



## Ranging of *Rhinopithecus bieti* in the Samage Forest, China. II. Use of Land Cover Types and Altitudes

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**Abstract** We investigated composition and structure of a temperate montane forest called Samage at Baimaxueshan National Nature Reserve in Yunnan, one of the last refuges for the highly endangered black-and-white snub-nosed monkeys (*Rhinopithecus bieti*). There is a patchwork of vegetation types at Samage, and we distinguished 6 major land cover types within the home range of the focal group. We tracked the semihabituated Gehuaqing band for a full annual cycle to study their habitat utilization and altitudinal ranging. We analyzed the group's selective use of particular habitat types via selection ratios. We calculated habitat availability from a GIS database. We found that they used mixed deciduous broadleaf/conifer forest disproportionately to its availability in all months. Subjects completely avoided meadows. Pine and evergreen broadleaf forests acted as corridors between patches of mixed forest and monkeys visited them occasionally, but at low frequencies and mostly in transit. The focal band stayed at elevations ranging from *ca.* 2600 m to 4000 m, and the mean elevation used

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is 3200 m. We found evidence for seasonal variation in use of elevational zones. The band stayed at significantly higher elevations in summer than in spring. The descent in spring was likely related to a flush of immature leaves at low-lying elevations. Availability of preferred fruits also had a highly positive influence on altitudinal ranging, i.e., during months with high fruit availability (late summer, early fall), the band stayed at medium elevations where preferred fruits were most abundant. Higher concentrations of lichens and the snub-nosed monkeys' search for not yet depleted fruits probably caused them to remain at mid-elevations in winter. There is no significant correlation between climate parameters and elevation used. One of the main inferences of this investigation is that, contrary to previous accounts, *Rhinopithecus bieti* is not universally associated with high-elevation dark fir forest, but at Samage exhibits an overwhelming preference for mixed forest. Moreover, our analyses support the hypothesis that elevational migration, in this temperate-subtropical forest, is influenced by the temporal fruiting of major food trees and that climate has only a negligible effect on elevation use.

**Keywords** altitudinal migration · conifer · elevation · GIS · golden monkey · GPS · habitat use · lichen · mixed forest · *Rhinopithecus* · seasonality · temperate forest · Yunnan

## Introduction

Broadly speaking, temperate forests with relatively low productivity are an atypical environment for nonhuman primates. Only very few primate species inhabit forests in temperate regions, e.g., Nepal gray langurs (*Semnopithecus schistaceus*) in the Nepal Himalayas (Curtin 1975; Sayers and Norconk 2006) and Japanese macaques (*Macaca fuscata*) at several localities in Japan (Hanya 2004; Izawa and Nishida 1963). The 4 species of snub-nosed monkeys are semiarborescent and large-bodied leaf monkeys with markedly differing habitat requirements: gray snub-nosed monkeys (*Rhinopithecus brelichi*) are connected with subtropical-temperate mixed deciduous and evergreen broadleaf forest (Bleisch *et al.* 1993; Wu *et al.* 2004), Tonkin snub-nosed langurs (*R. avunculus*) inhabit tropical-subtropical hilly evergreen broadleaf forest on karst limestone formations (Dong and Boonratana 2006; Le Khac Quyet 2003), and golden snub-nosed monkeys (*R. roxellana*) range mostly in mixed deciduous broadleaf/conifer forests, with slight interpopulation differences in habitat association (Kirkpatrick *et al.* 1999; Li *et al.* 2002).

Researchers have long considered *Rhinopithecus bieti* (black-and-white or Yunnan snub-nosed monkeys), which are geographically restricted to the Hengduan Mountains of Northwestern Yunnan and Southeastern Xizang (Tibet), to be primarily associated with high-elevation evergreen fir-azalea forests (Li *et al.* 1982; Kirkpatrick 1996; Zhao *et al.* 1988). More recent studies, though, have demonstrated that the habitats used by *Rhinopithecus bieti* are more diverse than previously thought: they also include forests with deciduous and evergreen angiosperm trees (Ding 2003; Huo 2005; Liu 2003). Kirkpatrick and Long (1994), Tan *et al.* (2007), and Yang (2003) suggested that *Rhinopithecus bieti* use their montane and highly seasonal habitat not only relative to the distinct major forest types, but also adjust

altitudinal ranging in relation to seasonal food availability, human activities, and temperature, a phenomenon that we refer to as altitudinal migration *sensu lato*. Altitudinal migration *sensu stricto* refers to vertical movement from low elevation winter range to high elevation summer range, a pattern that researchers have particularly studied in cervids (Albon and Langvatn 1992; Oosenbrug and Theberge 1980; Robin 1975).

