Factors Affecting the Ranging Behavior of White-headed Langurs (*Trachypithecus leucocephalus*)

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Abstract Ranging behavior is an important aspect of animal behavior that researchers use to investigate ecological influences on individual behavior. We studied the influence of diet, water resources, and sleeping sites on the ranging behavior of 2 groups of white-headed langurs (*Trachypithecus leucocephalus*) in a limestone habitat at Fusui Nature Reserve, China, between August 2007 and July 2008. During the study period, the total home range sizes for the 2 focal groups were 23.8 ha and 33.8 ha, the mean daily path lengths were 491 m and 512 m, and leaves accounted for 83.4% and 91.0% of the diet, which are well within the range of variation reported for other *Trachypithecus*. One focal group traveled significantly longer distances in the rainy season months than in the dry season months. This variation may be related to the seasonal difference in food availability and diet. The langurs did not use their home ranges uniformly, and 50% of their activities occurred within 11% (group 1) and 20% (group 2) of their home ranges. The most heavily used quadrats in the home ranges were located near the most frequently used sleeping sites. Moreover, the core areas (>70% of location records) of both groups' home ranges included ≥1 permanent water pool. The langurs ventured to these pools for drinking when surface water became scarce in the dry season. These results suggest that sleeping sites and water scarcity may be significant influences on the ranging behavior of white-headed langurs in limestone habitat.

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Introduction

Resources documented to influence the ranging behavior of primates include food (Buzzard 2006; Clutton-Brock 1975; Di Fiore 2003; Olupot *et al.* 1997), water resources (Sigg and Stolba 1981; Scholz and Kappeler 2004), and sleeping sites (Harrison 1983; Matsuda *et al.* 2009). Researchers usually consider food quality and its distribution to be the most important of these (Buzzard 2006; Clutton-Brock 1975; Di Fiore 2003; Olupot *et al.* 1997). In general, folivorous species have smaller home ranges and shorter daily path lengths than frugivorous primates (Chapman and Chapman 2000; Clutton-Brock and Harvey 1977). These patterns may be related to the relatively poor nutrition in the diet of folivorous primates as well as the relative ubiquity of their food resources. Seasonal variation in food availability can also have large influence on the ranging behavior of primates (Buzzard 2006; Di Fiore 2003; Olupot *et al.* 1997). Some primates increase daily path length when high-quality foods are scarce, e.g., *Colobus angolensis*: Bocian (1997) and *C. satanas*: McKey and Waterman (1982). In contrast, other species decrease their daily path length during the lean period for high-quality foods, e.g., *Hylobates lar*: Bartlett (1999) and *Trachypithecus pileatus*: Standford (1991). This variation probably reflects a difference in foraging strategy. Primates can either increase foraging efforts, e.g., moving farther and covering larger seasonal home range, to search for high-quality foods under conditions of scarcity or adopt a strategy for saving energy, e.g., decreasing daily path lengths, and rely on lower quality foods until condition improve (Di Fiore 2003).

In dry environments, water availability also has a large impact on primate ranging behavior. For example, hamadryas baboons (*Papio hamadryas*) in semidesert areas travel several kilometers each day to visit water holes within their home ranges (Sigg and Stolba 1981). Other species focus their activities around permanent water resources, e.g., *Papio cynocephalus ursinus* at De Hoop: Hill (1999). Primates may also change their home ranges in response to seasonal water scarcity. For example, redfronted lemurs (*Eulemur fulvus rufus*) switched their activity center to an area close to the water holes during the periods of critical water scarcity (Scholz and Kappeler 2004).

Primate ranging behavior can also be influenced by the location and availability of sleeping sites (Harrison 1983). For example, the ranging patterns of proboscis monkeys (*Nasalis larvatus*) are affected by the location of sleeping sites because they typically sleep adjacent to riverbanks to protect themselves from terrestrial predators (Matsuda *et al.* 2009). Moreover, sleeping sites are often concentrated in the area most used by a group (Anderson 1984), and using sleeping sites as central places for foraging is a strategy to maximize economic foraging (Chapman *et al.* 1989).

