±0.2	439.2±78.9

Group	Season	Diet composition (% of feeding time, mean±SD)					Dietary diversity index
		Young leaves	Mature leaves	Flowers	Fruits	Other	
G-DS	Annual	71.6±12.2	14.8±7.9	1.1±1.1	6.6±6.0	5.8±5.9	5.11±0.57
G-ZWY	Annual	71.4±14.2	15.2±12.2	2.4±2.8	4.8±2.8	6.2±3.7	4.94±0.57
G-LZ	Annual	68.7±11.8	17.8±11	1.6±1.3	6.9±5.5	5.1±3.3	4.82±0.48
G-NN	Annual	67.5±7.9	15.6±9.0	3.8±2.8	8.1±5.3	4.9±3.8	4.99±0.28
Mean	Annual	69.8±11.5	16.7±9.9	2.2±2.3	6.6±5.0	5.5±4.2	4.96±0.49
	Dry	62.3±10.5	23.4±8.6	2.1±2.6	5.2±3.7	7.1±5.3	4.98±0.63
	Rainy	77.4±6.5	10.0±5.8	2.4±2.1	8.0±5.8	3.9±1.8	4.95±0.30

Season	Climatic factors, temperature (°C), humidity (%), rainfall (mm), and daylength (min) (mean±SD)							
	HTF	MTF	RHF	HTR	MTR	RHR	Rainfall	Daylength
Annual	26.9±4.5	22.5±4.7	84.9±5.3	41.9±6.8	26.3±5.1	73.7±4.9	365.2±291.3	774.2±59.8
Dry	24.8±5.2	20.0±5.1	81.3±5.2	39.2±5.5	23.6±4.9	72.6±4.9	167.9±125.8	725.4±31.7
Rainy	29.1±2.7	25.0±2.8	88.5±2.4	44.8±7.2	29.1±3.9	74.8±5.1	562.5±278.3	823.1±33.9

Season	Food availability index (FAI) (mean±SD)			
	Young leaves-FAI	Mature leaves-FAI	Flowers-FAI	Fruits-FAI
Annual	10 870.4±4 664.2	31 775.3±5 613.8	1 126.3±1 357.7	2 265.2±1 855.2
Dry	7 489.8±4 272.9	30 358.0±5 027.5	500.8±196.8	912.3±524.2
Rainy	14 250.9±1 474.4	33 192.6±6 263.8	1 751.7±1 754.4	3 618.1±1 704.1

HTF: Mean highest temperature of forest; MTF: Mean temperature of forest; RHF: Mean relative humidity of forest; HTR: Mean highest temperature of bare rock; MTR: Mean temperature of bare rock; RHR: Mean relative humidity of bare rock.

short, consistent with the energy minimization strategy (Agetsuma, 1995; Li et al., 2020c).

We found that white-headed langurs increased their moving time and ranging distance with the dietary diversity index. They consumed a variety of plants throughout the year, resulting in a high dietary diversity index (Table 1). Thus, increasing the variety of plant food species appears to be an important way for langurs to cope with shortages in preferred foods. This may be due to the lack of food resources in our study area. Compared to the habitat of other populations of white-headed langurs in the Fusui and Nonggang areas of Guangxi, our study area shows higher habitat fragmentation (Huang et al., 2008) and reduced habitat quality, which can affect primate behavior patterns (Arroyo-Rodríguez & Mandujano, 2006). Previous studies have shown that habitat fragmentation is an important factor that affects langur ranging behavior (Huang et al., 2017). Although there were seasonal variations in the availability of preferred food (young leaves and fruits) in our study area (Figure 1), the total amount of food was scarce. In regard to food resource shortages, these langurs have very little scope in food selection (especially food part selection) (Zhang et al., 2017). Instead, they increased their moving time and distance to search for additional food

species. Studies have shown that increasing the number of food species is an effective way for many primates to cope with food shortages (Hemingway & Bynum, 2005), and primates can benefit from high food diversity (Fan et al., 2015).