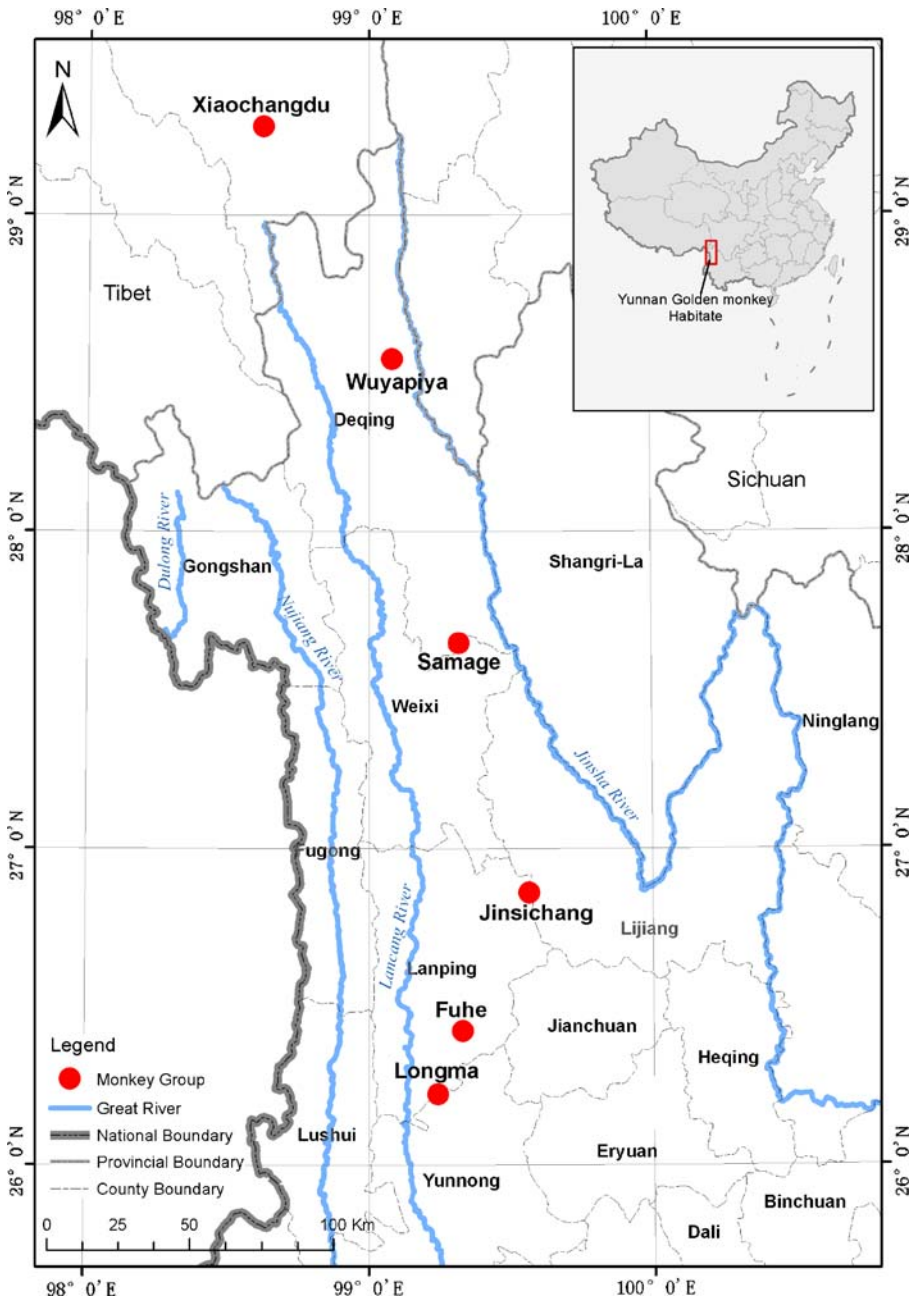
In temperate-living *Rhinopithecus*, the evidence regarding seasonal variation in altitudinal distribution is conflicting. Some researchers have noted differential utilization of altitudinal belts among seasons (Cui 2003; Happel and Cheek 1986; Hu *et al.* 1980; Li *et al.* 2000; Liu 1959; Liu *et al.* 2004; Wu *et al.* 2004; Yang 2003). Conversely, other researchers found no indication that altitudinal ranging occurs on a seasonal basis (Bleisch *et al.* 1993; Huo 2005; Kirkpatrick and Gu 1999; Kirkpatrick and Long 1994; Kirkpatrick *et al.* 1998; Ren *et al.* 2000; Tan *et al.* 2007). There are similarly inconsistent results for Hanuman langurs (*Semnopithecus* spp). Bishop (1977) postulated (but did not observe) migration to lower winter grounds for *Semnopithecus schistaceus* at Routang, as did Dolhinow (1972) for southern plains gray langurs (*S. dussumieri*) at Nainital, and Curtin (1975) observed this migration in *S. schistaceus* at Junbesi (Vogel 1971). However, other populations, such as *Semnopithecus schistaceus* at Simla and Melemchi, did not descend (Bishop 1979; Sugiyama 1976).

We present data on the vegetation structure of the different land cover types in the temperate Samage Forest, an uncommon environment for primates. We studied the snub-nosed monkeys' range use in relation to vegetation type and investigated whether there are seasonal disparities in habitat exploitation. Researchers had based inferences on altitudinal ranging in *Rhinopithecus bieti* on small or incomplete sample sizes and/or indirect evidence such as distribution of fecal pellets. We draw on a long-term study to illuminate the phenomenon of altitudinal migration in *Rhinopithecus bieti* and to identify the factors influencing their seasonal shifts in altitude. Considering that *Rhinopithecus bieti* are at the brink of extinction because of a long history of hunting, logging, and other forms of encroachment (Long *et al.* 1994; Xiao *et al.* 2003) and are still poorly known in terms of its ecological adaptations, their habitat requirements need urgent investigation. Ours is the first detailed study that quantitatively examines habitat association patterns of *Rhinopithecus bieti*.

## Methods

### Study Site

We conducted the study in the vicinity of the village of Gehuaqing (27°34'N, 99°17'E), which is in the Samage Forest in Yunnan's Baimaxueshan (Baima Snow Mountain) National Nature Reserve (Fig. 1). The Samage Forest harbors the largest subpopulation of *Rhinopithecus bieti*, a geographically distinct part of the whole population comprising 2–3 groups of *ca.* 700 individuals (Ding *et al.* 2003; Grüter 2004) and representing *ca.* one-third of the total remaining population (Grueter *et al.* 2008; Long and Wu 2006).



**Fig. 1** Map of Northwest Yunnan indicating the locations of all investigated groups of *Rhinopithecus bieti*, including the one at the Samage Forest that is the focus of our study.

## Data Collection

**Climatological Monitoring** We recorded daily minimum and maximum temperatures (in °C), precipitation (in mm) and humidity (in %) at the base camp (2448 m) which was equipped with a wireless weather station and a professional weather shelter. We measured the amount of precipitation (usually rain, sometimes melted snow) via a gauge connected with the data-logger and transmitted data automatically. We classified seasons as follows: spring (March–May), summer (June–August), fall (September–November), and winter (December–February).

**Description of Vegetation** We applied stratified random sampling, i.e., we subdivided the forest/habitat into 5 distinct forest types or strata (Mueller-Dombois and Ellenberg 1974). We established 67 20 m × 20 m plots in total (area: 26,800 m<sup>2</sup>); we laid out 10 plots in pine forest, 12 in evergreen broadleaf forest, 3 in montane sclerophyllous oak forest, 35 in mixed forest, and 7 in fir forest. We allocated plots to the available strata according to the proportional availability of different vegetation types (stratum weight) within the central part of the study area (cf. Krebs 1999). We determined the availability of strata via reconnaissance surveys and a geographic information system (GIS) vegetation map. Within each stratum, we placed plots with an objective of sampling at different altitudinal belts (200-m intervals). Within the belts, we laid out plots along existing trails via a random walk procedure, whereby we drew a random number (100–999) and then located a sample plot by taking this number of paces at 500-m intervals.

For each plot, we investigated both abiotic and biotic variables. We assessed aspect of slopes via an electronic compass (E=east=45°–135°; S=south=135°–225°; W=west=225–315°; N=north=315–360° and 0°–45°). We measured slope inclination in the center of a plot with a clinometer. For slope inclination, we used the following classes: 0°–10°, 10°–20°, 20°–30°, 30°–40°, 40°–50°, 50°–60°. We considered trees to be individuals with girth >40 cm. We recorded the following physical dimensions for all trees in the plots: tree height, crown diameter, bole height, and girth. We estimated both tree height and bole height, i.e., height from ground to base of crown, by eye. We paced off crown diameter directly beneath the tree. To estimate the area of each crown (C), we calculated 2 diameters taken perpendicularly to each other as:

$$C = (D_1 + D_2/4)^2\pi$$

We computed crown volume via formulae specific to the crown shape. We modeled the crown shape of conifers as a cone:

$$C_V = \pi(D^2L/12)$$

We modeled the crown shape of broad-leaf trees as an ellipsoid:

$$C_V = 4/3(D/2)(L/2)(H/2)\pi$$

wherein  $C_V$ =crown volume (m<sup>3</sup>);  $D$ =crown width (m);  $L$ =crown depth (m);  $H$ =crown height (m). We approximated canopy cover in plots via the categories: <20%, 20–40%,

40–60%, 60–80%, >80%. We identified tree specimens in plots *in situ* ( $n=1851$ ) to specific or generic level via reference books (*Iconographia Cormophytorum Sinicorum* 1972; Raven and Wu 1994–2005). If identification *in situ* was not feasible, we collected vouchers that staff of the Alpine Botanical Garden in Shangri-La, Yunnan inspected.