Previous studies suggest that the ranging behavior of white-headed langurs (*Trachypithecus leucocephalus*), one of the 25 most endangered primate species in the world (Li *et al.* 2003) is mainly influenced by the spatial distribution of foods

(Huang 2002; Li and Rogers 2005). However, very little is known about the influence of other resources, e.g., sleeping site and water resource, on the ranging behavior of this species. Here, we examine the influences of diet, water resources, and sleeping sites on their ranging behavior. The langurs are highly folivorous, and young leaves account for the bulk of monthly diet almost all year (Huang 2002; Li and Rogers 2006). However, in limestone habitat young leaves become scarcer in the dry season (Li and Rogers 2006; Zhou *et al.* 2006), and langurs rely on more low-quality mature leaves in response to this scarcity (Li and Rogers 2006). Accordingly, they may be expected to reduce foraging effort by decreasing daily path length so as to save energy. Because of seepage, the limestone habitat is a very dry environment, and surface water is scarce in the dry season (Huang 2002). Although white-headed langurs can obtain water requirement mainly from food, they still need to drink water from permanent pools in the dry season (Huang and Li 2005; Li 2000). Thus permanent water pools may be an important resource and langurs may be expected to focus their activities around permanent water pools in the dry season. Finally, the limestone habitat has some unique features that differentiate it from mountain forests, such as steep cliffs, which represent about 10–20% of the area (Huang 2002). White-headed langurs typically use caves on cliffs as their sleeping sites to protect themselves against terrestrial predators (Huang *et al.* 2003). Thus, we predict that the locations of sleeping sites will play an important role in determining the ranging behavior of white-headed langurs.

Methods

Study Site and Subjects

We conducted this study at Fusui Nature Reserve, Guangxi province, China (22°24′ 51″–22°36′20″N and 107°23′–107°41′43″E, Fig. 1), which was founded in 1981 to protect white-headed langurs and François' langurs (*Trachypithcus francoisi*). The reserve consists of limestone hills, ranging from 400 m to 600 m above the sea level. The vegetation is characterized by limestone seasonal rain forest (Guangxi Forestry Department 1993), but the remaining habitats in the reserve have become highly fragmented as a result of sugarcane plantations, roads, and settlements and further degraded by firewood collection (Huang 2002; Li and Rogers 2005). The main potential predators in the reserve are crested serpent eagles (*Spilornis cheela*), which are large enough to catch infant langurs (Li 2000).

Our study site is located in the central part of Fusui Nature Reserve. We focused on 2 neighboring groups of white-headed langurs that ranged near our camp. Group 1 consisted of 14 individuals initially (1 adult male, 8 adult females, 2 juveniles, and 3 infants), and increased to 18 individuals after the birth of 4 infants. Group 2 contained 11 individuals (1 adult male, 5 adult females, 3 juveniles, and 2 infants) throughout the study period.

Data Collection

We collected climatic data, including rainfall and minimum and maximum temperatures, daily from August 2007 to July 2008 with a rain gauge and maximum and
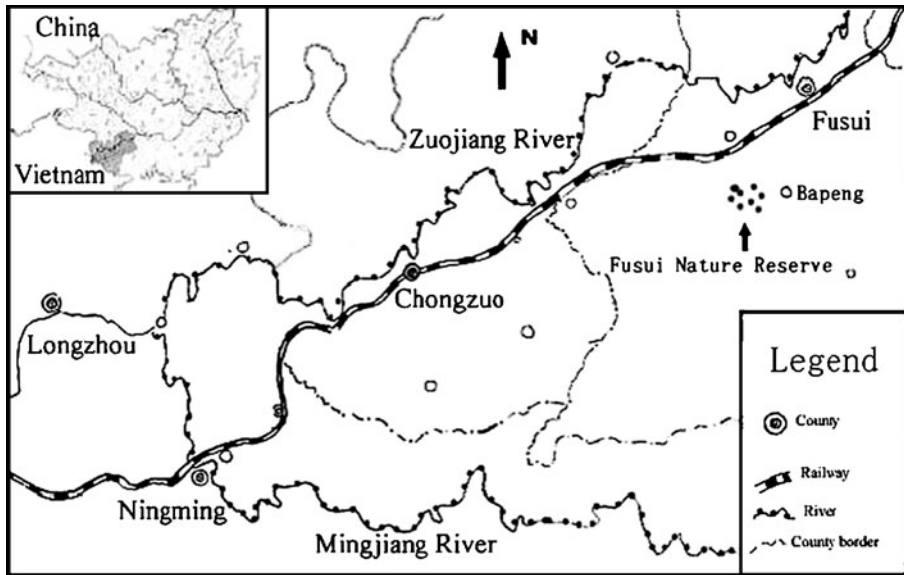
Fig. 1 Map of Fusui Nature Reserve.

