



Ranging of *Rhinopithecus bieti* in the Samage Forest, China. I. Characteristics of Range Use

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Abstract We quantified the home range and explored the style of ranging of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) in the subtropical-temperate montane Samage Forest (part of Baimaxueshan Nature Reserve) in the vicinity of Gehuaqing. Over 14.5 mo, we took positional records of the study band via a GPS receiver at 30-min intervals, and found that they covered an area of 32 km². Over a 10-yr period, the group even ranged in an area of 56 km², which is among the largest home range estimates for any primate. The large home range was probably due to the combined effects of large group size ($N > 400$) and forest heterogeneity, with seasonally food-rich areas interspersed with less valuable areas. The subjects did not use their home range uniformly: 29% of the grid cells had more location records than expected based on a uniform distribution, thus representing a core area, albeit a disjunct one. A continuous 1-mo group follow in the fall revealed that the band traveled on average 1.62 km/d and that days of concentrated use of a particular forest block were followed by more extensive marches. Neither climate nor human disturbance parameters correlate significantly with monthly estimates of the group's home range size. Even though there is no significant correlation between temporal availability of plant phenophases and range size, our observations implicate temporal and spatial availability of food as a determinant of home range use of the focal group. Winter,

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spring, and summer home ranges are equally large: 18.2, 17.8, and 18.6 km², respectively. Home range decreased markedly in fall (9.3 km²), probably because the band obtained sufficient food resources (fruit) in a smaller area. The large winter range is best attributed to the exploitation of dispersed clumped patches of mature fruits.

Keywords Colobinae · home range · *Rhinopithecus* · temperate environment · Yunnan

Introduction

Range use in Colobinae and other Primates is determined by an assortment of eco-behavioral factors, including precipitation (McKey and Waterman 1982; Raemaekers 1980), temperature (Yang 2003), the quality, availability, and distribution in time and space of food (Agetsuma and Noma 1995; Barton *et al.* 1992; Bennett 1986; Clutton-Brock 1975; Curtin 1982; Fleury and Gautier-Hion 1999; Pages *et al.* 2005; Zhang 1995), group size (Fashing *et al.* 2007b; Ganas and Robbins 2005; Strier 1987), sleeping site or resting site location (Davies 1984; Liu *et al.* 2004; Rasmussen 1979; Zhou *et al.* 2007; Zinner *et al.* 2001), proximity of conspecific groups (Fashing 2001; Struhsaker 1974; Waser 1976), predation pressure (Boinski *et al.* 2000; Treves 2002), anthropogenic disturbance (Li *et al.* 1999, 2005), polyspecific associations (Holenweg *et al.* 1996), and day length (Li 2002). Researchers have long known that colobines have shorter daily path lengths and smaller home ranges than those of most other primates (Chapman and Chapman 2000). The typically small range sizes and short daily travel distances of many colobines may be caused by energetic constraints attributable to their specialized digestive tracts and relatively folivorous diets, and their dependence on uniformly distributed and ubiquitous food resources (Kay and Davies 1994).

Nevertheless, colobines exhibit a tremendous variety of ranging styles: on the one extreme, some populations of guerezas (*Colobus guereza*; Schenkel and Schenkel-Hulliger 1967; Leskes and Acheson 1971) and purple-faced langurs (*Trachypithecus vetulus*) occupy very small home ranges and are almost stationary (Hladik 1977), whereas populations of Angolan colobus (*Colobus angolensis*) in Rwanda (Fashing *et al.* 2007b), black colobus (*Colobus satanas*) in Gabon (Fleury and Gautier-Hion 1999), and black-and-white snub-nosed monkeys (*Rhinopithecus bieti*; Kirkpatrick *et al.* 1998) occupy vast areas, show long-term range expansions, and are seminomadic.

The question arises as to why some colobines exhibit large home ranges and even are semimigratory. It is not simply that large range sizes are a feature of colobines in resource-poor environments such as temperate forests, even though this is demonstrated by some species including pale-armed Himalayan langurs (*Semnopithecus schistaceus*) and *Rhinopithecus bieti* (Curtin 1975; Kirkpatrick *et al.* 1998). *Colobus angolensis* at Nyungwe and *C. satanas* in the Forêt des Abeilles follow a comparable strategy, but live in more productive tropical habitats, i.e., in montane mixed moist forests and lowland moist forests, respectively (Fashing *et al.* 2007b; Fleury and Gautier-Hion 1999). The large ranges in *Colobus satanas* are assumed to be caused by the irregular fruiting of the Caesalpinaceae, an essential food source (Fleury and Gautier-Hion 1999). Based on established socioecological theory (van Schaik *et al.* 1983), we should expect larger groups to occupy larger home ranges to satisfy their energy requirements. In Nyungwe, it is probably the very large group sizes of >300 that necessitate such

wide ranges (Fashing *et al.* 2007b). Kirkpatrick *et al.* (1998) considered lichens to be a critical factor influencing ranging of a band of *Rhinopithecus bieti* in an alpine-temperate and very seasonal forest in North Yunnan, China: they argued that, because lichens replenish very slowly, monkeys need to forage nomadically to allow lichen-depleted patches to recover to a harvestable level between visits. Further, they hypothesized that the “readily digestible energy in lichens may release *R. bieti* from the short travel distances associated with leaf-eating (Kirkpatrick *et al.* 1998, p.40).”

Black-and-white snub-nosed monkeys (golden monkeys) are characterized by behavioral and ecological strategies that differ in many respects from those of other colobines, the aforementioned large ranges being just one of them. They live at the upper limit of elevation (≤ 4700 m) and latitude for any nonhuman primate and inhabit subtropical-temperate or purely temperate forests (Long *et al.* 1994). Their use of food resources reaches an extreme in some populations that rely almost exclusively on tree lichens (Kirkpatrick 1996); however, other populations in more productive environments have a more diversified diet largely molded by phenology. Moreover, groups of *Rhinopithecus bieti* are invariably large and can contain up to several hundred members (Grüter and Zinner 2004).

Only *ca.* 17 groups of *Rhinopithecus bieti* remain in the wild (Long and Wu 2006), and only a few of them are suitable for obtaining an unbiased estimate of their range use. Some groups are restricted to forest islands in a sea of farmland/grazing land (Xiao *et al.* 2003) and thus are no longer able to exhibit a natural ranging pattern. One group is regularly herded by humans for tourist viewing, thus obscuring natural ranging tendencies (Grüter 2004), and others are so elusive that even a long-term study does not permit more than a handful of sightings (Yang 2000). To overcome the last problem, other researchers investigated the distribution of feces as evidence of the ranging of snub-nosed monkeys (Cui 2003) or used global positioning system (GPS) collars to track them (Ren *et al.* 2004). We directly followed a single band of *Rhinopithecus bieti* for a prolonged period spanning >1 yr.

We aimed to characterize the spacing system of *Rhinopithecus bieti* at a locality in the central area of their geographic distribution, verify initial reports of their semi-nomadism, document whether they use their home range in an even manner or exhibit seasonal range compression/expansion, and tackle the question of why home ranges in the species are so extraordinarily large. Because one of the main determinants of their ranging may be the seasonally variable abundance of specific food items, we assessed temporal availability of food by monitoring phenology of food trees monthly throughout the study period. We also investigated the correlation between ranging and climatological parameters as well as anthropogenic factors that are assumed to interfere with the natural range use of the monkeys.