Measuring epiphyte biomass is difficult, and we did not conduct large-scale destructive sampling, i.e., felling of trees. Instead we gave each of the marked trees a lichen-load category, *viz.*, none, sparse, light, moderate, or heavy. We assigned each category a rank from 0 for none to 4 for heavy to provide a subjective scale to allow comparison among trees. We derived the sampling design from Kirkpatrick (1996) and MacLennan (1999).

*Group Follows* We usually located the focal group every 2 or 3 d based on its signs of presence: scat, food leftovers, prints, etc. We typically stayed with the group for several hours, and on an average of 4 d/mo also from morning until evening. Observation conditions permitting, we made a record of the group's position every 30 min. The location records included a reading of the geographical latitude and longitude with a Garmin® eTrex Summit GPS (geographic positioning system) receiver. We also recorded the habitat type in which we encountered the estimated center of mass of the monkey band during a location record. We usually ended follows when the group retreated to its sleeping spot or crossed the crest of a hill and moved into another valley. Over the entire 12-mo period, we lost track of the study group on only 3 occasions: in January 2006 for a 3-wk period (when both field researchers were absent), in February 2006 for a 2-wk period (due to heavy snowfalls and celebration of Chinese New Year), and in June 2006 for another 2-wk period. We have the impression that all forest types were equally easy or difficult for finding and maintaining visual contact with the monkeys. When a physical barrier prevented us from approaching the group, we could still visually locate them from bare hilltops or rocky outcrops at a few hundred meters. We frequently conducted such distance observations, which not only allowed us to have a good overview of the various forest types and see into forest patches that were difficult to reach on foot, but also precluded the possibility that our presence interfered with the group's natural movements.

Every month, we recorded presence/absence of fruits, flowers, and young leaves for 157 food trees and calculated the percentage of trees bearing each of the phenophases every month (Grueter *et al.* 2008).

We conducted field work between September 2005 and November 2006 during which we had contact with the focal group for *ca.* 800 hours. We used the following data sets for the analyses: total and monthly/seasonal habitat selection ratios: 1-yr data, November 2005–October 2006 (because sampling effort in September/October 2006 was much higher than in September/October 2005); relationships between seasonal/monthly altitudinal ranging and seasonal/monthly climate/human disturbance: 1-yr data, September 2005–August 2006 (because fall 2006 data are insufficient owing to an early termination of field work in November 2006); and relationship between monthly altitudinal ranging and phenology: 1-yr data, November 2005–October 2006 (because phenological records of September/October 2005 are incomplete).

## Data Processing

The Institute of Ecology, Yunnan University generated vegetation cover maps in ArcView 3.3 via a 4-step procedure summarized as follows: 1) georeferencing satellite images (Landsat TM), 2) generating polygons by clustering the pixels with similar attributes with a programmed protocol, 3) labeling each type of polygon based on the image interpretation, and 4) ground-truthing to verify and revise the labels. Availabilities of resources (vegetation types) can be treated as known because they were derived from maps that were partitioned into vegetation types. We digitally assessed resource availability, i.e., proportion of each vegetation type within the home range, via GIS (*cf.* McClean *et al.* 1998). The total home range estimate based on the minimum convex polygon (MCP) method used for this analysis is 50.99 km<sup>2</sup>.

Via Manly's terminology, we applied a study design 1 to measure resource selection (Manly *et al.* 2000), i.e., we made all measurements at the population level and did not recognize distinct individuals. Habitat selection is a hierarchical process (Erickson *et al.* 1998; Johnson 1980). First-order selection refers to the selection of a geographical area, second-order selection is the habitat composition of the home range, and third-order selection (also called point-range selection) pertains to utilization of habitats within the home range. We assessed habitat use at the third order level, i.e., via the home range *per se* as a definition of availability. We assessed home range during a 14-mo study (Grueter *et al.* 2008).

Per Lopez *et al.* (2004), we applied habitat-selection ratios versus other inferential statistics because researchers have questioned the efficacy of testing point-null hypotheses known to be false *a priori*, e.g., that the monkey band uses available habitat randomly (Anderson *et al.* 2000; Guthery *et al.* 2001; Johnson 1999). We calculated habitat-selection ratios of the group for each habitat type by dividing observed use by availability (Lopez *et al.* 2004; Manly *et al.* 2000). We determined observed use by vegetation type from group follows and associated location records taken at half-hour intervals. The selection ratio for a given habitat type is the ratio of the percentage used to the percentage available (Manly *et al.* 2000). Ratios close to 1 indicate no selectivity. Values <1 indicate selection against that vegetation type whereas larger values indicate selection for the vegetation type. We determined expected availability by multiplying total location records by the proportion of a given vegetation type/stratum in the monkeys' home range. We then calculated a selection ratio ( $S$ ) as

$$S = ([U + 0.001]/[A + 0.001])$$

wherein  $U$ =observed use and  $A$ =expected use (availability). To avoid 0 in the numerator or denominator, we added 0.001 to both use and availability (Aebischer *et al.* 1993; Bingham and Brennan 2004; Lopez *et al.* 2004).

We calculated the Shannon-Weaver index of species diversity ( $H'$ ) to evaluate differences in tree biodiversity among habitat types. The formula is:

$$H' = - \sum p_i \ln p_i$$

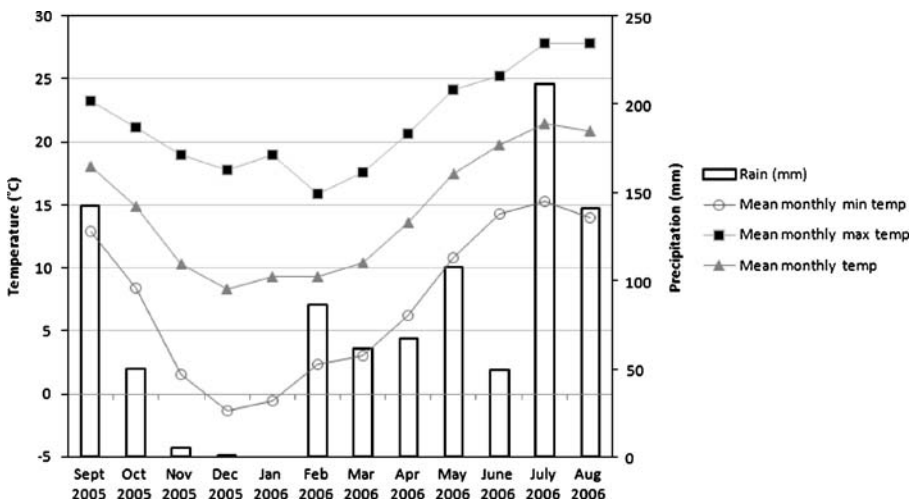
wherein  $p_i$  is the proportion of individuals of the  $i$ th plant species. We primarily used SPSS 12.0 for statistical data analysis. Tests for significance are 2-tailed.