minimum thermometer. We made behavioral observations of group 1 for 54 full days (2–9 full/mo), and of group 2 for 39 full days (2–5/mo; Table I). We also followed groups on a partial basis on the other days to maintain a picture of all the areas visited during the study period. For full-day follows, we began observation when the langurs left their sleeping sites and ended when they entered the sleeping sites again.

Table I Monthly ranging size, mean daily path length, and sampling days of the 2 focal groups at Fusui Nature Reserve between August 2007 and July 2008

Month	Group 1					Group 2				
	No. of quadrats used	Mean daily path length (m)	No. of full-day follows (d)	No. of days of follows	No. of location records	No. of quadrats used	Mean daily path length (m)	No. of full-day follows (d)	No. of days of follows	No. of location records
August 2007	29	499	4	6	84	20	565	2	3	50
September 2007	52	536	9	10	209	14	970	2	3	52
October 2007	36	616	5	5	129	40	535	5	7	126
November 2007	35	584	4	4	90	15	403	4	5	98
December 2007	32	427	4	5	119	29	412	3	3	69
January 2008	13	300	2	3	45	16	405	2	3	57
February 2008	31	369	4	4	96	48	438	5	5	129
March 2008	25	396	4	6	106	37	403	3	4	100
April 2008	40	560	5	5	124	37	548	4	4	108
May 2008	22	559	4	4	58	37	658	5	6	146
June 2008	32	386	4	4	108	12	553	2	3	73
July 2008	38	437	5	6	140	17	545	2	2	51
Mean	32	472	5	5	109	27	536	3	4	88
SD	10	100	2	2	42	13	160	1	1	34

Partial-day follows began when we first encountered the focal group. The duration of contact was variable, with an average of 4.04±2.29 h (range=2.5–9).

We collected behavioral data using scan sampling with 15-min intervals (Altmann 1974a, b). Scans lasted 5 min, followed by 10 min of inactivity until the next scan began. We recorded the activity of each individual seen during each scan. We watched each individual for 5 s after detection and recorded its predominant behavior, e.g., resting, moving, feeding, and social behavior, during that interval. To avoid sampling bias toward certain individuals or a particular age–sex class, we collected behavioral records on as many different individuals as possible during a scan so that we included all individuals in the focal group, but we sampled no individual more than once. When the individual was feeding, we recorded plant species and parts eaten as mature leaves, young leaves, fruits, flowers, seeds, and other items, including petioles and stems. We plotted the location of the focal group on a topographic map (1:10,000) every 30 min and recorded of the group's activity at the same time, e.g., resting, moving, or feeding. During the study period, we collected 1308 location records for group 1 and 1059 for group 2 (Table I). When possible, we marked the locations of sleeping sites on the topographic map (1:10,000).

Data Analysis

We calculated the percentage of different plant parts in the monthly diet of the focal group using monthly total feeding records. We obtained annual dietary composition by taking the mean of the monthly percentages. We excluded records for dependent infants and juveniles from analysis because they did not forage independently, and infant and juvenile mouthing of prospective foods often cannot be differentiated from actual feeding.

To assess a group's home range size and pattern of range use, we superimposed a grid of 50×50 m quadrats (0.25 ha) on the map of the study area. We estimated range size as the total number of different quadrats entered each month (monthly range size) and throughout the study (total home range size). We expressed the pattern of range use as the percentage of the total location records that fell into each 0.25-ha quadrat of the grid. We defined a core area as the sum of all quadrats of the home range in which langur residence exceeded the expected uniform percentile value (Samuel *et al.* 1985). We assessed the overall intensity of quadrat use across the home range using 5 use-intensity categories: ≥3.0% total use, 2.0–2.9% use, 1.0–1.9% use, 0.1–0.9% use, and no use. We used only full-day follows for analyses of daily ranging behavior. We calculated daily path length by summing the straight-line distances between successive chronological locations for each day.