Range use is often linked to demography (Chapman and Chapman 2000), and the interrelation between the 2 is another focus of our study. Specifically, we compared group size and home range size of different groups and checked for effects of scramble competition, which occurs in several primate taxa (Barton *et al.* 1992). Environmental variables such as floristic diversity and composition, elevation, and climate vary substantially across sites within the distribution of *Rhinopithecus bieti* (Long *et al.* 1994). We therefore asked whether such differing environmental conditions lead to intraspecific variation in range sizes. In particular, we tested whether there is a negative relationship between range size and habitat quality or pro-

ductivity, as found in previous studies of primates in temperate forests (Bishop 1979; Jiang *et al.* 1991).

Methods

Study Area and Subjects

We conducted our study between September 2005 and November 2006 in the Samage Forest near the town of Tacheng and the village of Gehuaqing in Weixi County of Yunnan Province, PRC (27°34'N, 99°17'E). The Samage Forest forms the southernmost part of Baimaxueshan Nature Reserve. The research area encompasses *ca.* 40 km² of subtropical to temperate forest interspersed with clearcuts and cattle grazing land and spans 2500–4000 m elevation. The mountains are part of the Hengduan Mountain Range at the Eastern margin of the Tibetan Plateau. Annual rainfall was 921 mm, and mean annual temperature was 14.5°C at 2448 m (800 m below the most frequently used altitude of the study group). Temperature and precipitation vary strikingly with seasons (Li *et al.* 2008). Forest cover at the research area is a mosaic of mixed coniferous and deciduous-broadleaf forest, high-elevation fir forest (*Abies georgei*), evergreen oak forests of different kinds (mesophytic lowland *Cyclobalanopsis* spp. and montane xerophytic *Quercus pannosa*), and pine forest (*Pinus yunnanensis*). Topography is composed of precipitous slopes. Parts of the Samage Forest have been selectively logged, and human encroachment in the form of livestock grazing and harvest of nontimber forest products is commonplace. The focal group (Gehuaqing group) comprises *ca.* 410 members. The group has become fairly well habituated after years of continued surveillance by reserve staff. Another large group (Xiangguqing group) lives *ca.* 10 km to the east of the Gehuaqing group. The only other sympatric primate is *Macaca mulatta*.

Data Collection

We located the study group based on their position during previous observation days and information about their location from field assistants. After establishing visual or auditory contact (vocalizations, sound of breaking branches) with the group, we took a location record of the group's center every 30 min via a GPS receiver (Garmin® eTrex Summit), unless dense vegetation and deep valleys made it impossible. Because we usually observed the group from lookout points up to several hundred meters away, we corrected positions for distance to the group via a laser rangefinder (Bushnell®) and an electronic compass.

The lifestyle of *Rhinopithecus* called for a somewhat flexible study design. Instead of undertaking conventional dawn-to-dusk group follows during several consecutive days, we trailed the group whenever conditions were favorable and established contact with them on an average of 12 d/mo (Table II). A conventional 5 d/mo sampling regime would have resulted in a drastic underrepresentation of the monthly home ranges because the group covers much larger areas monthly. Similarly, it would have been unsuitable for estimating daily travel distance in the species for 2 reasons: 1) The group sometimes spent time in areas not accessible to researchers, resulting in missing

data in that month. 2) *Rhinopithecus bieti* alternates between long-distance movements and concentrated use of relatively small areas. Such uneven ranging may cause strong biases in monthly estimates of daily travel distance if based on only a few days per month.

We were seldom able to make full-day follows and to obtain accurate data on daily travel distance because continuous tracking of the group is challenging when the subjects engage in long-distance travel. They are fast moving, sometimes go out of sight, and may wander into areas that are off-limits to researchers. In addition, group spread is often large, and determining the group center is often difficult when following them. Hence, daily travel distance calculation based on consecutive GPS points are probably not very exact because the georeferenced portion of the group need not be the group center. Nevertheless, in September 2006, when additional manpower was available, we followed the group continuously for a whole month. We chose September because it seemed to be a representative month in terms of day range and day-to-day travel (based on our data from September 2005 and additional data on daily travel distance collected in other seasons after the termination of the study).

Data Analysis

Range Use For calculation of the total home range size, we recorded the grid cells the focal group entered. We chose 250×250 m grid cells because the usual spread of the band was ca. 200 m. We calculated range size as:

$$(\text{number of cells entered}) \times (0.0625 \text{ km}) / \cos(40^\circ)$$

The $\cos(40^\circ)$ represents the approximate average angle of slope obtained from a field survey at Samage (*cf.* Tan *et al.* 2007). We based the total home range both on sightings of the group itself and on signs of their presence such as fresh scat. We also took coordinates of positions where the group had been seen by forest guards, whose accounts were reliable given their familiarity with the terrain and their year-long experience in tracking (and formerly also hunting) monkeys from the study group. The grid cell method often produces underestimates of range sizes (Singleton and van Schaik 2001; Sterling *et al.* 2000), which can be circumvented by including cells that monkeys did not enter, but that were surrounded by other cells entered into the total home range estimate (lacunae elimination: Albernaz 1997; Kirkpatrick *et al.* 1998). We linked isolated cells by connecting them with the minimum number of intervening cells of suitable habitat, and filled lacunae provided they contain supposedly suitable habitat. We excluded 3 grid cells known to be pastures in the calculation of the home range size even though they were surrounded by cells monkeys had visited.

We applied the minimum convex polygon (MCP) to calculate monthly and seasonal home ranges. We based monthly and seasonal home ranges on sightings of the study group and fresh scat. Because minimum convex polygons can incorporate large areas that are never used, we adjusted monthly and seasonal polygons (adjusted polygons) by removing unsuitable habitat such as alpine pastures and areas never visited based on our 15-mo data set (*cf.* Li and Rogers 2005).

We entered GPS readings in longitudes/latitudes for group location into the GIS application ArcView®. We did all subsequent home range analyses via an extension to ArcView® named YGM (Yunnan Golden Monkey)-TOOL developed by Ruidong

Wu, a program that implements a suite of movement and home range analyses functions within the GIS. We edited maps in ArcMap®.

We estimated intensity of utilization by the number of 30-min location records per grid cell, via GIS. We defined a core area as the sum of all grid cells of the home range that are used more heavily than would result from a uniformly distributed use (Samuel *et al.* 1985). Via ArcView®, we recorded daily travel distance as the sequence of coordinates taken at every location record, and calculated the sum of distances between each set of coordinates. Even though we followed the group from morning to evening (*ca.* 0700–1900 h), sometimes the group had changed position between the last sighting of one day and the first sighting of the next. In that case, we apportioned the distance between the sightings on a 50/50 basis and added it to the estimate for the respective daily travel distances on those days (*sensu* Kirkpatrick and Gu 1999).

