

## RESEARCH ARTICLE

## Influence of Day Length, Ambient Temperature, and Seasonality on Daily Travel Distance in the Yunnan Snub-Nosed Monkey at Jinsichang, Yunnan, China

REN BAOPING<sup>1</sup>, LI MING<sup>1</sup>, LONG YONGCHENG<sup>2</sup>, AND WEI FUWEN<sup>1\*</sup><sup>1</sup>Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, China<sup>2</sup>The Nature Conservancy, China Program, Kunming, Yunnan, China

This article examines the effect of ambient temperature, day length, weather conditions, and seasonality on daily path length (DPL) of a free-ranging group of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) using an auto-released GPS collar. Data were collected from December 17, 2003 to October 22, 2004 at Laojunshan in northwestern Yunnan province, China. The average DPL of the monkey group was  $909 \pm 472$  m ( $n = 291$ ), with the shortest distance being 180 m and the longest distance 3,626 m. Ambient temperature and day length were found to affect DPL. Both factors were positively correlated with DPL, which means that the monkey group traveled greater distances on longer and warmer days. At the study site, three distinct seasons were identified, and DPL did not vary significantly across these periods. The time of sunrise was not correlated with DPL. Nevertheless, we sometimes observed the group starting its daily trip later on cloudy days than on sunny days. Furthermore, weather conditions (e.g. rainy, cloudy, and sunny) did not influence the average DPL of the study group. Overall we found that the primary factors affecting DPL in *R. bieti* were day length and ambient temperature, especially daily highest temperature. *Am. J. Primatol.* 71:233–241, 2009.

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**Key words:** the Yunnan snub-nosed monkey; daily path length; ambient temperature; day length; seasonality

## INTRODUCTION

The distance a primate group travels in a day is generally a tradeoff between travel costs and energy intake. A wide variety of factors influence daily travel length in primates including food availability and distribution [Clutton-Brock, 1977; Dasilva, 1992; Isbell, 1983; Li, 2001; Ostro et al., 1999; Pages et al., 2005; Stanford, 1991; Suarez, 2006; Yamagiwa & Mwanza, 1994]; group size [Chapman & Chapman, 2000; Dias & Strier, 2003; Isbell et al., 1999; Li et al., 2005]; seasonal patterns of temperature and rainfall [Altmann & Altmann, 1970; Goodall, 1977; Li, 2001; Li et al., 2005]; astronomical sunrise (day length) [Sigg & Stolba, 1981]; and human activities such as habitat disturbance and hunting [Kirkpatrick et al., 1998; Li et al., 2005].

It has been argued that owing to increased dietary needs, primates residing in larger groups travel farther than primates living in smaller groups [Chapman, 1990; Isbell et al., 1999; but see Sussman & Garber, 2007 for an alternative perspective]. However, studies in several species of folivorous primates fail to support this contention. In these primates, daily travel distances do not vary with group size [e.g. *Brachyteles arachnoides hypoxanthus*, Dias & Strier, 2003; *Procolobus badius*,

Isbell, 1983; *Rhinopithecus roxellana*, Li et al., 2005]. Although heavy rain may temporarily stop a primate group's movement, rainfall is not directly correlated with daily travel length [Altmann & Altmann, 1970; Goodall, 1977]. Daily travel length can be affected by seasonal changes in the availability and distribution of resources and thermoregulatory requirements associated with extremes in temperature [Hall, 1962; Kirkpatrick et al., 1998; Li, 2001; Stoltz & Saayman, 1970]. For example, a group of chacma baboon (*Papio ursinus*) traveled farther in winter than in summer [Hall, 1962]. It was argued

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\*Correspondence to: Wei Fuwen, Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, China.  
E-mail: weifw@ioz.ac.cn

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that increased travel was directly related to the more abundant food supply in summer. In another group of this species in the northern Transvaal, despite seasonal differences in air temperature, daily travel distance did not vary markedly between summer and winter [Stoltz & Saayman, 1970]. In contrast, snub-nosed monkeys (*Rhinopithecus* spp.) were found to travel greater distances in warmer months [Kirkpatrick et al., 1998; Li, 2001], which suggests that ambient temperature may affect daily path length (DPL).