We used Mann-Whitney tests to compare daily path length and mean monthly range size for the 2 groups, and to test for seasonal differences in these variables. We used Spearman correlations to examine the relationship between monthly mean daily path length and the proportion of young leaves, mature leaves, and fruits in the diet, and to compare monthly mean path length to rainfall. We used χ^2 tests to compare the observed frequencies of quadrat use to the frequencies expected by chance, calculated using the total number of quadrats used and the total number of location records, and to compare the observed frequencies of sleeping sites use to the frequencies expected by chance, calculated using the total number of sleeping sites

and the total number of observed nights. All tests are 2-tailed, with a significance level of $p<0.05$.

Results

Climate

The total rainfall during the study period was 1035 mm. There were 2 seasons: a dry season from October 2007 to March 2008 with <50 mm monthly rainfall and a rainy season in the remainder of the year with >50 mm monthly rainfall. Mean annual temperature was 23.2°C, ranging from a mean monthly minimum of 6.2°C in January 2008 to a mean monthly maximum of 34.9°C in August 2007 (Fig. 2).

Home Range Size and Overlap

During the study period, group 1 entered 94 0.25-ha quadrats whereas group 2 used 124 quadrats (Fig. 3). Six quadrats (1 for group 1 and 5 for group 2), which were bordered on each side by the quadrats visited by langurs, were never entered by any member of the focal groups, but should be included in the home ranges because the forests within them did not differ from the surrounding vegetation. There were an additional 6 quadrats (lacunae) linking isolated quadrats visited by group 2. Including these quadrats, the total home range size was 23.8 ha for group 1 and 33.8 ha for group 2. When we plotted the cumulative number of new quadrats entered by langurs with each successive month, the curve reached asymptote for group 1 and group 2 (Fig. 4), suggesting that these were accurate estimates of total home range size.
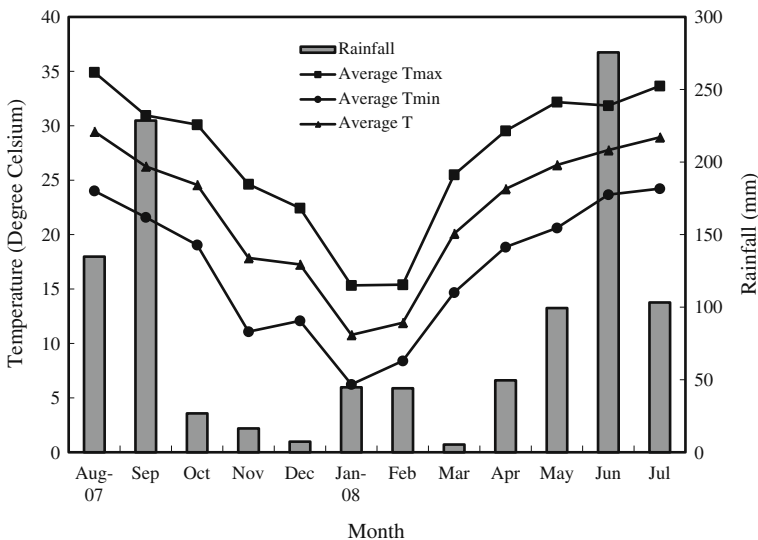