Our results showed that langur ranging behavior was significantly affected by food availability and climatic factors. As the availability of fruit increased, the langurs showed an increase in moving time and travel distance and a reduction in resting time. Primates demonstrate a variety of responses when fruit is abundant, including changes in moving time (Li et al., 2020b; Ning et al., 2019), which involve energy strategy selection and behavioral optimization to maximize feeding benefits (Barrett, 2009; Fan et al., 2012). Although langurs showed a preference for fruits, fruit availability did not affect their fruit consumption, which was likely due to the limitation of overall resources (Zhang et al., 2017). Notably, they depended on leaves, especially young leaves, more heavily and maintained a stable active behaviors (feeding and moving) and a short daily travel distance. For folivorous primates, maintaining a small home range and short daily travel distance can aid in energy conservation (Stephens et al., 2007).

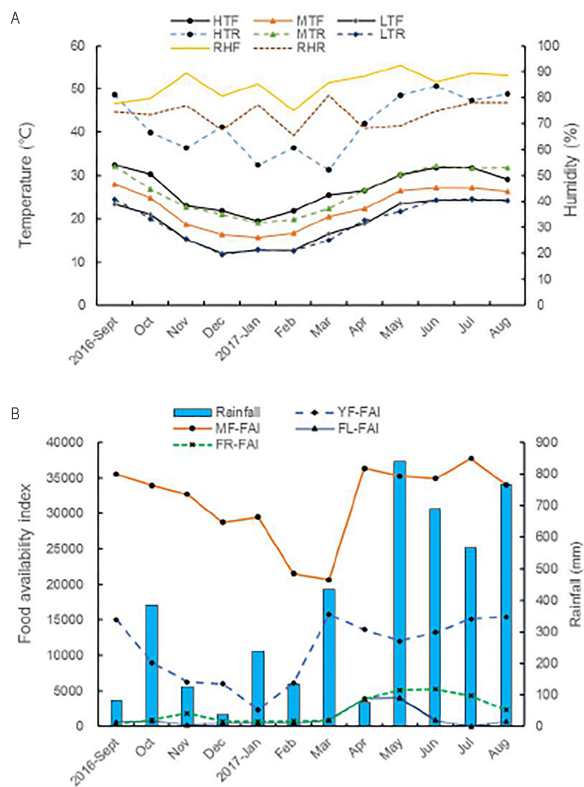


Figure 1 Monthly temperature, relative humidity, rainfall, and food availability index during study period

A: Monthly temperature (°C) and relative humidity (%). HTF: Mean highest temperature of forest; LTF: Mean lowest temperature of forest; MTF: Mean temperature of forest; RHF: Mean relative humidity of forest; HTR: Mean highest temperature of bare rock; LTR: Mean lowest temperature of bare rock; MTR: Mean temperature of bare rock; RHR: Mean relative humidity of bare rock. B: Monthly rainfall (mm) and food availability index. YL-FAI: Food availability index for young leaves; ML-FAI: Food availability index for mature leaves; FL-FAI: Food availability index for flowers; FR-FAI: Food availability index for fruits.

In addition, the ranging behavior of white-headed langurs was strongly influenced by temperature and relative humidity, consistent with other studies on limestone forest-residing primates (Li et al., 2020a, c). The langurs reduced their moving time and travel distance when temperature increased. The cost of performing activities at high temperatures is expensive. In addition to the energy required by the exercise itself, the animal also requires additional energy for body temperature adjustment (Hanya, 2004). Therefore, when the temperature of the bare rock increased, langurs reduced their activity to conserve energy (Li et al., 2020a; McLester et al., 2019). Generally, as the temperature increased, the relative humidity of the bare rock decreased, while an increase in the humidity of bare rock was usually caused by rainfall. Additionally, rainfall had a negative effect on primate activity across the daytime. Similarly, Hanya et al. (2018) also found that even a small amount of rainfall can have a negative effect on Japanese macaque activity. Moreover, with the increase in