In environments with marked seasonal differences in day length, diurnal primates may need to modify their activity pattern in order to have sufficient time to accomplish social and maintenance activity. In this regard, day length has been found to influence activity scheduling and habitat choice in chacma baboons [*P. ursinus*, Hill et al., 2003]. For example, these baboons spent more time in feeding, moving, and resting on longer days than they did on shorter days. Given the results of these previous studies, the effect and relative importance of environmental temperature (rather than group size, food availability, and rainfall) on DPL of folivorous primates remain unclear and require further investigation.

Yunnan snub-nosed monkeys (*R. bieti*) are confined to a narrow habitat in the Yunling Mountains between the Yangtze River to the east and the Mekong River to the west [Long et al., 1994]. The extreme ecological conditions associated with high altitude (3,000–4,500 m asl) and cold temperatures (−13~−16.2°C) may have led to important changes in social behavior and patterns of habitat exploitation. For example, Yunnan snub-nosed monkeys live in large “nested” or multilevel social groups of 100–200 individuals [Grueter & Zinner, 2004]. These primates occupy a larger home range [ $> 20 \text{ km}^2$ , Kirkpatrick et al., 1998] and have a larger group than do most other Asian colobines [most colobines have home ranges of  $< 1 \text{ km}^2$  with *Presbytis entellus* occupying the largest home range of  $12 \text{ km}^2$ , Bennett & Davies, 1994].

Lichens [especially *Bryoria* spp., Kirkpatrick, 1996] and bamboo leaves [*Fargesia* spp., Yang & Zhao, 2001], both ubiquitous and nonseasonal resources, dominate the diet of *R. bieti*. Food supply appears to play only a minor role in the ranging behavior of *R. bieti* because lichens and bamboo leaves were found not to be depleted after the group left each feeding site [Kirkpatrick, 1996]. In addition, most natural groups of *R. bieti* remain spatially isolated from each other [Long et al., 1994], and intergroup interactions are extremely rare. Thus, aspects of territorial behavior and range defense, which characterize many primate species, have virtually no influence on the daily travel pattern of *R. bieti*.

Published data on daily travel distances of wild groups of *R. bieti* are scarce, and sample sizes are

limited [Kirkpatrick, 1996; Liu et al., 2004] owing to the difficulty of locating the monkeys in the field [Wu, 1991]. For this study, we employed GPS collar technology to monitor a free-ranging group of *R. bieti* on Laojunshan Mountain, Yunnan Province from December 2003 to October 2004. The main goal of this study was to investigate the impact of ambient temperature, day length, weather conditions, and seasonality on DPL across an annual cycle.

## METHODS

### Study Site

The study area, Jinsichang (26°53'N, 99°37'E), lies approximately 80 km to the northwest of Lijiang city in the Yunnan province of China. The site represents an area of  $280 \text{ km}^2$  and is not located within a natural reserve. The study group (170–180 individuals) remained within the Jinsichang site throughout the entire study period of December 17, 2003 to October 23, 2004.

Three forest types are found along an elevation gradient ascending from 3,000 to 3,900 m asl: (1) deciduous broad leaf forest; (2) mixed coniferous and broad leaf forest; and (3) coniferous forest. Dense bamboo (*Fargesia* spp.) and *Rhododendron* spp. are scattered between 2,900 and 3,900 m in the area [Yang, 2000]. The mean annual ambient temperature during the study period was 5.8°C, ranging from −13°C in February 2004 to 20°C in July 2004. Snow covered the ground from November to April.

### Environmental Data Collection

Ambient temperature was measured and recorded with a kerosene minimum–maximum thermometer (LX-198, China Lanxi, made in Changzhou city, Jiangsu province) at our field camp (3,280 m asl.). The thermometer recorded highest ( $T_h$ ) and lowest ( $T_l$ ) temperatures each day, with data recorded each morning before the instrument was re-set by a magnet. The daily mean temperature ( $T$ ) was calculated as  $(T_h + T_l)/2$ .

Era Shuttle<sup>®</sup> calendar (Wuhan, Hubei Province, China), free software owned by Liu Anguo in 2005, supplied the daily times of sunrise and sunset. Day length was calculated as the interval between sunrise and sunset in hours. Day length (mean:  $12.3 \pm 1.1$  hr,  $N = 291$ ) varied seasonally from a minimum of 10.5 hr in December to a maximum of 13.8 hr in June (one-way ANOVA:  $F_{2,291} = 248.607$ ,  $P = 0.000$ ). Daily mean ambient temperature and day length during the study period are illustrated in Figure 1.