To predict whether a primate species would be territorial, Mitani and Rodman (1979) devised an index of defendability that relates day journey length to the diameter of a circle equivalent to the home range area. Because no datum on mean annual day journey length is available, we used the data obtained from the 1-mo follow in September 2006.

The degree of human activities and the number of livestock inside the reserve boundaries vary seasonally and are thus bound to have a changing impact on the monkeys' ranging behavior. We noted all sightings of people and livestock inside the home range on tracking days to obtain a crude estimate of how the presence of humans and domestic animals might affect ranging. Because we recorded only activities detected along the way, we certainly may have missed activities elsewhere, e.g., at elevations above us, that might have affected the subjects' movements. We developed a relative index of disturbance to take into account the differential degree of disturbance caused by different human activities and different domestic animals (Table I). The classification is admittedly somewhat arbitrary, but it provides a crude measure of perceived disturbance.

Table I Different values of the disturbance index based on different disturbances caused by humans and livestock

Origin of disturbance	Disturbance index	Rationalization
1 dog	2	Sound of barking is far-reaching, and dog is closest to a natural predator
1 person of which activity/ purpose not determined	1	Less than dog because of partial habituation to humans
1 person cutting tree	1.5	Noise of wood chopping makes disturbance higher
1 person looking for medicine, mushrooms	1	More unobtrusive activity than tree cutting
1 cow in forest	0.5	Higher than cow on meadow because forest habitat is shared by golden monkeys
1 cow on meadow	0.25	Lower than cow in forest because monkeys usually do not visit meadows
1 sheep in forest	0.25	Lower than cow in forest because of smaller size and less damage in terms of food consumption/ vegetation destruction

There is no comparable direct measure of habitat quality at different study sites of *Rhinopithecus bieti*. However, habitats can be divided simply into marginal and productive ones. Features of marginal habitats versus more productive ones are lower temperature, less rainfall, lower specific diversity, higher elevation, and poorer soils. Based on these criteria, Tibet (Xiaochangdu) and Baimaxueshan North (Wuyapiya) are marginal habitats while Baimaxueshan South (Samage) and Jinsichang, Longma, and Fuhe are relatively productive habitats (Long *et al.* 1994; Xiang *et al.* 2007). The marginal sites lie at latitudes $>28^{\circ}30'N$, while the productive sites lie at latitudes $<27^{\circ}36'N$. Via ANCOVA, we tested for a relationship between productivity (productive vs. marginal) and log-transformed home range size (dependent variable) while including log-transformed group size as a covariate.

We performed statistical procedures in SPSS 12.0. Tests for significance are 2-tailed. We classified seasons as spring (March–May), summer (June–August), fall (September–November), and winter (December–February). We used the following data sets for analyses: calculation of total home range size: September 2005–November 2006; calculation of seasonal home ranges: September 2005–August 2006; and relation between phenology and home range size: November 2005–October 2006 (because phenological records for September/October 2005 were incomplete).

Phenology

To assess abundance of different tree species, we quantitatively inspected and identified 1851 trees in 67 20×20 m botanical plots within the focal group's home range (Li *et al.* 2008). Of the 1851 marked trees, we selected 307 trees for monthly phenological monitoring, and then selected another subset of 157 trees from 21 general that contribute significantly to the diet for analysis. These last phenological records were intended to characterize seasonal changes in the availability of food resources for *Rhinopithecus bieti*. Trees selected for phenological monitoring were mature individuals with girth >40 cm that offered a good view of their crowns. We conducted phenological sampling at monthly intervals, when we visually inspected each marked tree, and recorded the presence of fruits, flowers, and young leaves. We calculated the proportion of monitored trees bearing each of the phenophases every month (*cf.* Yeager 1989; Li 2006).

Results

Home Range Size and Temporal Variability

The focal group of *Rhinopithecus bieti* entered 269 grid cells (16.81 km²) over 14.5 mo in 2005/2006 (Fig. 1). We saw the group in 205 of the map cells, and detected signs of their presence, i.e., feces, remnants of discarded food and prints, in an additional 64 map cells. A 24.75-km² area (396 grid cells) represents the total home range estimate after including grid cells surrounded by visited cells (lacunae) and linking isolated grid cells. Applying a correction factor for terrain resulted in a final home range size estimate of 32.31 km². For comparative purposes, the annual home range size would be 21.25 km² (27.7 km² with correction for terrain).