Fig. 2 Monthly mean temperature (maximum and minimum) and rainfall at Fusui Nature Reserve between August 2007 and July 2008.
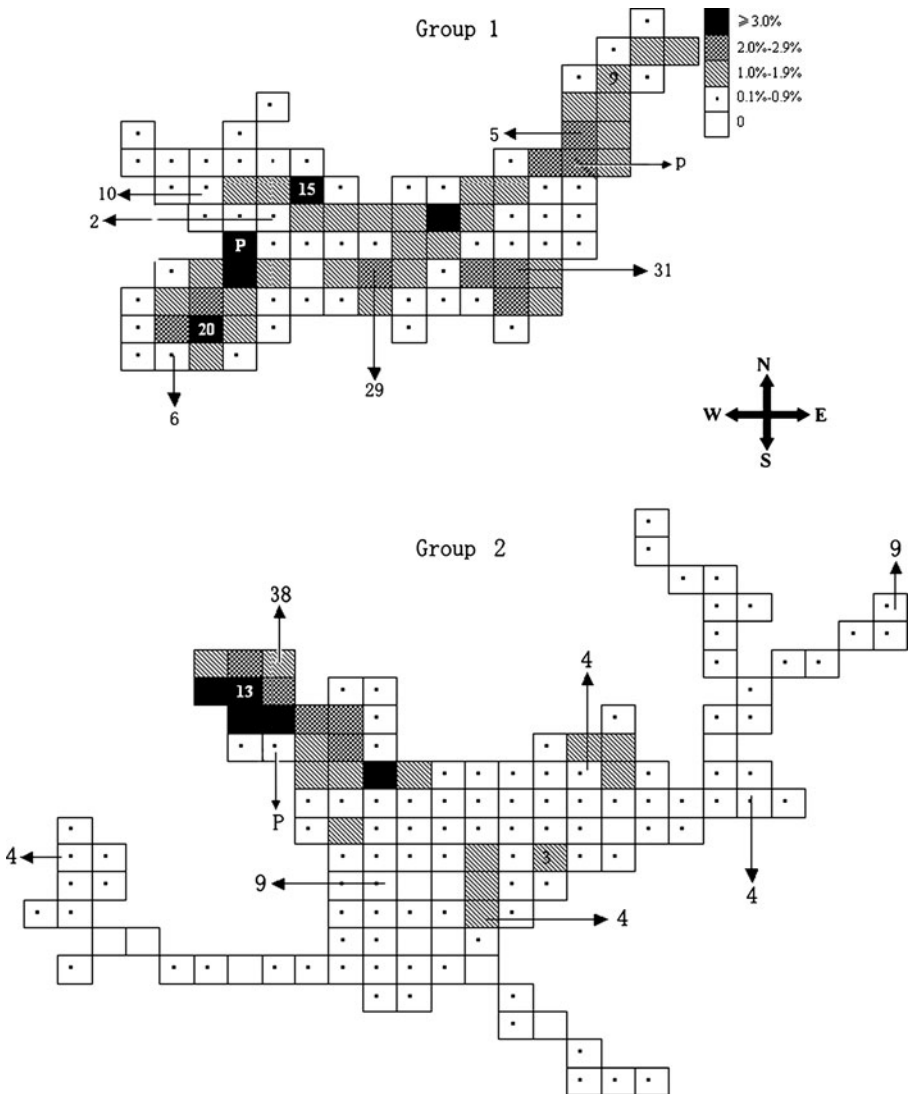
Fig. 3 Patterns of home range use and sleeping site use for the 2 focal groups at Fusui Nature Reserve. The numbers in the quadrats or behind arrows are the number of times the site was used for sleeping during the study period. *P* represents the location of permanent water pools.

The 2 groups were separated by a road and sugarcane plantations and never entered one another's home range. Group 1 shared 3.8 ha at the northwestern edge of its range with another unstudied group, which accounted for 16% of group 1's range. A 15.8-ha area (47%) of group 2's home range overlapped with that of an all-male group.

Daily Path Length

Daily path length varied widely between days in the focal groups (group 1: 270–840 m; group 2: 215–970 m). However, mean daily path length was not significantly

Fig. 4 Cumulative quadrats entered by the 2 focal groups during the study period.
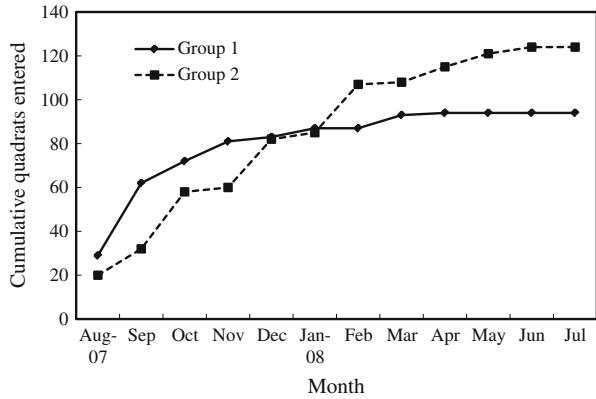
different between groups (group 1: 491±134 m, $n=54$; group 2: 512±153 m, $n=37$; $U=920.0$; $p=0.523$). Monthly mean daily path lengths varied from 300 to 616 m for group 1, and 403–970 m for group 2 (Table I). There was a significant seasonal variation in monthly mean daily path length for group 2 ($U=0.0$, $n_1=6$, $n_2=6$, $p=0.004$), which traveled farther in the rainy season months than in the dry season months, but not for group 1 ($U=14.0$, $n_1=6$, $n_2=6$, $p=0.522$).