Weather conditions were recorded each day to test their influence on DPL. Descriptors used to record weather conditions were sunny, cloudy, light rain (including minimal snow), and heavy rain (or snowstorms). These were ranked (sunny = 4, heavy rain = 1) and Spearman's correlation rank tests were

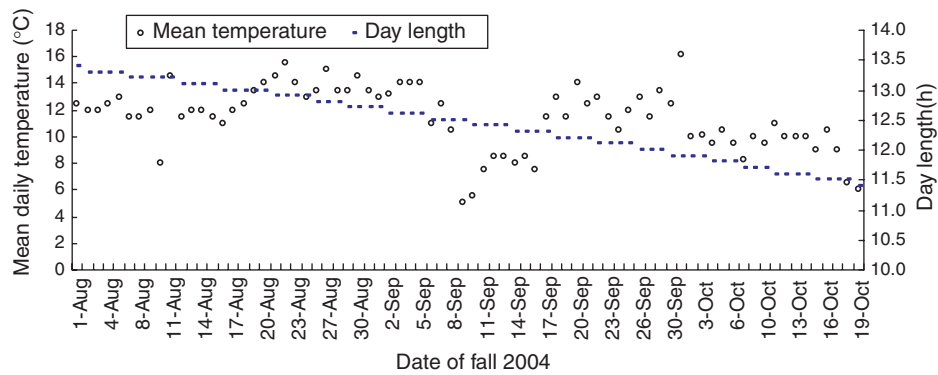


Fig. 1. Changes in mean daily ambient temperature (range:  $-7.0\sim 20^{\circ}\text{C}$ ) and day length (range: 10.5~13.8 hr) at Jinsichang from December 17, 2003 to October 19, 2004.

used to detect a correlation between DPL and weather conditions. Principal component analysis was used to detect possible interactions among ambient temperature ( $T_h$ ,  $T_1$ , and  $T$ ), day length, and weather conditions on DPL.

In order to test our intuitive impression that waking time and morning foraging were influenced by sunlight, we recorded whether or not there was sunshine or cloud cover in the early morning. These data were used to investigate whether the group began its daily travel later on cloudy days, and if so, whether the combined influence of time of sunrise and degree of cloud cover were important factors in DPL.

### DPL Calculation

A store-on-board GPS collar (TGW-3580, Tenolics Com. Ltd., Arizona; gross weight: 890 g) with a five-site positioning schedule was fitted on a healthy adult male in the group on December 17, 2003. The five-site positioning schedule limits the maximum number of recorded positions to five each day (range: 0–5). An adult male *R. bieti* typically weighs more than 30 kg [Bai et al., 1987], so the gross weight of the collar was below the 5% tolerable weight limit suggested for primates [Gursky, 1998]. An auto-release function was added to the collar to free the monkey after monitoring was completed. The collar automatically released on the preprogrammed date of October 22, 2004. A detailed description of capture and release to fit the GPS collar, the group positioning schedule, parameters stored on the collar, manipulation of GPS fixes, and setting of the GPS dilution of precision (DOP) values is available elsewhere [Ren et al., 2008]. The collar was retrieved on October 24, 2004 and the positional data were downloaded into ArcView3.2a (ESRI, Redlands, CA) Geographic Information System. Two officials from the Forestry Bureau of Yulong County as the third party, entrusted by the State Bureau of Forestry of China, supervised the process of marking the monkeys. This research complied with the legal

requirements for ethical animal research in the Laojunshan area of China.

A map (1:50,000) of the study area was digitized on the ArcView3.2a platform. A SPOT5 satellite image taken in November 2004 (60 × 60 km, resolution: 2.5 m) unified the geo-reference of subjects using the projection of WGS\_1984\_UTM\_ZONE\_47N. Accordingly, all GPS positions were converted from latitude–longitude to UTM map coordinates. Only the GPS fixes with DOP value  $\leq 6$  were used to calculate DPL in this study.

The DPL was calculated by the Animal Movement Extension V.1.1 [Hooge & Eichenlaub, 1997] in ArcView 3.2a. The data were then imported into Microsoft Excel<sup>®</sup> (Microsoft Corporation, Washington), and statistical analyses were performed in SPSS 13. We obtained four types of daily travel distances: 2-site displacements, and 3-, 4-, and 5-site summed distances. Because 2-site displacements were significantly shorter than the multisite distances (3-, 4-, and 5-site distances) [Ren et al., 2008], DPL was calculated using only days on which more than two positions were fixed by the collar. The 2-site displacement data were not used in the calculation of daily travel distance. As no significant differences were detected among the three types of summed distances [Ren et al., 2008], the multisite distances were integrated into a single variable. Regression (curve estimation) was used to examine relationships between DPL and day length, and between DPL and ambient temperature ( $T_h$ ,  $T_1$ , and  $T$ ). Daily travel distances (in meters) were displayed as means  $\pm$  standard deviations. Minimum level of significance was set at 5% and all statistical tests were two-tailed.