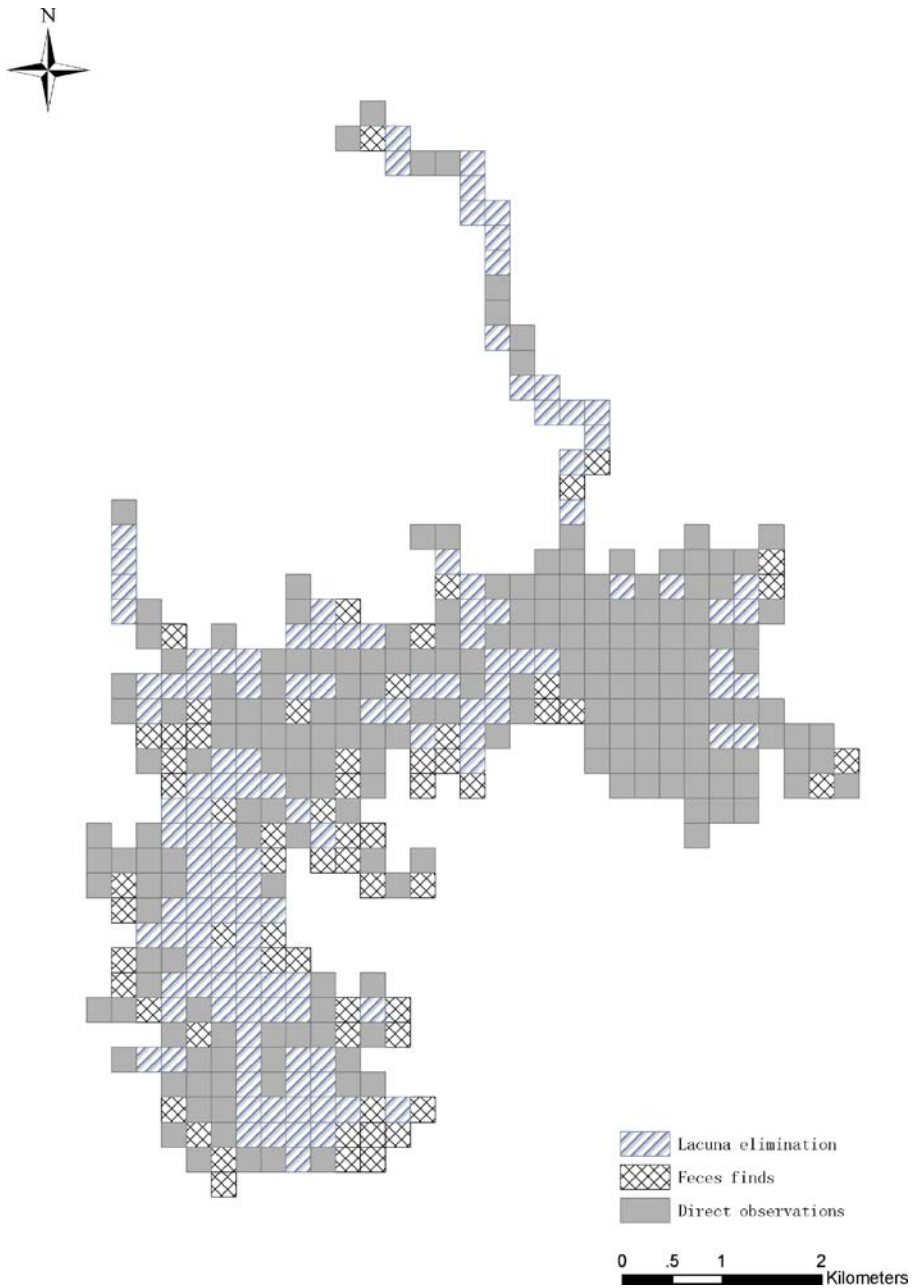


Fig. 1 Total home range of the Gehuaqing band of *Rhinopithecus bieti* at the Samage Forest, Baimaxueshan Nature Reserve in 14 1/2 mo (September 2005–November 2006). The figure contains not only grid cells where we spotted the group, but also grid cells where we found feces and grid cells surrounded by visited cells.

The cumulative number of new grid cells our focal group visited with each successive month is in Fig. 2. The group continually entered new grid cells, and the curve had not yet reached an asymptote by October 2006; however, additional data that field assistants collected in November and December 2006 indicated that the focal band did not venture into new areas. Nevertheless, the group had occasionally made excursions into peripheral areas in previous years. Including areas where forest guards have seen the band in the previous 10 years (1996–2005), the size sums to 43 km² (56.1 km² with correction for slope).

Sampling effort was uneven among months, ranging from 4 d of observation in January to 17 d of observation in August (Table II). However, there is neither a significant correlation between the number of observation days per month and monthly home range size (Spearman rank correlation, $r_s=0.477$, $p=0.117$, $n=12$ mo) nor between monthly number of location records and monthly home range size ($r_s=0.343$, $p=0.275$, $n=12$ mo), implying that the uneven sampling effort only marginally affected data comparability and interpretation.

The mean monthly home range area of *Rhinopithecus bieti* based on the adjusted minimum convex polygon method is 6.7 km². Polygon-based sizes of seasonal and monthly and also home ranges varied considerably (Table II). Home ranges are: spring, 17.8 km²; summer, 18.6 km²; fall, 9.3 km²; and winter, 18.2 km² (Fig. 3).

Intensity of use of grid cells varied markedly. Subjects entered many cells only once, whereas others had ≤ 64 location records. The difference between the observed and expected distributions of location records across the home range is highly significant (Kolmogorov-Smirnov 1-sample test, $Z=9.199$, $p<0.001$, $n=205$). Range use of *Rhinopithecus bieti* surpassed the expected uniform distribution in 60 core cells (29.3% of all grid cells with location records; Fig. 4). The cells constitute a core zone, albeit not a contiguous one. Fifty percent of all location records occurred in only 29 cells, which corresponds to 1.81 km². Seventy-five percent of all location records occurred in 69 cells, which corresponds to 4.31 km² (Fig. 5).

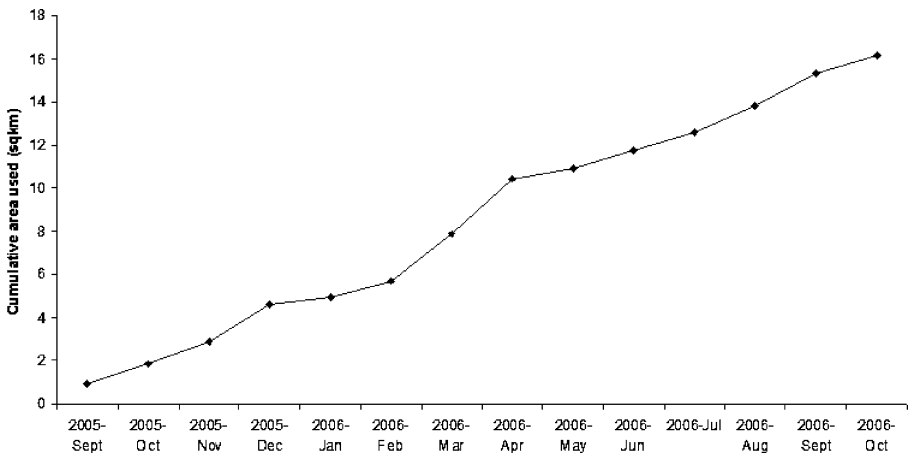


Fig. 2 Cumulative increase of the home range of the Gehuaqing band, based on group sightings, i.e., location records, and feces.

Table II Number of location records and observation days per month as well as monthly home range estimates (based on the adjusted minimum convex polygon method) for the band of *Rhinopithecus bieti* in the Samage Forest

Month and year	Observation days	Location records	Adjusted MCP ^a (km ²)
September 2005	9	55	5.13
October 2005	10	107	1.27
November 2005	7	76	7.36
December 2005	14	90	5.83
January 2006	4	40	0.73
February 2006	6	42	5.13
March 2006	12	120	8.95
April 2006	16	124	12.77
May 2006	12	89	1.75
June 2006	9	53	14.52
July 2006	14	83	6.03
August 2006	17	103	10.48
September 2006	30	505	6.51
October 2006	15	107	9.7
November 2006	9	104	NA
Total	184	1698	NA

^a Not corrected for slope.

Fig. 3 Adjusted minimum convex polygons of seasonal home ranges of *Rhinopithecus bieti* at Samage. We excluded unsuitable and never visited areas from the polygon.

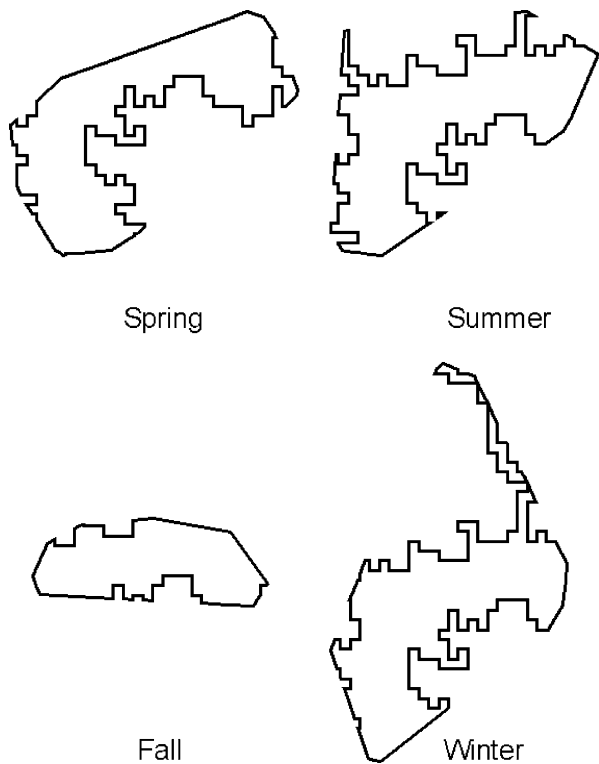




Fig. 4 Total home range of *Rhinopithecus bieti* at Samage. The subjects obviously utilized parts of their range unevenly. They used the eastern part frequently and the western and southwestern parts less frequently. *Rhinopithecus bieti* used the northern part only once when they made an excursion. Darker tones indicate a higher number of location records, i.e., more frequent use.