Effect of Diet

Leaves accounted on average for 83.4% of the diet in group 1 and 91% in group 2. Young leaves were by far the most important, whereas fruit constituted a small proportion of the langurs' diet (Table II). There is no significant correlation between monthly mean daily path length and the proportion of young leaves, mature leaves, and fruits in the diet (group 1: $r_s=0.182$, $n=12$, $p=0.572$ for young leaves; $r_s=-0.014$, $p=0.966$ for mature leaves; $r_s=-0.049$, $p=0.880$ for fruit; group 2: $r_s=0.364$, $n=12$, $p=0.245$ for young leaves; $r_s=-0.430$, $p=0.163$ for mature leaves; $r_s=0.382$, $p=0.220$ for fruit). There is a significant and positive correlation between monthly mean path length and rainfall for group 2 ($r_s=0.839$, $p=0.001$), but not for group 1 ($r_s=0.267$, $p=0.401$).

Home Range Use

Monthly range size varied widely between months in the 2 focal groups (Table I), but mean monthly range size was not significantly different between groups (group 1: 32 quadrats, $n=12$; group 2: 27 quadrats, $n=12$; $U=57.0$; $p=0.386$). There was no significant seasonal variation in monthly range size (group 1: $U=11.500$, $n_1=6$, $n_2=$

Table II Annual dietary composition of the 2 focal groups at Fusui Nature Reserve (percentage of feeding records for each item)

	Young leaves	Mature leaves	Fruits	Flowers	Seeds	Other	No. of feeding records
Group 1	72.1	11.3	9.9	3.5	2.5	0.7	2072
Group 2	76.8	14.2	5.7	1.3	0.3	1.7	1250

6, $p=0.297$; group 2: $U=11.000$, $n_1=6$, $n_2=6$, $p=0.259$). Monthly range size of the study groups does not significantly correlate to either the proportion of main items in the diet (group 1: $r_s=0.186$, $n=12$, $p=0.564$ for young leaf; $r_s=-0.298$, $p=0.347$ for mature leaf; $r_s=-0.312$, $p=0.324$ for fruit; group 2: $r_s=0.211$, $n=12$, $p=0.510$ for young leaf; $r_s=-0.184$, $p=0.566$ for mature leaf; $r_s=-0.286$, $p=0.367$ for fruit) or rainfall (group 1: $r_s=0.231$, $p=0.470$; group 2: $r_s=-0.514$, $p=0.087$).

Intensity of use of quadrat varied markedly. The langurs entered many quadrats only once or twice, whereas others had 90 location records. There was a highly significant difference between observed and expected frequencies of quadrat use for both groups (group 1: $\chi^2=874.03$, $n=94$, $p<0.001$; group 2: $\chi^2=2663.04$, $n=124$, $p<0.001$), indicating that the langurs showed a preference in home range use. For group 1, 50% of location records occurred in only 19 quadrats, and 37 core quadrats together accounted for 74% of location records. For group 2, only 14 quadrats contributed to 50% of location records, and 32 core quadrats contributed to 72% of location records (Fig. 3). Moreover, the 2 focal groups showed similar seasonal trends in home range use, with increased use of the northeastern part of their home ranges in the dry season (Fig. 5).