### Classification of Jinsichang Seasons

Seasons classified using daily mean temperatures ( $T$ ) [Zhang, 1934] in mainland China are as follows:  $T \geq 22^{\circ}\text{C}$  was scored as summer,  $T \leq 10^{\circ}\text{C}$  was scored as winter, and  $10^{\circ}\text{C} < T < 22^{\circ}\text{C}$  spring and autumn. In this study, we adopted Zhang's classifica-

tion to divide seasons at Jinsichang into spring (May to July), autumn (August to October), and winter (November to April). Summer temperatures are absent at Jinsichang. These seasonal classifications are consistent with descriptions of 4–6 months of snow cover [Xiao et al., 2003] in the monkey's habitat (November to April at Jinsichang). Therefore, the local three-season model is considered more suitable for interpreting seasonal changes in the ranging patterns of *R. bieti* than a four-season model. To facilitate comparison with other researchers [Kirkpatrick et al., 1998; Liu & Zhao, 2004; Liu et al., 2004], however, the data are examined using both the three-season and the four-season models.

## RESULTS

### Multipoint Summed DPL and its Seasonality

Annual mean DPL of the monkey group was  $909 \pm 472$  m (mean  $\pm$  S.D.,  $n = 291$ ). The DPL ranged from 180 to 3,626 m. Seasonal mean DPLs for both models are listed in Table I. Seasonal DPLs showed significant differences using a four-season model (one-way ANOVA:  $P = 0.035$ ) but not using a three-season model (one-way ANOVA:  $P = 0.076$ ). With the exception of summer, mean DPLs of the same season did not differ significantly for either model (independent sample  $T$  test:  $P > 0.1$ ). Given that seasonality, as defined by ambient temperature did not influence DPL using the locally appropriate three-season model, we conclude that DPL of our study group was nonseasonal.

### Monthly DPL Variations of the Jinsichang Group

Monthly mean DPL of the Jinsichang group varied significantly (one-way ANOVA test:  $F_{10,290} = 3.155$ ,  $P = 0.001$ , two-tailed). A post hoc test showed that mean DPLs in January, April, and June of 2004 were responsible for this significant result (Dunnett  $T_3$  test: January mean/April mean,  $P = 0.014$ ; January mean/June mean,  $P = 0.003$ ; no significant difference between the June/April means). The monthly mean DPL for January 2004 represented the shortest distance the group covered

throughout the study period. Mean DPLs in April and June were neither the shortest nor the longest distances compared with other monthly mean DPLs (Table II, Fig. 2). The causes of this statistical difference are discussed below.

No significant correlation was found between monthly mean DPLs and monthly mean  $T_h$  (Pearson correlation:  $r = 0.089$ ,  $N = 11$ ,  $P = 0.796$ ), between monthly mean DPLs and monthly mean  $T_l$  (Pearson correlation:  $r = 0.112$ ,  $N = 11$ ,  $P = 0.744$ ) or between monthly mean DPLs and day length (Pearson correlation:  $r = -0.036$ ,  $N = 11$ ,  $P = 0.917$ ). Thus, monthly mean temperature and monthly mean day length appear not to be suitable or sensitive measures influencing monthly DPL.

### Influences of Ambient Temperatures and Day Lengths on DPL Day to Day

Daily mean ambient temperatures significantly affected the DPL of the study group (Pearson correlation:  $r = 0.165$ ,  $N = 291$ ,  $P = 0.005$ , two-tailed): the group traveled farther on warmer days and shorter distances on colder days (Fig. 3). The daily highest temperatures ( $T_h$ , Pearson correlation:  $r = 0.141$ ,  $N = 291$ ,  $P = 0.016$ , two-tailed) and the daily lowest temperatures ( $T_l$ , Pearson correlation test:  $r = 0.168$ ,  $N = 291$ ,  $P = 0.004$ , two-tailed) showed the same positive correlations with DPL so did daily ambient temperatures ( $T$ ).  $T_h$ , however, contributed more strongly (eigenvalue: 76.6%) than the other two temperature measures ( $T$  and  $T_l$ , sum eigenvalues: 21.4%) to longer DPLs (principal component analysis, abbreviated as PCA test later).