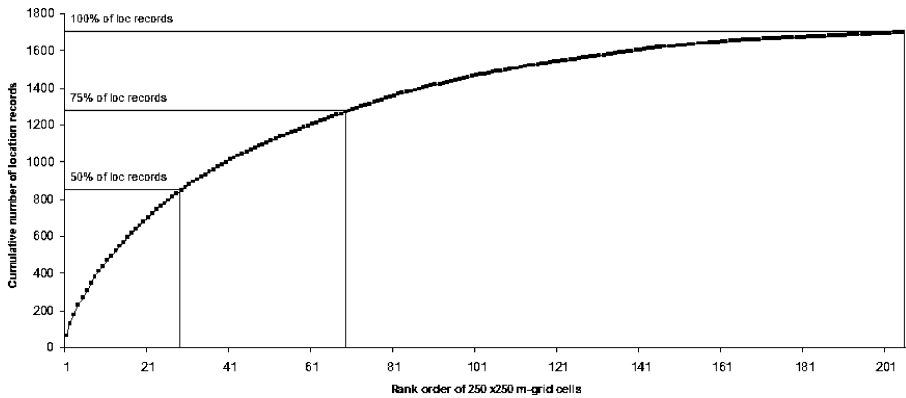


Fig. 5 Cumulative number of location records of the Gehuaqing band in 250-m grid cells. Cells are arranged in rank order of use. The areas accounting for 50%, 75%, and 100% of all location records are designated.

Correlates of Range Use

Availability of new leaves, flowers, and fruit varied across the annual cycle (Fig. 6). Fruit abundance reached a peak in August, and we recorded a flush of immature leaves in May. There is no significant correlation between presence of young leaves and monthly range size ($r_s=0.312$, $p=0.324$, $n=12$ mo), presence of fruits and monthly range size ($r_s=0.277$, $p=0.384$, $n=12$), or presence of flowers and monthly range size ($r_s=0.120$, $p=0.710$, $n=12$).

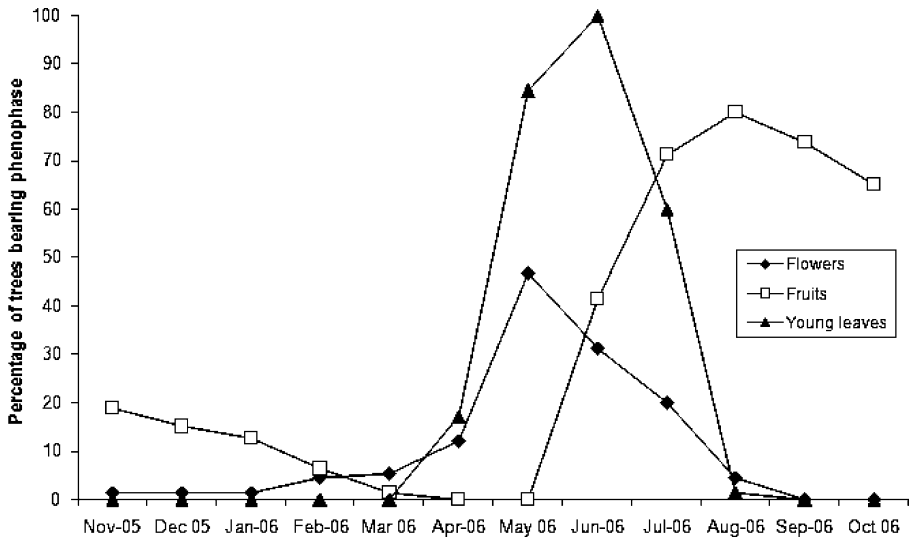


Fig. 6 Availability of fruits, young leaves, and flowers of food trees of *Rhinopithecus bieti* at the Samage Forest, South Baimaxueshan Nature Reserve in 2005/2006. Data are from 157 sampled tree specimens. According to our phenological data, fruit availability is meager in winter, but the finding may be due to the fact that our phenology trees lie within the heavily utilized core area of the band where fruit resources became almost depleted. Some trees outside the core areas still bore fruit in late winter (*pers. obs.*).

Monthly home range size significantly correlates neither with the number of people ($r_s=.411$, $p=0.185$, $n=12$ mo) nor with the total disturbance index ($r_s=0.340$, $p=0.280$, $n=12$) (Table III).

There is no significant correlation between monthly range size and temperature ($r_s=0.339$, $p=0.282$, $n=12$ mo) or between monthly range size and rainfall ($r_s=0.109$, $p=0.737$, $n=12$; Li *et al.* 2008). Monthly variation in day length is not associated with variation in monthly home range sizes ($r_s=0.473$, $p=0.121$, $n=12$).

Daily Moving Distance Based on Full-Day Follows

There is a conspicuous variance in daily travel distance in September 2006. The band showed concentrated use of certain confined areas and short daily travel distances (<1500 m) for 3 consecutive days twice that month. On the days before and after the relatively stationary phases, the band engaged in long distance travels of >1500 m (Fig. 7). The mean daily travel distance in September was 1620 m (range 578–4216 m, SD=798 m) (Fig. 8). The largest elevational range covered in one day was 400 m. Overall movements in that month were characterized by a zigzag pattern with frequent returns to previously visited areas. Distances traveled fluctuated with day-time. There were 3 peaks of travel (1030–1130 h, 1330–1630 h, 1830–1930 h) and 3 periods of relative immobility (0630–0930 h, 1130–1330 h, 1630–1730 h).

Territoriality and Home Range Overlap Between Bands

A comparatively low index of defendability of the Gehuaqing group at Samage (0.29; 0.25 if the home range estimate corrected for slope is applied) suggests that the group is unable to defend an exclusive territory (Mitani and Rodman 1979). We found indirect

Table III Average number of people encountered per day for each month and total monthly disturbance index

Month and year/season	No. of people	Total disturbance index
September 2005	3.3	6.8
October 2005	0.6	2.15
November 2005	0.7	3
December 2005	0.2	1.2
January 2006	0.7	0.7
February 2006	0	0
March 2006	1.2	1.4
April 2006	4.1	5.05
May 2006	5	9.65
June 2006	2.7	5.9
July 2006	2.2	2.9
August 2006	6.2	9.55
Fall 2005	1.7	4.2
Winter 2005/06	0.1	0.8
Spring 2006	3	4.3
Summer 2006	3.5	5.3

The total monthly disturbance index is derived from an evaluation of different human activities and different domestic animals.