## Results

### Climate

The study area is characterized by marked seasonality in precipitation and temperature. Winters are generally dry and cold; summers are wet and warm. The wet season is controlled by the southwest monsoon. In winter, a polar front ensures cold and dry conditions with often very strong N-NW winds behind it (*cf.* Walker 1986). Seventy-eight percent of the rain fell between April and September 2006, the wet season. Annual rainfall was 921 mm. Number of days with precipitation was 140. The highest monthly rainfall was 211 mm in July 2006, the lowest 0 mm in January 2006 (Fig. 2). There was a prolonged dry season from November 2005 to February 2006 with minimal precipitation. We recorded the highest humidity (90%) in May 2006 and the lowest (11%) in December 2005 and February 2006. Most snowfalls occurred in February 2006, during which snow accumulated  $\leq 80$  cm in depth at an elevation of 3100 m. Higher areas were temporarily off limits owing to even greater snow depth.

Mean annual temperature was 14.5°C. Temperatures fell between 2 extremes of  $-3.6^{\circ}\text{C}$  in December and  $35.4^{\circ}\text{C}$  in July. The month with the highest average temperature ( $21.5^{\circ}\text{C}$ ) was July, and the month with the lowest average temperature ( $8.3^{\circ}\text{C}$ ) was December (Fig. 2). There were considerable day-night fluctuations in temperature, especially in winter. The greatest daily temperature range was  $24.4^{\circ}\text{C}$  in February; the greatest daily humidity range was 65% in November. Because temperature decreases with elevation, the temperature within the core area of the band's home range at *ca.* 3200 m was *ca.*  $4^{\circ}\text{C}$  lower than at base camp.



**Fig. 2** Mean monthly temperature, mean monthly minimum and maximum temperature as well as monthly precipitation at Gehuaqing (2448 m), Samage Forest, in 2005/2006. Precipitation in February was mainly in the form of snow. Data from 3 d in September are deficient.



## Composition of Vegetation

We explicitly defined 6 major vegetation types based on dominant tree taxa, vegetation physiognomy, and ratio of gymnosperms to angiosperms: 1) warm-temperate, monodominant and largely secondary pine forest on lower south- and west-facing slopes; 2) subtropical, mesophytic evergreen broadleaf forest along valleys; 3) montane, monodominant, evergreen sclerophyllous oak forest on upper (south and west) slopes and along ridges; 4) polydominant mixed deciduous broadleaf/conifer forest on middle and upper slopes (includes stands of bamboo [*Fargesia* spp.]); 5) monodominant cool temperate fir forest (dark conifer forest) mainly on ridge-tops (includes selectively logged forest with dense underbush); 6) open areas, i.e., alpine herbfields, mountain shrublands, summer grazing land, grassy meadows, scree, and agricultural land. Various azaleas (*Rhododendron* spp.) are widespread in all vegetation communities. Altitude and topography are strongly related to vegetation type and are major factors in differentiating the various habitat forms across the Samage Forest. Additional data on the different strata are in Table I.

Average canopy cover of all plots combined is 58.4%. Average height of all sampled trees is 16.8 m and average diameter at breast height (DBH) is 28.5 cm. The distinguished forest strata are noticeably different in terms of overall structure and composition and architectural properties of trees (Table II). All tree parameters in Table II vary significantly among the different vegetation types (DBH:  $F_{4,1893}=14.736$ ,  $p<0.001$ ; bole height:  $F_{4,1893}=19.562$ ,  $p<0.001$ ; tree height:  $F_{4,1893}=19.357$ ,  $p<0.001$ ; lichen load:  $F_{4,1893}=199.771$ ,  $p<0.001$ ; crown area:  $F_{4,1893}=31.846$ ,  $p<0.001$ ; crown volume:

**Table I** Distribution, composition, and structure of different forest types in the Samage Forest, Baimaxueshan Nature Reserve

Variables	Mixed deciduous broadleaf/conifer forest (n=969)	Pine forest (n=325)	Evergreen broadleaf forest (n=249)	Cool temperate fir forest (n=241)	Montane sclerophyllous oak forest (n=114)
Altitude [m]	2900–3600	2500–3100	2500–3000	3500–4000	3200–3500
Main canopy species	Various <sup>a</sup>	<i>Pinus yunnanensis</i>	<i>Cyclobalanopsis</i> spp.	<i>Abies georgei</i>	<i>Quercus pannosa</i>
Density of trees [ha <sup>-1</sup> ]	697.8 (248.1)	812.5 (239.0)	518.8 (146.6)	860.7 (190.3)	950.0 (413.1)
No. fallen log	3.4 (1.9)	3.5 (2.8)	5.3 (3.8)	2.7 (3.0)	2.3 (2.5)
Tree stumps	2.6 (2.9)	1.8 (1.7)	3.4 (2.0)	1.3 (2.2)	0
Canopy cover [%]	56.9 (17.5)	60.0 (10.5)	60.0 (20.0)	67.1 (13.8)	50.0 (0.0)
Shannon-Weaver index (H')	3.42	1.27	2.48	0.46	1.13
No. tree species	58	10	36	4	10
Ratio gymnosperm/angiosperm <sup>b</sup>	0.38	2.14	0.12	8.27	0.11

Data are means ( $\pm$  standard deviation).

<sup>a</sup>Main overstory species are *Acanthopanax evodiaefolius*, *Sorbus* spp., *Acer* spp., *Betula utilis*., *Salix* spp., *Quercus rehderiana*, *Rhododendron* spp., *Picea likiangensis*, *Tsuga dumosa*.

<sup>b</sup>Number of gymnosperm stems over number of angiosperm stems.