forest humidity, the langurs increased their moving time, feeding time, and travel distance, indicating that they preferred the comfortable microclimate under the forest rather than the high temperatures. Studies have confirmed that selecting a thermally favorable microenvironment is an important way for primates to regulate body temperature (Hanya et al., 2007). In high-temperature seasons, François' langurs use their understory habitat and avoid high-temperature bare areas (Li et al., 2020a). A previous study found that white-headed langurs like to rest on exposed rocks and sunbathe during the cold months (Huang, 2002), thus adopting an energy-conserving strategy during low-temperature periods (Guan et al., 2018; Ning et al., 2019). Other primates have adopted a similar strategy in response to cold temperatures, i.e., François' langurs (Li et al., 2020a; Zhou et al., 2007), Assamese macaques (Li et al., 2020b), western black crested gibbons (*Nomascus concolor*) (Ning et al., 2019), and ring-tailed lemurs (*Lemur catta*) (Kelley et al., 2016). Thus, similar to other primates (Fan et al., 2012; Li et al., 2020b), temperature was a determinant of white-headed langur ranging behavior in the limestone forest.

Ranging behavior was also influenced by daylength (Supplementary Table S3). Moving time decreased with the increase in daylength, while grooming time increased with the increase in daylength. This may be related to the energy-saving strategy adopted by langurs, as moving is a high-energy activity and grooming is a relatively low-energy activity (Dunbar et al., 2009). In the longer day season (high temperature, rainy season), reducing moving and increasing grooming may reduce thermal stress levels under high-temperature conditions (Dunbar et al., 2009; Li et al., 2020b).

In summary, white-headed langurs primarily consumed leaves throughout the year and fed on a variety of plant species, likely benefiting from high food diversity. On this basis, they maintained a stable moving time and feeding time, retained a short daily travel distance, and adjusted their resting and grooming times, which aided in conserving energy. In addition, the langurs increased moving time and daily path lengths in response to the increase in high-quality food and decreased moving time and travel distance under high-temperature environments. They used energy minimization strategies in response to food shortages and high and cold temperatures in a fragmented habitat. The current study highlights the importance of food availability and temperature in shaping the ranging behavior of this karst-dwelling primate, and the importance of vegetation protection and restoration in fragmented habitats, as habitat loss and fragmentation can impact species diversity and microclimate.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Permission to conduct fieldwork in the Banli area was granted by the Guangxi Chongzuo White-Headed Langur National Nature Reserve. Data collected for this project were purely observational. The authors have no ethical conflicts to disclose.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Z.H.H. designed the research. K.C.Z. collected data and wrote the manuscript. H.L.X., Q.H.Z. and Z.H.H. revised the manuscript. All authors read and approved the final version of the manuscript.

ACKNOWLEDGEMENTS

We are very grateful to the Guangxi Forestry Bureau and the Guangxi Chongzuo White-Headed Langur National Nature Reserve for permitting us to conduct our research. We are also grateful to Zhi-Zhang Liang, Shao-Quan Huang, Jin-Long He, Gao-Wen Nong, and Mei-Shu Liang for their logistical assistance.

Ke-Chu Zhang^{1,2,3}, Qi-Hai Zhou^{2,3}, Huai-Liang Xu^{1,*},
Zhong-Hao Huang^{2,3,*}

¹ College of Life Science, Sichuan Agricultural University, Ya'an, Sichuan 625014, China

² Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection (Guangxi Normal University), Ministry of Education, Guilin, Guangxi 541004, China

³ Guangxi Key Laboratory of Rare and Endangered Animal Ecology, Guangxi Normal University, Guilin, Guangxi 541004, China

*Corresponding authors, E-mail: xuhuail@sicau.edu.cn; hzh773@126.com

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