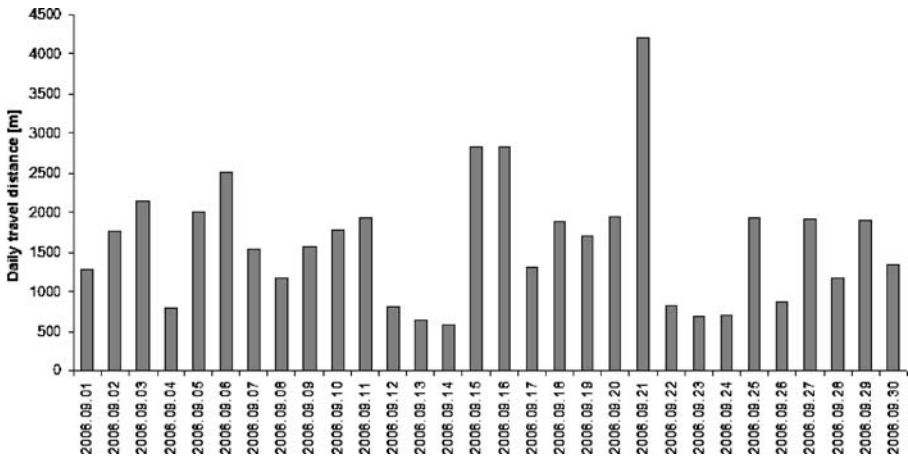


Fig. 7 Daily travel distance of the Gehuaqing group in September 2006. The long distance on September 21 may be erroneous and may have been caused by falsely following a splinter group from the main band.

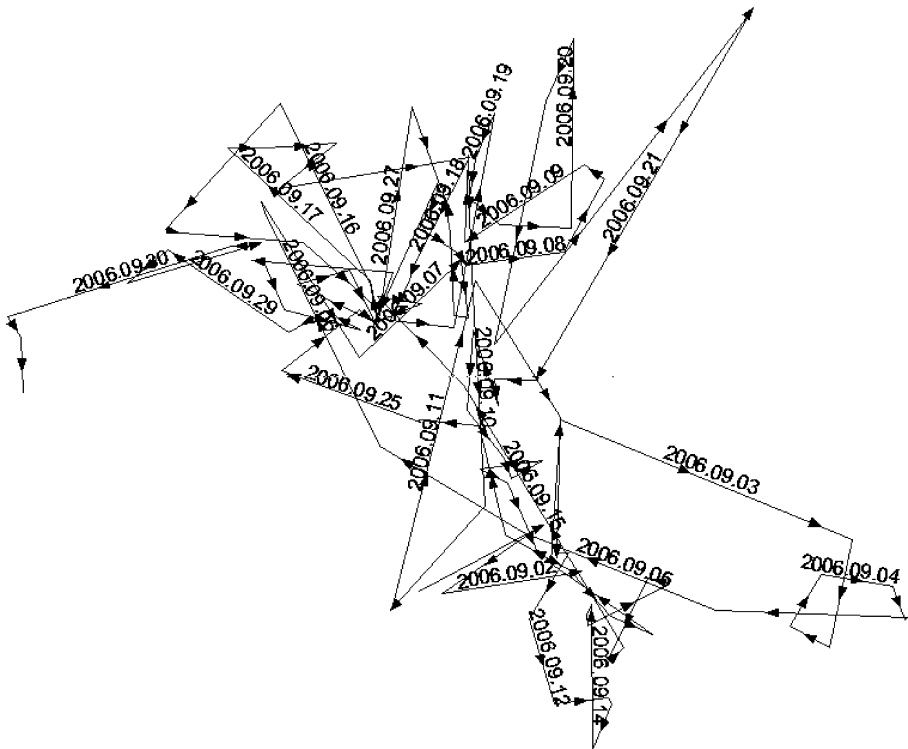


Fig. 8 The daily travel distances of Fig. 7 in a directional context. Arrows indicate direction of travel. Dates are indicated.

evidence of another small group (Shikuadi) that partially shared the same space, but difficult observation conditions and lack of individual identification made it impossible to identify intergroup encounters clearly.

Relationship Among Group Size, Home Range, and Productivity

Table IV provides data on group size and home range size of all groups of *Rhinopithecus bieti* studied at the various sites. Via ANCOVA, we tested for a relationship between productivity (productive vs. marginal) and home range size (dependent variable) while including group size as a covariate. Because the interaction group size * productivity did not have a significant effect on home range size ($p=0.162$), we calculated the ANCOVA model without the interaction effect. Group size had a significant positive effect on home range size ($F=33.176$, $p=0.010$, $df=1$). There is a trend toward larger home ranges in marginal habitats: productivity has a nearly significant effect on home range size ($F=8.439$, $p=0.062$, $df=1$).

Discussion

Temporal Variability in Ranging

In many cases, temporal variation in primate range use is related either to utilization of valuable rare localized resources or major food items, or both factors (Fashing 2007). Major dietary components clearly influence ranging in Ugandan red colobus (*Ptilocolobus tephrosceles*; Clutton-Brock 1975), Tana River red colobus (*P. rufomitratus*; Marsh 1981), *Colobus satanas* (McKey and Waterman 1982; Fleury

Table IV Group size and home range size of all studied groups of *Rhinopithecus bieti*

Site	Group size	Home range size (ha)	Notes	Geographical distribution ^a	Reference
Fuhe	80	1070	250×250 m grid used; group size approximate; data obtained during an unspecified number of months over a 11/4-year period	S	Liu <i>et al.</i> 2004
Jinsichang	180	1730	250 m x 250 m grid used; group size approximate; data from 11 continuous months	S	
Longma	80	956	250 m×250 m grid used; group size approximate; data from 14 more or less consecutive months	S	Huo 2005
Samage	410	2475 ^b	250 m×250 m grid used; data from continuous 141/2 mo	M	This study
Wuyapiya	175	2525	500×500 m grid used; data from 12 mo over 2 yr	N	Kirkpatrick <i>et al.</i> 1998
Xiaochangdu	210	2125	500×500 m grid used; data from 13 mo over a 22-mo period	N	Xiang 2005

^a S = southern part of the geographical range of *Rhinopithecus Bieti*; M = middle part; N = northern part.

^b Estimate not corrected for slope to ease comparability.

and Gautier-Hion 1999), king colobus (*C. polykomos*: Dasilva 1989), white-thighed surilis (*Presbytis siamensis*: Bennett 1986), southern plains gray langurs (*Semnopithecus dussumieri*: Newton 1992), maroon leaf monkeys (*Presbytis rubicunda*: Davies 1984), capped langurs (*Trachypithecus pileatus*: Stanford 1991), white-bellied spider monkeys (*Ateles belzebuth*; Nunes 1995) and mountain gorillas (*Gorilla beringei beringei*: Watts 1998). However, for several populations, range use is not clearly related to the primary dietary variables (Fashing 2001; Oates 1977; Sangchantr 2004; Struhsaker 1974), but seems to be more affected by scarce resources, e.g., swamp plants and eucalyptus bark in *Colobus guereza* (Fashing 2001; Fashing *et al.* 2007a; Harris and Chapman 2007; Oates 1978), saltlicks in Phayre's leaf monkeys (*Trachypithecus phayrei*: Pages *et al.* 2005), and water in hamadryas baboons (*Papio hamadryas*: Zinner *et al.* 2001). We detected no statistical relationship between monthly availability of main food items and home range size of the Gehuaqing band. Nevertheless, it is still possible that a careful fine-grained, albeit logistically challenging, study of the band's daily travel distance would reveal positive correlations between monthly availability of food and daily travel distance. Moreover, monthly consumption of fruit (vs. monthly availability) may have an effect on range use. Two of our findings, i.e., the substantially smaller home range in fall and the large winter home range, were unexpected and require explanation.