Day length at Jinsichang was found to significantly influence the DPL of the monkey group (Pearson correlation:  $r = 0.121$ ,  $N = 291$ ,  $P = 0.039$ , two-tailed). Our study group traveled farther on longer days than on shorter days. This positive correlation between day length and DPL is illustrated in Figure 4. Temperature was found to play a more important role in influencing the group's DPL than did day length: the group reduced its DPL on colder days when day length was longer than the annual mean ( $12.3 \pm 1.1$  hr). A PCA test showed that temperature together with  $T_l$ ,  $T_h$ , and  $T$  contributed

TABLE I. Average Daily Path Lengths (Mean  $\pm$  SD in Meters) of the Study Group by Season

Seasons	Three-season DPL		Four-season DPL*		Independent sample $T$ test	
	Mean DPL	$N$	Mean DPL	$N$	$P$ -value	df
Spring	$931 \pm 435$	81	$870 \pm 385$	88	0.190 ( $t = 1.315$ )	167
Summer	–	–	$1,023 \pm 542^{**}$	81	–	–
Autumn	$997 \pm 520$	76	$940 \pm 384$	47	0.759 ( $t = -0.307$ )	155
Winter	$847 \pm 460$	134	$814 \pm 514$	75	0.569 ( $t = 0.571$ )	213

Three seasons: spring, May to July; autumn, August to October; winter, November to April. Four-seasons style: spring, December to February; summer, March to May; autumn, June to August; winter, September to November. \* $P < 0.05$  of one-way ANOVA test. \*\*Significant difference detected because of summer ( $P = 0.035$ ).

98% influence on DPL whereas day length contributed only 2% influence.

There was no significant correlation between weather conditions and DPLs (Spearman correlation rank test:  $r_s = 0.110$ ,  $N = 291$ ,  $P = 0.060$ ). DPL did not vary among sunny, cloudy, or rainy days, including days of heavy precipitation (one-way ANOVA:  $F_{3, 290} = 0.758$ ,  $P = 0.518$ ). We observed several times during the GPS collar-positioning period that the monkeys halted their movement when it rained heavily. After the rain stopped, however, the group continued on its route. Similarly, the one snowstorm we observed did not stop group movement. On December 29, 2003, it snowed heavily for 4 hr (9:00–13:20) and the ambient temperature was 1°C. However, the group traveled 1,111 m that day and 1,226 m the following day (December 30, 2004) when it was sunny and the temperature

increased to 3°C. December 28, 2003 was cloudy and the monkeys traveled 726 m. Finally, the group traveled 669 m on December 31, 2003, a sunny day. The GPS collar recorded the full five points on each of these 4 days. DPL on the snowstorm day (December 29, 2003) was significantly greater than the mean DPL for the other days (December 28 and 31, 2003) (Chi-square test:  $\chi^2 = 138.403$ ,  $df. = 2$ ,  $P = 0.000$ ).

Although a significant negative correlation was detected between  $T$  and weather conditions (Spearman correlation rank test:  $r_s = -0.481$ ,  $N = 291$ ,  $P = 0.000$ ), weather conditions did not exert a strong influence on DPL of the study group (eigenvalue:  $-0.616$ , PCA test). Finally, the presence or absence of morning sunlight did not have an influence on DPL (Spearman correlation rank test:  $r_s = 0.040$ ,  $N = 291$ ,  $P = 0.494$ ). During the study period, sunrise was visible in the morning on 95 days and the sun was obscured by cloud cover on 196 days. Time of sunrise on sunny days did not influence DPLs (independent sample  $T$  test:  $t = -0.070$ ,  $df. = 289$ ,  $P = 0.944$ ).

**TABLE II. Monthly Variation in Mean DPL (m) of the Jinsichang Group (Annual Mean DPL:  $909 \pm 472$  m)**

Month	N	Mean	S.D.	Minimum	Maximum
Dec <sup>a</sup>	15	1,149	803	546	3,626
Jan	31	625	235	310	1,342
Feb	29	842	463	249	2,594
Mar	31	820	363	203	1,758
Apr	28	964	393	324	2,155
May	29	832	397	180	2,024
Jun	26	1,137	518	365	2,614
Jul	26	835	307	484	1,663
Aug	29	1,089	683	359	3,271
Sep	29	911	376	280	1,764
Oct	18	986	401	353	1,961
Annual	291	909	472	180	3,626

<sup>a</sup>December of 2003, all other months were in 2004.