Sleeping Sites

We observed the langurs entering their sleeping sites on 127 nights for group 1 and 88 nights for group 2. We recorded 9 sleeping sites for each group, which they used unevenly (Fig. 3). We found significant differences between the observed frequencies of sleeping sites and the frequencies expected by chance (group 1: $\chi^2=80.91$, $n=9$, $p<0.001$; group 2: $\chi^2=101$, $n=9$, $p<0.001$). The frequently used sleeping sites tended to be located either within or adjacent to the most frequently used quadrats (Fig. 3).
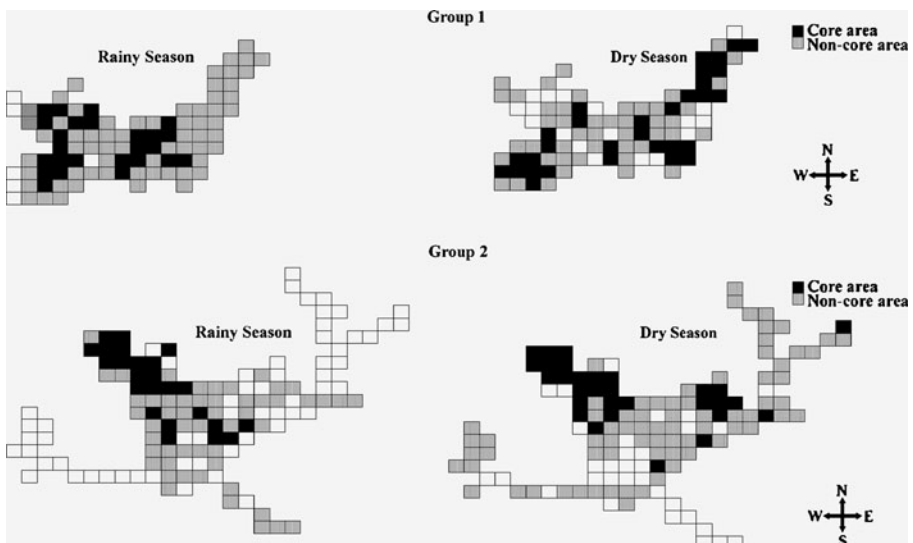

Fig. 5 Seasonal variations in home range use by the 2 focal groups.

Drinking Behavior

In the rainy season, we often observed white-headed langurs licking leaves early in the morning and sometimes observed them putting their heads into stone hollows. These stone hollows were the only places that may have contained rainwater after a downpour. In the dry season, the langurs often ventured to the foot of the hills for drinking because there are some small water pools containing permanent water. There were 2 permanent water pools in the home range of group 1 and one in group 2's home range (Fig. 3). These pools were all located in or neighboring quadrats used frequently.

Discussion

The ranging behavior of white-headed langurs at Fusui followed the typical pattern for *Trachypithecus* sp.: a small home range size and short daily path length (Table III). This pattern seems to be related to their fiber-rich foliage diet (Clutton-Brock and Harvey 1977; Yeager and Kool 2000). Leaves accounted on average for 83.4–91.0% of the annual diet of white-headed langurs at Fusui, whereas fruits contributed to only 6–10% of the annual diet. Compared to fruits, leaves are abundant and evenly distributed food resources but poor in nutrition and energy

Table III Diet, home range size, and daily path length of *Trachypithecus* sp.

Species	Percentage in diet				Home range size (ha)	Daily path length (m)	Reference
	Leaves	Fruits and seeds	Flowers	Others			
Trachypithecus auratus	50.2	32.3	13.7	4.1	5.5	550	Kool 1989[a]
T. cristatus	91	9	–	–	20	350	Bernstein 1968; Hock and Sasekumar 1979[a]
T. francoisi	52.8	31.4	7.5	7.4	69.3	541	Zhou 2005
	94.5	3.1	0.5	2.0	19	438	Zhou et al. 2007; Huang et al. 2008
T. leucocephalus	83.4–91.0	6.0–12.4	1.3–3.5	0.7–1.8	23.8–33.8	491–512	This study
	87.9	7.7	2.4	2.2	28–48	–	Li and Rogers 2005, 2006
	75.3	22.5	2.3	–	52	585	Huang 2002
T. johnii	59.4	26.3	13.4	1	24	–	Oates et al. 1980[a]
T. obscuras	58	35	7	–	33	559	Curtin 1980[a]
	48.2	47.3	4.5	–	28.5	950	MacKinnon and MaKinnon 1980[a]
T. phayrei	68.1	24.4	–	7.5	27.5	500	Stanford 1988, 1991[a]
T. pileatus	66.8	33.7	7	–	21.6	324.5	Standford 1991
T. vetulus	60	28	12	–	2–3	–	Hladik 1977[a]
Semnopithecus entellus	49.1	24.4	9.5	4	74.5	1083	Newton 1987, 1992[a]

[a] Cited in Yeager and Kool (2000).