**Table II** Variables of measured trees in different forest types at the Samage Forest Means ( $\pm$  standard deviation) are given

Variables	Mixed deciduous broadleaf/conifer forest ( <i>n</i> =969)	Pine forest ( <i>n</i> =325)	Evergreen broadleaf forest ( <i>n</i> =249)	Cool temperate fir forest ( <i>n</i> =241)	Montane sclerophyllous oak forest ( <i>n</i> =114)
DBH <sup>a</sup> (cm)	29.3 (19.5)	24.5 (11.6)	34.9 (25.5)	26.0 (11.8)	24.8 (9.4)
Bole height (m)	10.4 (6.0)	12.5 (6.2)	10.7 (5.2)	12.5 (5.5)	12.7 (4.6)
Tree height (m)	15.3 (6.6)	18.8 (7.3)	17.7 (7.4)	18.9 (7.4)	17.1 (4.9)
Crown area (m <sup>2</sup> )	27.4 (23.1)	25.9 (18.1)	40.8 (37.4)	21.5 (14.8)	15.7 (9.5)
Crown volume (m <sup>3</sup> )	99.7 (151.8)	82.4 (97.8)	242.0 (406.0)	58.4 (72.8)	47.5 (43.9)
Lichen load <sup>b</sup>	1.3 (0.9)	1.1 (0.8)	0.5 (0.6)	2.4 (0.5)	2.2 (0.8)

Data are means ( $\pm$  standard deviation).

<sup>a</sup> DBH=diameter at breast height.

<sup>b</sup> See text for details.

$F_{4,1893}=40.211$ ,  $p<.001$ ). DBH is largest in evergreen broadleaf forest and smallest in pine forest. Small DBH in pine forest may be due to the fact that the forest contains a sizable amount of secondary vegetation including young trees. Both bole and tree height are largest in cool temperate fir forest and smallest in mixed forest. The 2 monodominant gymnosperm strata pine and fir forests are structurally very similar: DBH, bole height, and tree height are almost identical. Trees within the evergreen broadleaf forest stratum have the largest crown areas and volumes.

In mixed forest, broadleaf trees form a rather closed canopy through which the more widely spaced conifers emerge, as demonstrated by the density of trees per ha in mixed forest. The mean density of broadleaf trees ( $n=708$ ) is 505 stems/ha, and mean density of conifers ( $n=263$ ) is 187.5 stems/ha. Moreover, broadleaf trees are shorter than conifers in mixed forest. Mean DBH of broadleaf trees is 25.6 cm ( $\pm 14.5$ ), and mean DBH of conifers is 39.2 cm ( $\pm 26.7$ ). Mean tree height of broadleaf trees is 13.6 m ( $\pm 4.8$ ), and mean tree height of conifers is 21.0 m ( $\pm 8.5$ ). These differences are highly significant (DBH: independent-samples *t*-test,  $T=10.127$ ,  $p<0.01$ ,  $df=969$ ; tree height:  $T=17.094$ ,  $p<0.01$ ,  $df=969$ ).

Number of stumps indicate past logging (highest in the low-lying forest and lowest in the higher strata). None of the forest types is primary *sensu stricto* because selective logging has affected all of them. Diversity varies greatly among forest types, with mixed forest being the most species-rich (58 species) and fir forest the most species-poor (4 species).

Lichen abundance is higher in temperate strata than in the subtropical stratum and increases with elevation. The only subtropical stratum is the low-altitude evergreen oak forest, which has only marginal lichen cover (lichen load index 0.5). Lichen cover is highest in high-altitude fir forest (2.4). Medium-altitude mixed forest has moderate lichen cover (1.3).

#### Overall Preferences for Floristic Strata

At Samage, *Rhinopithecus bieti* use mixed forest most frequently, followed by pine forest, sclerophyllous oak forest, and evergreen broadleaf forest. They use fir forest

**Table III** Percentage of each vegetation type at the Samage Forest within Minimum Convex Polygon-based home range of the Gehuaqing group of *Rhinopithecus bieti* and observed number of location records per stratum in relation to availability

Vegetation type	Percentage	Expected no. of location records <sup>a</sup>	Observed no. of location records per stratum	Selection ratio	Preference, non-selection or avoidance
Pine forest	16.0	193.0	118	0.611	Avoided
Evergreen broadleaf forest	10.7	129.0	31	0.240	Avoided
Fir forest	37.8	455.9	22	0.048	Avoided
Mixed forest	25.8	311.1	993	3.19	Preferred
Sclerophyllous oak forest	9.7	117.0	42	0.359	Avoided

Open areas make up 22.5 % of the area, but were never used and thus we excluded them from the analyses.  $n=1206$  location records.

<sup>a</sup>Based on proportional availability of habitat types.

(excluding open areas; Table III). They avoided clearcuts. We only very rarely encountered the band in severely degraded/altered forest. In our evaluation of habitat-selection ratios, they preferred mixed forest ( $S=3.19$ ), whereas they avoided all other vegetation types (Table III).

#### Habitat Use Across Seasons

We found a preference for mixed forest in all seasons and all months (Table IV) and avoidance or no selection of sclerophyllous oak, evergreen broadleaf, fir, and pine forest in all seasons/months. There is one exception: in September, they preferred pine forest ( $S=1.44$ ).

#### Vertical Migration Along an Altitudinal Gradient

Use of elevations by *Rhinopithecus bieti* varies significantly among seasons (Kruksal-Wallis,  $\chi^2=194.69$ ,  $df=3$ ,  $p<0.001$ ). The lowest recorded elevation is 2625 m; the highest one is 3793 m. We also found scat at 4014 m. The most frequently used altitudinal belt is 3000–3400 m, and the mean elevation is 3218 m. The range of elevations they used is widest in summer and narrowest in winter. The group stayed at higher elevations in summer than in other seasons, and at lower elevations in spring than in other seasons (Table V). The onset of winter did not result in use of lower elevations relative to fall (Mann-Whitney,  $U_{238,172}=18687$ ,  $Z=-1.505$ ,  $p=0.132$ ). However, the group descended temporarily in winter as a result of severe snowstorms; e.g., on March 11, 2006, we located them at 3500 m, and after 32 mm of snow had fallen at base camp in the meantime, the group was at 3100 m on March 13. The range of elevations covered was higher in spring/summer (1168 m) than in fall/winter (880 m).

Grueter *et al.* (2008) presented data on phenology. Monthly mean altitude is not correlated with availability of young leaves ( $r_s=0.055$ ,  $p=0.866$ ,  $n=12$  mo). This relationship is obscured because the time of emergence of sprouts depends on elevation, i.e., leaves appear to mature earlier at lower elevations. However, monthly

**Table IV** Location records ( $n=1206$ ) of the group of *Rhinopithecus bieti* in the Samage Forest in 2005/06 with note on habitat type used in different months and seasons

	Mixed forest	Pine forest	Sclerophyllous oak forest	Evergreen broadleaf forest	Fir forest
November	69	7	0	0	0
December	89	1	0	0	0
January	33	0	0	4	0
February	28	0	0	0	7
March	103	11	0	6	0
April	97	19	0	7	0
May	85	0	0	0	0
June	51	0	0	0	0
July	75	0	0	4	0
August	78	3	4	0	15
September	206	71	31	0	0
October	79	6	7	10	0
Winter	150	1	0	4	7
Spring	285	30	0	13	0
Summer	204	3	4	4	15
Fall	354	84	38	10	0

Meadows are excluded.

mean altitude correlates highly positively with availability of fruits ( $r_s=0.729$ ,  $p=0.007$ ,  $n=12$  mo; Fig. 3). In months with high fruit availability, the band stayed at mid-altitudes where favored fruits such as *Acanthopanax evodiaefolius* (Araliaceae), *Sorbus* spp. (Rosaceae), and *Cornus macrophylla* (Cornaceae) are most common (Grueter *et al.*, *in prep.*; Fig. 4).