**DISCUSSION**

**Absence of Seasonal Variation in DPL**

Our results show that despite living in a cold, high altitude habitat, the Jinsichang group of *R. bieti* exhibited a ranging pattern in which DPL did not vary significantly across the three locally recognized seasons of the year. Our results using the locally appropriate three-season model were not consistent when we analyzed the data using a four-season model. During the year of our study, local temperatures did not reach summer levels during those months typically classified as summer in other parts

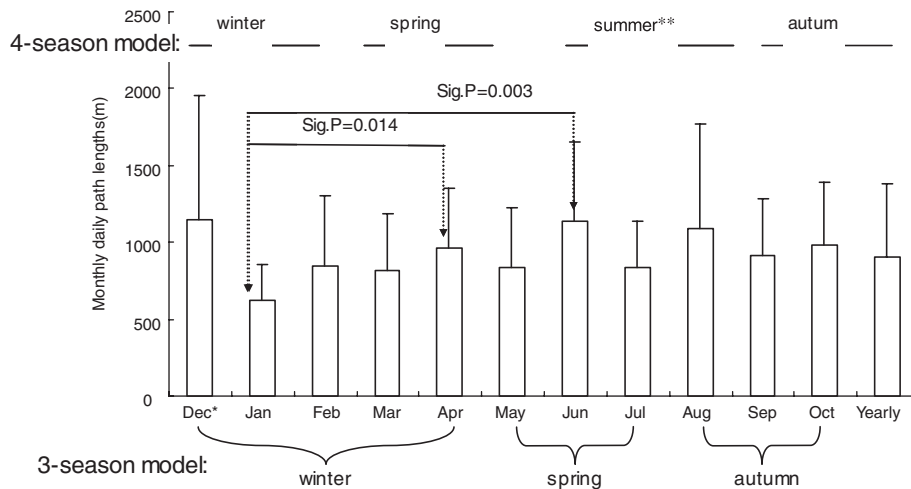


Fig. 2. Monthly daily path length (+SEM) of the study group from December 2003 to October 2004. The presence of a significantly different pattern was owing to differences in monthly mean DPL between January vs. April and June (Dunnnett’s  $T_3$  test). \*December of 2003. \*\*Significant seasonal variation detected in the four-season model was owing to values recorded for the season, summer (one-way ANOVA test:  $P = 0.035$ ). No significant difference was found in the three-season model.

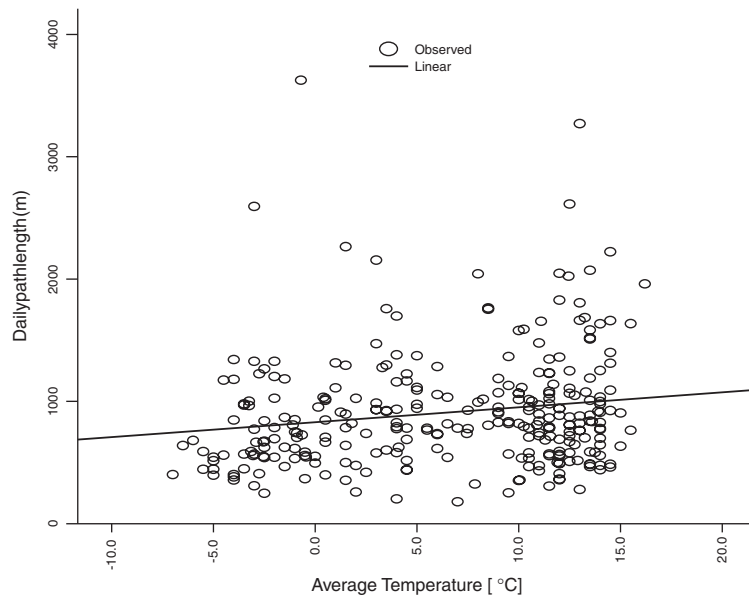


Fig. 3. Correlation between daily path length and daily average temperature at Jinsichang site from December 17, 2003 to October 19, 2004 (Pearson correlation:  $r = 0.165$ ,  $N = 291$ ,  $P = 0.005$ ).