(Richard 1985; Waterman and Kool 1994), so only a small home range and short daily path length are needed for foraging (Clutton-Brock and Harvey 1977; Yeager and Kool 2000).

In this study, group 2 had larger home range than group 1. This variation probably reflects difference in the distribution of preferred food resources in habitat. White-headed langurs preferred less common plant species as food (Li and Rogers 2006). Group 2 obtained more food from preferred plant species (65.7% of total feeding records) than group 1 did (60.9% of total feeding records, *unpubl. data*). In other words, group 1 spent more time foraging preferred foods and needed a larger area. Data on the distribution of preferred food species are needed to examine the intergroup variation in ranging behavior.

As we predicted, white-headed langurs decreased daily path lengths in the dry season months vs. the rainy season months. This may reflect the influence of seasonal dietary variation on ranging behavior. When preferred young leaves became scarcer in the dry season, white-headed langurs at Fusui consume more mature leaves (Li and Rogers 2006; Zhou *unpubl. data*). Compared to young leaves, mature leaves have more structural components— fiber and lignin— and less nitrogen content (Waterman and Kool 1994). When the langurs fed on nutrition-poor mature leaves, they may have decreased their travel distance to conserve energy. On the other hand, the langurs may not need to travel far because mature leaves are a relatively ubiquitous food resource (Richard 1985). However, there was no relationship between monthly mean daily path length and the percentage of mature leaves in the diet.

The ranging behavior of white-headed langurs at Fusui may also be influenced by seasonal water scarcity. We found a significant positive relationship between monthly mean daily path length of group 2 and rainfall. Water availability in limestone habitat is closely correlated with monthly rainfall (Huang 2002). Increased water availability may allow the langurs to be more flexible in their ranging behavior because they can obtain drinking water in various ways, such as dewdrop on leaves and rainwater in stone hollows. However, when water is scarce in the dry season, langurs' ranging behavior appears to be influenced by the locations of permanent water resources. Both study groups had ≥1 permanent small water pool in or near to their core areas in the dry season. Moreover, group 1 increased their use of areas that contained another permanent small water pool in the dry season. As long as there were no people in the vicinity, the langurs often visited these water pools to drink in the dry season. When they did so, they often showed goal-directed movement, with rapid, coordinated travel to the side of the water pool (Zhou *pers. obs.*). Thus, these water pools appear to dictate the movement of white-headed langurs in the dry season, and we suggest that water is an important resource for white-headed langurs in limestone habitat.

Our results suggest that sleeping sites play an important role in determining the ranging behavior of white-headed langurs. The 2 focal groups focused their activities on a small part of their home ranges, and frequently used sleeping sites tended to be located in or near to the most heavily used quadrats. Moreover, we found that most feeding activities of the focal groups were concentrated near the sleeping sites (Zhou *unpubl. data*). This pattern is similar to that in spider monkeys (*Ateles geoffroyi*), which use sleeping trees as central places for foraging, a behavioral strategy to

maximize economic foraging (Chapman *et al.* 1989), François' langurs (*Trachypithecus francoisi*), close phylogenetic relatives occurring in the same reserve (Zhou *et al.* 2007), and other primate species, e.g., *Macaca nemestrina*: Caldelott (1986); *Saguinus midas*: Day and Elwood (1999); and *S. fuscicollis* and *S.mystax*: Smith *et al.* (2007).

In conclusion, our results suggest that the ranging behavior of white-headed langurs is affected not only by the spatial and temporal distribution of food resources, but also by the location of sleeping sites and permanent water pools. However, habitat fragmentation has become the main influence on white-headed langur behavior at Fusui (Li 2000). Many researchers have documented that primates can respond to habitat fragmentation by decreasing the sizes of their home ranges (Onderdonk and Chapman 2000; Irwin 2006). White-headed langurs in large continuous habitat fragments occupy larger home ranges than those in small habitat fragments, suggesting white-headed langurs may adopt a similar strategy in response to habitat fragmentation (Li and Rogers 2005). However, research in continuous habitats is necessary for understanding better the influence of habitat fragmentation on the ranging behavior of white-headed langurs because researchers conducted all previous studies in fragmented habitats.

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