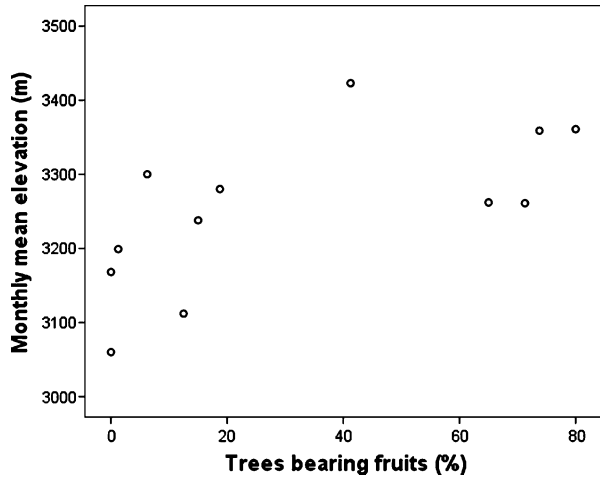
**Table V** Monthly variation in elevational ranging of the Gehuaqing band of *Rhinopithecus bieti* in the Samage Forest in 2005/2006

Month	No location records	Mean elevation (m)	SD <sup>a</sup>	Minimum elevation (m)	Maximum elevation (m)	Elevational range <sup>b</sup>
January	40	3112	98	2951	3225	274
February	42	3300	199	3100	3747	647
March	120	3199	154	2748	3600	852
April	124	3060	187	2625	3375	750
May	89	3168	97	2962	3400	438
June	53	3423	126	3088	3604	516
July	82	3261	187	2674	3546	872
August	103	3361	154	3147	3793	646
September	55	3381	182	3032	3756	724
October	107	3052	122	2876	3335	459
November	76	3280	128	3080	3568	488
December	90	3238	87	3023	3400	377
Spring	333	3139	167	2625	3600	975
Summer	238	3341	172	2674	3793	1119
Fall	238	3201	197	2876	3756	880
Winter	172	3224	142	2951	3747	796

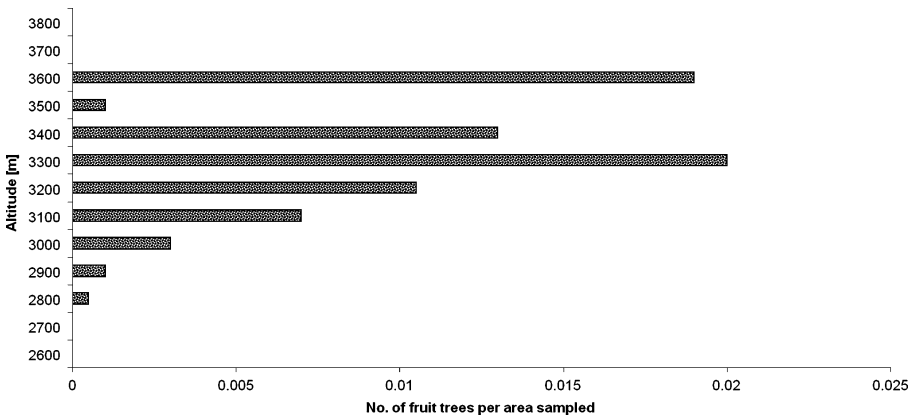
<sup>a</sup> Standard deviation.

<sup>b</sup> Highest elevation minus lowest elevation in any month.

**Fig. 3** Correlation between monthly mean elevation of the band of *Rhinopithecus bieti* at Samage and monthly fruit availability at the Samage Forest.



There is neither a significant correlation between monthly rainfall and monthly mean altitude used ( $r_s=0.294, p=0.354, n=12$  mo) nor between monthly temperature and monthly mean altitude ( $r_s=0.350, p=0.264$ ). Nevertheless, summer had the highest temperature and rainfall at base camp, and the group stayed at the highest elevations where temperature and precipitation were lower. Perhaps human activities affect the seasonal altitude of the band as well: the largest number of people in the forest occurs in summer, and the band stayed at the highest elevations then.



**Fig. 4** Abundance of major fruit trees (*Sorbus* spp., *Cornus macrophylla*, *Acanthopanax evodiaefolius*) among different altitudinal zones at the Samage Forest. The main fruit trees comprise 138 trees out of 1851 marked trees in vegetation plots. To take into account different sampling effort at each elevation, we calculated the number of fruit trees per area sampled. The number of fruit trees (FT) and the size of the area sampled at each elevation is: 2600 m, 0.2 ha, 0 FT; 2700 m, 0.2 ha, 0 FT; 2800 m, 0.2 ha, 1 FT; 2900 m, 0.2 ha, 2 FT; 3000 m, 0.44 ha, 14 FT; 3100 m, 0.28 ha, 20 FT; 3200 m, 0.4 ha, 42 FT; 3300 m, 0.08 ha, 16 FT; 3400 m, 0.2 ha, 26 FT; 3500 m, 0.16 ha, 2 FT; 3600 m, 0.08 ha, 15 FT; 3700 m, 0.2 ha, 0 FT; 3800 m, 0.04 ha, 0 FT.

**Table VI** Climate data compared among localities where researchers have studied *Rhinopithecus bieti*

Site	Altitude <sup>a</sup> (m)	Highest temperature (°C)	Month highest temperature (°C)	Lowest temperature (°C)	Month lowest temperature (°C)	Mean annual temperature (°C)	Annual precipitation (mm)	Reference
Wuyapiya	4250	16	Jun (5.7)	-13	Feb (-4.9)	0.9	936	Kirkpatrick 1996; Kirkpatrick <i>et al.</i> 1998
Xiaochangdu	3800	26.9	Aug (12.5)	-15.4	Jan (-3.6)	4.7	740	Xiang 2005
Longma			Aug (14.3)		Jan (1.9)	8.8	1501	Huo 2005
Xiangguqing/Tacheng	2800		Jun (14.9)		Jan (0)	7.5		Ding and Zhao 2004
Fuhe	3100	28.1	Jun (14.8)	-9.8	Jan (-0.5)			Liu and Zhao 2004
Jinshichang	3280	20	Aug (12.7)	-13	Jan (-3.8)	5.8	1624	Ren unpubl.; Yang 2000
Samage/Gehuaqing	2448	35.4	Jul (21.5)	-3.6	Dec (8.3)	14.5	921	This study

<sup>a</sup> Altitude at which researchers collected climatic data.