Large winter home range The group of *Rhinopithecus bieti* at Samage covered a relatively large area in winter. Conversely, other studies on *Rhinopithecus bieti* at more northern localities documented a reduction in home range size or daily travel distance in winter (Kirkpatrick *et al.* 1998; Xiang 2005). Data on monthly variation in daily travel distance are not (yet) available for Samage, but the size of the home range remained large in winter. One might best explain the dichotomy by the unequal availability of food resources in winter at different study sites. Climate is more adverse at Wuyapiya and Xiaochangdu at the northern tip of Yunnan, and food diversity is more restricted versus that at Samage.

At Samage, we assigned the lichen-load category heavy to only 0.2% of all investigated trees whereas at Wuyapiya 29% of the trees had heavy loads of *Bryoria* (Kirkpatrick 1996; Li *et al.* 2008). Thus, the relatively lower abundance of lichens may force the Gehuaqing band to cover wider areas in search of them, whereas there is no need for the Wuyapiya band to travel far because lichens are abundant and other high-quality food items are out of reach or in negligible supply.

The large winter range was partly a result of an excursion, i.e., visit to peripheral areas of the home range, and partly a result of traveling extensively to pursue the last remaining fruits. At Samage, the spatial distribution of arboreal fruit appeared to have changed from fall to winter after natural abscission and after fruit depletion in some areas had taken place. Our phenological data show that of 157 fruit trees, fallen fruit was beneath only 23 of them in November 2005, 27 trees in December 2005, and 20 trees in January 2006. We detected no fallen fruit in October 2005. The fact that we found surprisingly few fruits beneath trees implies that they had been eaten beforehand (fallen fruits decompose slowly in the dry season). On several occasions the monkeys fed on the phenological fruit samples, and we assume that after intense foraging in the most fruit-rich core areas of the band's range in fall, they needed to seek fruits actively in winter. Extensive ground surveys revealed that some trees in more remote areas, which the band visited in winter, were still largely covered with preferred fruits such as *Sorbus*

spp. (Rosaceae) and *Acanthopanax evodiaefolius* (Araliaceae) even in late winter. The higher costs of long travel associated with searching for fruit may be compensated by the presumably high nutritional and energy returns content of the fruits.

Home range reduction in fall In fall, when fruits were plentiful and constituted a major part of the diet, the band of *Rhinopithecus bieti* at Samage displayed more concentrated and restricted range use. When favorite fruit tree species are relatively abundant and spatially clumped in the home range, a primate group can economize on the time and energy of travel by intensively exploiting the resource within a small portion of its home range (Fashing 2001; Iwamoto 1992; Kaplin 2001; Terborgh 1983). At the Samage Forest, the key fruit species in the diet of *Rhinopithecus bieti*—*Acanthopanax evodiaefolius*, *Sorbus thibetica*, *Sorbus* spp., *Cornus macrophylla* (Cornaceae)—occurred at relatively high densities within clumps and showed overall synchrony in their fruiting patterns, thus enabling the band to feed largely on fruit within relatively small areas. The home range in fall was the smallest. In September, the group criss-crossed a relatively confined area and showed high return frequencies to previously visited areas. Such zigzagging may lead to increased daily travel distance, but not necessarily to increased monthly home range. Others have made similar observations: the spatially concentrated distribution of acorns, a seasonally preferred and ample food item for *Rhinopithecus roxellana* in the Qinling Mountains and *Semnopithecus schistaceus* at Simla, resulted in small ranges in fall (Guo 2004; Sugiyama 1976; Tan *et al.* 2007). We expected the Gehuaqing group to exhibit similarly concentrated use of space in summer when fruit availability reached a peak, which most likely would have produced a significant correlation between fruit availability and seasonal range sizes. The co-occurrence of juicy bamboo shoots in summer, which appeared in spatially separated patches, caused the group to move far and may have masked a statistical effect of fruit availability on range size.

Fluctuating Daily Travel Distances

Our limited data set on daily travel distance demonstrates that the focal group of *Rhinopithecus bieti* has among the longest day journey lengths of all leaf monkeys (Fashing 2007; Kirkpatrick 2007), and that the group alternated between short-distance and long-distance travels. Kirkpatrick *et al.* (1998) also observed that *Rhinopithecus bieti* show concentrated utilization of areas of 1–2 km² for *ca.* 1 week, at which time they proceeded 2–6 km to another area of concentrated utilization. Fleury and Gautier-Hion (1999) also reported alternating between long-distance movements and concentrated use among *Colobus satanas*. Along the same lines, *Semnopithecus schistaceus* follows a pattern of sweeps and concentrations, using only segments of their nearly continuous forest intensively and interspersing the periods with sweeps of the entire range (Bishop 1975, 1979). A comparable pattern is also prevalent in Tibetan macaques (*Macaca thibetana*) and Japanese macaques (*Macaca fuscata*), which forage within the group's most densely utilized areas for several days after which they move to more distant and less used areas/food patches (wandering and tripping) (Wada and Tokida 1981; Zhao and Deng 1988)).

Why Such a Large Home Range? Intraspecific Comparisons Among Sites

The golden monkeys' peculiarity of having extraordinarily large home ranges had already emerged from small-scale studies of Chinese scholars in the 1980s (Wu *et al.* 1988). Researchers have subsequently discovered large range sizes at all study sites of all Chinese *Rhinopithecus* spp. (Bleisch *et al.* 1993; Guo *et al.* 2004; Kirkpatrick and Gu 1999; Kirkpatrick *et al.* 1998; Li *et al.* 2000; Su *et al.* 1998; Xiang 2005). Home ranges of this magnitude usually occur only in ground-dwelling primates living in open environments *viz.*, *Papio anubis* (Barton *et al.* 1992; 44 km²), *P. hamadryas* (Swedell 2002; 30 km²), *Pan troglodytes* (Baldwin *et al.* 1982; >50 km²), and *Erythrocebus patas* (Enstam and Isbell 2007; 40 km²). In line with Kirkpatrick *et al.* (1998), the home range of the Gehuaqing band of black-and-white snub-nosed monkeys is one of the largest home ranges ever documented for a primarily tree-dwelling primate. Among the few other truly wide-ranging arboreal primates are male *Pongo abelii* (Singleton and van Schaik 2001; >25 km²) and Rwandan *Colobus angolensis* (Fashing *et al.* 2007b; 24 km²).