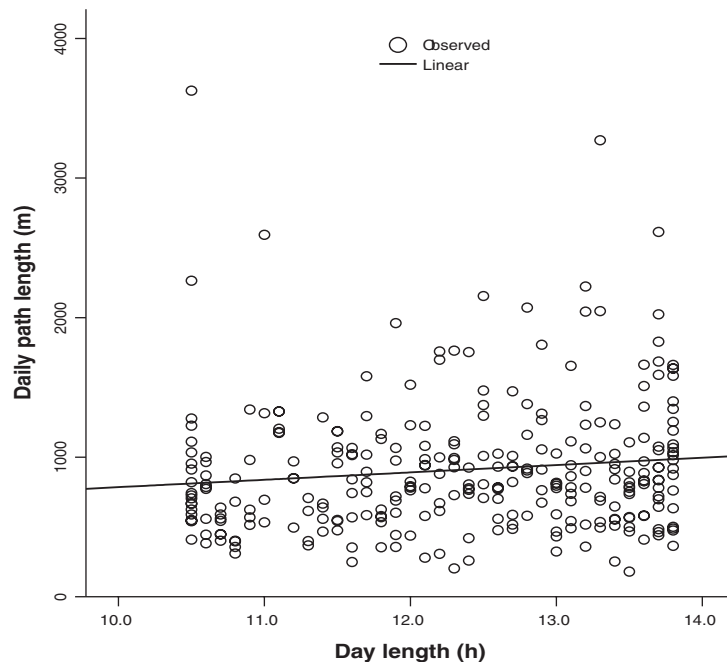


Fig. 4. Correlation between daily path length of the study group and day length at Jinsichang study site from December 17, 2003 to October 19, 2004 (Pearson correlation:  $r = 0.121$ ,  $N = 291$ ,  $P = 0.039$ ).

of China. No statistical differences were detected between DPLs in the three-season and the four-season models except when we included summer DPL (Table I). Thus, we feel that our data strongly support the contention that DPL in *R. bieti* was nonseasonal.

The two ubiquitous food sources primarily consumed by *R. bieti*, lichen [especially Ding & Zhao, 2004; *Usnea longissima*, Kirkpatrick et al., 1998;

Xiang et al., 2007] and bamboo leaves [*F. tenuilgenae*, Yang & Zhao, 2001], are characterized by a nonseasonal pattern of distribution and availability. This appears to have minimized the effects of seasonal food availability as a critical factor in affecting DPL. The January monthly DPL was significantly different from the mean DPL in April and in June of 2004, whereas the latter two did not differ significantly from the annual mean DPL. Furthermore, the shortest

monthly mean DPL occurred in January 2004, the coldest month of the study period. This suggests that cold temperatures may constrain *Rhinopithecus* movement patterns. The significantly different mean DPLs in April and June of 2004 from that of January are more difficult to explain. April is a time of seasonal change (from winter to spring) with temperature increasing. Thus, our study group tended to travel greater distances during these warmer months compared with the coldest month (January 2004). Bamboo shoots were sprouting abundantly during June 2004, and the group was observed feeding heavily on them. Competition for bamboo shoots between individuals in our study group was rarely observed [Ren et al., unpublished data]. Given the abundant and relative uniform distribution of bamboo shoots across the study groups' home range, we conclude that DPL in *Rhinopithecus* was not strongly influenced to the availability of this preferred food resource.

### Environmental Factors Impacting DPL of the Study Group

Low temperatures dominate the high-altitude montane habitat [Kirkpatrick et al., 1998; Long et al., 1994] of *R. bieti* during most of the year. Lower temperatures appear to be an important ecological constraint on the ranging behavior of *R. bieti*. To date, however, low temperatures only have been discussed in terms of sleeping site selection for this species [Liu and Zhao, 2004]. Our results show that low temperatures have a strong impact on the monkey's daily ranging patterns. Ambient temperature, especially highest daily temperature, is the main factor influencing DPL: the monkey traveled farther on warmer days [Kirkpatrick et al., 1998] and shorter distances on colder days. In contrast, a group of chacma baboons (*P. ursinus*) were found to travel greater distances on cooler days than on warmer days [Stoltz and Saayman, 1970]. The open savannah environment of the chacma baboon, in which high daytime temperatures reach almost 30°C [Hill, 2006] are likely to play a critical role in influencing both the timing and extent of baboon daily activity. *R. bieti* showed an opposite response to cold ambient temperature and traveled greater distances during warmer days. However, in the environment of this Asian colobine, the warmest daily temperatures are less than 20°C.