## Discussion

### Climate and Vegetation at Samage and other Localities

Striking seasonal variation in ambient temperatures typifies all localities where researchers have studied *Rhinopithecus bieti* (Table VI). The average ambient temperature at Gehuaqing/Samage is higher than at the other sites; however, one can partly attribute the divergence to the fact that we recorded the climatic data about 700 m below the most frequented elevation of the focal group. More northern areas, i.e., Wuyapiya and Xiaochangdu, tend to be colder than more southern areas owing to higher elevation.

George fir (*Abies georgei*) typically grows at the highest elevations at all study sites (Table VII). Stands of montane sclerophyllous oak are also major components of most sites. Samage appears to be the only locality where subtropical mesophytic evergreen broadleaf forest occurs (cf. Huo *et al. unpubl.*). At other sites, e.g., Wuyapiya, low-lying valleys have a completely different vegetation community, i.e., sparse dry scrub (MacLennan 1999) and chaparral (Kirkpatrick 1996).

Plant communities vary along an elevational gradient at a single site as well as along a north-south gradient across the whole geographical distribution of *Rhinopithecus bieti*. Specifically, botanical diversity and prevalence of angiosperm trees increases from north to south (cf. Long *et al.* 1994). Increased richness at more southern locations presumably relates to higher amounts of precipitation there.

### Seasonal and Overall Preferences for Particular Habitats and Comparison with other Studies

Preferences for particular macro- and microhabitats in primates as a whole depend largely on the availability of food (Gautier-Hion *et al.* 1981; Hashimoto *et al.* 1998) and risk of predation (Cowlshaw 1997; Enstam and Isbell 2004). We have no evidence of predation threat being lower in the frequently used forest types at Samage. The group of *Rhinopithecus bieti* at Samage did not use the study area homogeneously, but instead showed a clear preference for mixed forest.

The location records of mixed forest comprise 82% of all positions. Mixed forest is distributed between 2900 and 3600 m, which corresponds to the most frequently utilized altitudes of *Rhinopithecus bieti* at Samage. We suspect that food resource abundance in the stratum accounts for its preferred use. Mixed forest contains the highest diversity of tree species and the highest variety of food items. Ding and Zhao (2004) and Liu *et al.* (2004) previously documented the importance of mixed forest in providing food sources at other sites. Lichen load is intermediate there, but the temporal appearance of fruits and sprouts makes the stratum nutritionally valuable. Mixed forest is also the forest type where most of the sleeping sites occur (Li *et al.* 2007).

Researchers consider pine forest to be unsuitable habitat (Xiao *et al.* 2003; Huo *et al. unpubl.*) and use of the stratum as aberrant, e.g., induced by human herding. However, our results demonstrate that the Gehuaqing group spontaneously visits pine forest from time to time. Ding and Zhao (2004) also noted that the group at Xiangguqing occasionally spent time in secondary warm-temperate conifer forest,

**Table VII** Availability of vegetation types at other sites where researchers have studied *Rhinophilicus bieti*<sup>a</sup>

Vegetation types	Fuhe	Xiaochangdu	Longma	Jinsichang	Samage	Wuyapiya/ Namren
Montane conifer forest	<i>Abies</i> sp., <i>Tsuga</i> sp., <i>Larix</i> sp. 3100–3400 m	Primary and secondary forest with <i>Picea likiangensis</i> , <i>Abies squamata</i> 3000–4200 m	<i>Abies georgei</i>	Primary forest with <i>Abies georgei</i> , <i>Larix</i> sp., <i>Picea likiangensis</i> <i>Rhododendron</i> sp., <i>Fargesia</i> sp. 3300–3900 m	<i>Abies georgei</i> , <i>Rhododendron</i> spp. 3500–4000 m	<i>Abies georgei</i> , <i>Rhododendron</i> spp., <i>Larix</i> sp. ca. 3800–4400 m
Deciduous broadleaf forest	<i>Sorbus</i> sp., <i>Acanthopanax evodiaefolius</i> , <i>Fargesia</i> sp., <i>Betula</i> sp. 2700–3100 m	<i>Betula</i> sp., <i>Populus</i> sp. >3200 m	(Yes)	<i>Betula</i> sp., <i>Populus</i> sp., <i>Fargesia</i> sp. 3000–3200 m	No	Yes
Mixed broadleaf/ conifer forest	<i>Rhododendron</i> sp., <i>Abies</i> sp., <i>Tsuga</i> sp. 2900–3200 m	Not specified	Yes	<i>Betula</i> sp., <i>Populus</i> sp., <i>Picea likiangensis</i> , <i>Fargesia</i> sp. 3200–3300 m	<i>Acanthopanax evodiaefolius</i> , <i>Sorbus</i> spp., <i>Acer</i> spp., <i>Betula</i> spp., <i>Quercus rehderiana</i> , <i>Picea likiangensis</i> , <i>Tsuga dumosa</i> , <i>Rhododendron</i> spp., <i>Fargesia</i> spp. 2900–3600 m	<i>Abies georgei</i> , <i>Picea</i> sp., <i>Populus</i> sp., <i>Quercus</i> sp., <i>Rhododendron</i> sp., <i>Betula utilis</i> 3600–3800 m
Pine forest	No	No	<i>Pinus</i> spp.	No	<i>Pinus yunnanensis</i>	<i>Pinus</i> spp. <3600 m



Evergreen sclerophyllous oak forest	No	<i>Quercus aquifolioides</i> >3200 m	<i>Quercus pannosa</i>	Yes	2500–3100 m <i>Quercus pannosa</i> 3200–3500 m	<i>Quercus pannosa</i> Mainly 3600–3800 m
Bamboo	<i>Fargesia</i> sp., <i>Rhododendron</i> sp.	No	Yes	<i>Fargesia</i> sp. 2900–3900 m	<i>Fargesia</i> spp. <sup>c</sup>	No
Open areas	Not specified	<i>Sabina</i> and <i>Rhododendron</i> shrubs above treeline	Grasslands, shrubs	No	Alpine herbfields, mountain shrublands (e.g. <i>Rhododendron</i> ), summer grazing land, grassy meadows, scree, agricultural land	Alpine meadows, heath, scree, <i>Rhododendron</i> thickets >4200 m; Chaparral and barren rock <3400 m
Subtropical evergreen broadleaf forest	No	No	<i>Quercus acutissima</i> , <i>Lithocarpus dealbatus</i>	No	<i>Cyclobalanopsis</i> sp. 2500–3000 m	No
Other		Larch forest; <i>Larix griffithiana</i> , <i>Rhododendron</i> spp. 3000–4200 m	Stands of azalea; <i>Rhododendron</i> sp.(p.) <sup>b</sup>			

<sup>a</sup> We extracted data from the following sources: Samage; Ding and Zhao 2004; Li *et al.* 2007; this study; Wuyapiya/Namren: Cui 2003; Kirkpatrick 1996; MacLennan 1999; Jinsichang: Yang 2000; Ren B, *unpubl.*; Xiaochangdu: Xiang 2005; Xiang *et al.* 2007; Longma: Table II in Long *et al.* 1994; Fig. 9 in Huo 2005; Huo *et al.* *unpubl.*; Table V in Xiang *et al.* 2007; Fuhe: Liu and Zhao 2004; Liu *et al.* 2004.