Our home range estimate of 32 km² is based on data from *ca.* 15 mo. The larger estimate of *ca.* 56 km² is due to rare excursions into peripheral areas and is largely based on accounts of reserve staff and former hunters. Similarly, Kirkpatrick *et al.* (1998) found the home range of the Wuyapiya band to be 25 km² over 2 yr, but they state that the band may have covered >100 km² within a decade. The question arises why the monkeys have such extremely large home ranges.

Several researchers have discovered negative correlations between range size and habitat quality or productivity, e.g., *Macaca mulatta* (Jiang *et al.* 1991), or have found range size to be larger in areas of poor habitat quality, e.g., *M. sylvanus* (Mehlman 1989), *Semnopithecus* spp. (Bishop 1979), forest vs. savanna chimpanzees (Baldwin *et al.* 1982; Herbinger *et al.* 2001). Our results indicate a statistical trend toward larger home ranges of groups of *Rhinopithecus bieti* living in high-altitude cold depauperate habitats in the north versus those in low-lying warmer and productive habitats in the south. The effect would be highly significant without inclusion of our study at Samage that—contrary to expectations—revealed a very large home range in a fairly productive environment.

Intraspecific variation in habitat structure and resource availability offers a likely explanation for the unexpectedly large home range at Samage. The home range is configured to include a patchwork of fairly distinct vegetation types of which only the mixed forest appears to be of any significance in terms of resource procurability and that *Rhinopithecus bieti* utilized on a regular basis (Li *et al.* 2008). Patches of fruitful mixed forest are interspersed with other vegetational strata such as pine, oak, and fir forest, which may automatically lead to an enlargement of the home range because the band has to cross the less desired other forest types to reach their preferred forest type. Home range is thus expected to be larger where such fruitful patches are fragmented and dispersed (*sensu* Geffen *et al.* 1992).

Besides habitat heterogeneity, large group size appears to be another main factor that accounts for the overall large home range of *Rhinopithecus bieti*. Barton *et al.* (1992) and van Schaik *et al.* (1983) found a positive correlation between group size and home range size or group size and daily travel distance in several primate taxa. An increase in the size of a group causes a larger biomass per unit area. To sustain

per capita energy intakes, the quantity of available resources must be enlarged. We would thus anticipate that as group size increases there should be a corresponding increase in home range size (cf. Nunn and Barton 2000). Similarly, the enlargement of a group may necessitate increased travel to counter deficits in food supply. If such positive associations are present, as we found for *Rhinopithecus bieti*, they are an indication of scramble competition (Chapman 1990; Isbell 1991; Janson and van Schaik 1988).

Compared to other monkeys, evidence for intragroup scramble competition is less straightforward in colobines because their often relatively abundant and evenly spaced food supply may diminish scramble competition and not impose larger daily travel distances (Fashing 2001). For instance, in *Ptilocolobus tephrosceles*, there is no correlation between group size and daily travel distance (Struhsaker and Leland 1987). In Asian colobines as a whole, there is neither a positive correlation between daily path length and group size nor between home range size and group size (Yeager and Kirkpatrick 1998), implying that intragroup scramble competition is of minor importance in the species. However, others found a positive relationship between group size and daily travel distance (Gillespie and Chapman 2001; Steenbeek and van Schaik 2001). Another reason scramble competition may be difficult to identify in colobines is that ranging behavior may be influenced by irregularly distributed and scarce mineral-rich resources, which may force some groups to travel long distances to exploit them, while others living closer do not have to travel as far (Fashing *et al.* 2007a; Harris and Chapman 2007).

Kirkpatrick (1996) assumed that reliance on slow-growing lichens, the prime feeding resource of *Rhinopithecus bieti*, dictates range utilization in the temperate and very seasonal forests of Wuyapiya to a considerable degree. Because lichens need years or even decades to regenerate after consumption (Kirkpatrick 1996; Wu 1987), Kirkpatrick and Gu (1999) hypothesized that the monkeys need an extensive home range and forage seminomadically to avoid depletion and to allow overutilized patches to recover. Similarly, Watts (1991) proposed that mountain gorillas may harvest fibrous foods in such a way as to replenish the food supply and return later to the same site after regeneration has taken place. Compared to mountain gorillas, renewal rate is much slower for lichens than for herbaceous vegetation. Hence, if the strategy of snub-nosed monkeys is to allow lichens to regrow to a harvestable length, they have to abandon areas for a decade or more. We clearly did not find this. Our observations indicate that the band of *Rhinopithecus bieti* returns to particular areas after several months, not years or decades. If the habitat were less fragmented, the band would possibly leave patches for a decade or more to allow lichen renewal to take place. At present, the monkeys still seem to have sufficient quantities of their dietary staple, but sustained consumption exceeding production would result in a decreased standing crop and may create dietetic problems in the future.

Home Range Overlap, Core Area, and Site Fidelity

Based on the Mitani-Rodman index, the Gehuaqing group is theoretically not capable of territoriality. We observed no territorial encounter. It is practically challenging to verify whether other neighboring bands have overlapping home ranges with the focal band, but partial home range overlap has been inferred for our focal group at Samage, in accord

with findings for the bands of *Rhinopithecus roxellana* at Shennongjia (Ren *et al.* 2000) and at Zhouzhi (Tan *et al.* 2007).

The Gehuaqing band used large parts of their range very infrequently. However, they used some grid squares very often. They visited outlying peripheral areas only once or twice over the entire study period (Fig. 4), which resembles the range use strategy of eastern gorillas, *Gorilla beringei*, which use their entire home range only on a long-term basis and limit their range to small fractions of their home range in any given week or month (Vedder 1984; Yamagiwa *et al.* 1996). Kirkpatrick *et al.* (1998) and Liu *et al.* (2004) also noted differential intensity of home range use. In the case of the group at Mt. Fuhe, the frequently used grid squares were usually the ones including sleeping sites (Liu *et al.* 2004). The core cells of the group of *Rhinopithecus bieti* at Samage are not continuous, and occur in patches across the band's home range. The discontinuous nature of the core cells is best explained by the heterogenous nature of vegetation distribution across the home range.

Some groups of *Rhinopithecus* show large-scale home range shifts. For example, the central core of the Wuyapiya band's range appears to have moved 8–10 km over a decade (Kirkpatrick *et al.* 1998), apparently because of a rise in mushroom collection and forest contamination after insecticide spraying among other factors (Forest Biodiversity Database System 2006; MacLennan 1999). At Shennongjia, road construction caused a band of *Rhinopithecus roxellana* to avoid a previously regularly utilized area (Su *et al.* 1998). In the Qinling Mountains, logging operations are most likely responsible for the change of the summer home range of a band of *Rhinopithecus roxellana* (Li *et al.* 1999). The Gehuaqing band seems to have exhibited site fidelity for decades (Shunkai Feng *pers. comm.*), with the exception of short-term forays into remote corners of their home range on rare occasions, suggesting that bands do not shift home ranges, unless forced by disturbance.

Past commercial logging had a highly disruptive effect on the physiognomy of the Samage Forest. Broad areas were cleared as a result of large-scale commercial logging operations in adjoining Deqin County, which rendered this area uninhabitable. If the habitat across the county border was still largely intact, it seems reasonable to assume that the group's home range would be wider and its pattern of ranging even more migratory.

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