Struhsaker [1975] reported a positive correlation between monthly mean DPL and monthly rainfall in *Colobus badius tephrosceles*. In *R. roxellana*, however, DPL was negatively correlated with percentage of time it rained or snowed in winter and spring [Li et al., 2005]. The study on *R. roxellana* showed a relationship between weather conditions and DPL per se but not between rainfall and DPL. In that study, rain or snow in winter and spring were associated with a marked decrease

in environmental temperature, which affected *Rhinopithecus* activity patterns. Although we did not collect data on daily rainfall (daily weather conditions were only descriptively recorded), qualitatively it is our impression that snowy or rainy conditions did not influence DPL in *R. bieti* in our study.

### Comparison of DPL in the Yunnan Snub-Nosed Monkey

Kirkpatrick [1996] conducted a systematic field investigation of *R. bieti* behavioral ecology in at Wuyapiya, which is a strongly seasonal habitat in the northern region of the monkey's distribution. He states that 1,310 m is the longest DPL recorded in previous studies, but argued that 1,590 m is a more appropriate annual mean DPL estimate [Kirkpatrick et al., 1998]. Subsequently, a mean DPL of 2.1 km has been recorded for a group of *R. roxellana* in the Qinling Mountains [Tan et al., 2007].

In contrast, our data show that the annual mean DPL of the Jinsichang group of *R. bieti* is the shortest so far recorded. The Wuyapuya *R. beiti* group studied by Kirkpatrick et al. [1998] traveled to higher elevations (up to 4,300 m) in severely colder ambient temperatures than our study group. Moreover, the Wuyapuya group was not tracked during in the coldest months of the year [Kirkpatrick et al., 1998], and therefore DPL values may represent maximum values. The long DPL of *R. roxellana* in Qinling is not consistent with our hypothesis that cold temperatures constrain *Rhinopithecus* travel. However, the Qinling group inhabits an area characterized by extensive anthropogenic habitat fragmentation that began in 1996 [Li et al., 1999; Tan et al., 2007]. Habitat fragmentation may lengthen DPL in some primate groups [Li et al., 2005; Umapathy & Kumar, 2000] owing to the fact that individuals suffered a reduction in food availability and needed to exploit a larger area to meet their basal daily energy intake. The Jinsichang group of our study, occupied a primary and unfragmented habitat, and was found to travel relatively short daily distances (<1,000 m).

A study of activity budget has shown that *R. bieti* groups spend most of their daily time resting (39%) and feeding (35%), with 10% of time spent traveling and 16% of time engaged in other activities [Long et al., 1998]. Although *R. bieti* devotes less time to rest per day than do other colobines [e.g. *C. polykomos*: 61%, Dasilva, 1992; *C. guereza*: 57% time for rest, Oates, 1977; *Trachypithecus francoisi*: 52% Zhou et al., 2007], their overall activity budget is consistent with a low-energy strategy [relatively short DPL, 10% time moving] [Bennett & Davies, 1994].

### Short DPLs in Winter

Several previous studies of *R. bieti* and *R. roxellana* groups [Grueter et al., 2008; Kirkpatrick et al., 1998; Li, 2001; Liu et al., 2004] have found that the shortest mean DPL occurred during winter. This study supports these results. The factors influencing this apparent season-based ranging pattern of *Rhinopithecus* spp. are complex. Studies of *R. roxellana* have argued that the short winter DPL was owing to a critical decrease in food availability and shorter day length than in other seasons [Li, 2001]. Further research showed that winter snow or rain also may be contributing factors [Li et al., 2005]. This interpretation is not consistent with the results of this study of *R. bieti*. We argue that low ambient temperature in winter is the main factor constraining DPL, with increased DPL during warmer days. We found in this study that long but cold days led to shorter travel distances, and short cold days reduced DPL even further. Long DPLs in winter can therefore be attributed to occasionally warmer days.

As ambient temperature influences DPL in *R. bieti*, it also must affect the monkey's daily activity budget. A group of *R. bieti* was found to spend more time resting on southwardly facing slopes during its daily siesta in winter [Liu & Zhao, 2004]. Sunning is a strategy used by monkeys to keep warm on cold days. Huddling has been observed in natural *R. bieti* groups. This behavior occurs throughout the year, however, and distinctions between the social function of huddling and the thermoregulatory function of huddling in *R. bieti* remain unclear. Given that *Rhinopithecus* reduced its DPL on coldest days, further studies need to examine the physiological, social, and behavioral mechanisms used by these primates to thermoregulate during cold periods of the year.

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