<sup>b</sup> Whether these are trees or shrubs or both is not specified.

<sup>c</sup> Bamboo is found in the undergrowth of virtually every forest type.

i.e., pine forest. The underlying cause for the preference of pine forest in September remains unclear. However, as a whole, no selection is shown for pine forest in fall and annually. The main canopy species—*Pinus yunnanensis*—has no food value for the snub-nosed monkeys. Seeds of *Pinus armandii* are an important part of the late fall/winter diet for both *Rhinopithecus bieti* at other sites (Huo *et al.* unpubl.) and *R. roxellana* (Li 2006), but we have not witnessed ingestion of the seeds at Samage. *Pinus armandii* is equally associated with mixed forest and pine forest at Samage, and occurs at fairly low stem densities in both strata. Pine forest has a moderate lichen density. Pine forest often covers some of the lower ridges, and some of the band's frequently used travel routes leading from one patch of mixed forest to another cross the stratum. Accordingly, we assume that pine forest acts as a corridor and is visited by the band in transit. Yunnan pine forest also has an economically precious resource for humans: the highly prized Matsutake mushrooms. It is thus frequently visited by mushroom hunters in summer and fall, which may prevent the monkey group from moving into pine forest and may obstruct their passage to other patches of mixed forest.

Researchers have viewed *Rhinopithecus bieti* as inseparable from cool fir forest or dark conifer forest. However, dark conifer forest is evidently not the preferred habitat type at Samage. Occasional visits to this stratum in winter may be to obtain omnipresent beard lichens of *Usnea* and *Bryoria*, which are more abundant in fir forest than in other strata and form the staple food of the Gehuaqing band (Grueter *et al.*, submitted). Contrary to groups living in the north, the group at Samage is not as strictly dependent on lichens; they use a range of alternative nonlichen food items such as fruits, which may explain why fir forest is uncommonly visited by them. Owing to the fir forest's location on semi-isolated hilltops at the highest elevations, the band is obliged to traverse through this forest when crossing ridges and thus use it transiently. Several investigations at different localities provided evidence that high-elevation conifer forest is rarely (mostly in summer) or never used by *Rhinopithecus roxellana* in relation to deciduous broadleaf forest and (to a lesser degree) mixed forest (Hu *et al.* 1980; Li and Liu 1994; Li *et al.* 2000; Tan *et al.* 2007; Zhang 1995). Similarly, *Macaca fuscata* in the Shiga Heights avoid the conifer zone and stay in the broadleaf zone (Wada and Ichiki 1980).

Lush semihumid evergreen broadleaf forest is confined to valley bottoms, and the monkeys use it often in passage from one mountain slope to another. The forest also contains ample water sources, and group members drink from streams there. Further, the season with the highest number of positional records in the stratum is spring. In early spring, shoots emerge first at lower elevations (Ding and Zhao 2004), possibly causing the band to move along this low-lying altitudinal zone, which inevitably results in visits of evergreen broadleaf forest. Current anthropogenic activities such as illegal logging may have caused the overall avoidance of this forest type, and it seems that it was also avoided in the past when mass killings of snub-nosed monkeys for food and commercialization took place there in the 1960s and 1970s (Feng Shunkai, *pers. comm.*).

We have only rarely observed feeding on acorns at our site, but Xiang *et al.* (2007), noted that the group at Xiaochangdu visited sclerophyllous oak forest for acorns in fall and winter. High lichen availability and seasonal occurrence of acorns may explain why the Gehuaqing band used the forest type particularly often in fall.

A probable explanation for the total avoidance of open areas includes the absence of tall trees providing cover and the cattle grazing during the warmer months. At Samage, grasslands have a few bushes with berries, but are otherwise of minor importance with regard to food sources. Li (2004) also found that groups of *Rhinopithecus roxellana* at Shennongjia did not use grassland. At Zhouzhi, monkeys used clearcuts and heavily logged forests in transit (Guo 2004; Tan *et al.* 2007).

### Seasonal Altitudinal Migration

The Gehuaqing group showed seasonal adjustments in use of altitudes and basically stayed at relatively high elevations in summer, low elevations in spring, and moderate elevations in winter and fall. Our data precisely correspond to Cui (2003), whose results are based on indirect estimations using distribution of feces of a monkey group at Baimaxueshan North. Yang (2003) investigated seasonal distribution of feces of the Jinsichang group along an elevational gradient and found a comparable result: summer > fall > winter/spring. Liu *et al.* (2004) lumped 2 seasons together and found the following pattern for the group at Fuhe: summer/fall > winter/spring. In addition, the West Ridge troop of *Rhinopithecus roxellana* exhibited an analogous pattern of altitudinal ranging: summer > fall > winter/spring (Li *et al.* 2000). The results of the latter 3 studies diverge from ours insofar as they also demonstrated use of lower elevations in winter. Apart from the discrepancy as to the descent in winter, the existing evidence indicates that altitudinal ranging in snub-nosed monkeys may follow a general underlying principle, i.e., it is influenced primarily by diet and only marginally by climate and human encroachment.

Evidence for a descent in winter as a response to cold has been mixed. For instance, Yang (2003) found a positive correlation between temperature and elevational distribution of the Jinsichang band, whereas others found that the monkeys constantly chose the upper forest sections, even in cold snowy winters (Cui and Zhao 2002; Zhao *et al.* 1988). Even though movements to low elevations do not appear to be a general feature of ecology of *Rhinopithecus*, researchers have observed short-term descents to lower altitudes as a result of heavy snowstorms (Cui 2003; Kirkpatrick and Long 1994; Li *et al.* 2000; Shi *et al.* 1982; Tan 1985; Xiang 2005; this study). Our observation that snub-nosed monkeys remained at fairly high elevations when temperatures dropped in winter lets us conclude that they do not fine-tune their altitudinal ranging pattern in a systematic way to climate by staying at lower elevations when temperatures drop in winter and staying at higher elevations when temperatures rise in spring. However, inclement weather conditions such as heavy snowfalls and snowstorms seem to force them to move temporarily down into the valley with milder temperatures and shallower snow.

Winter cold did not affect altitude use; conversely, summer heat may have had an effect. In summer, the band possibly sought refuge at high elevations and thereby escaped the heat at lower elevations. Even though the correlations are not significant, summer had the highest temperature and rainfall at base camp, and the Gehuaqing group stayed at the highest elevations where temperature is *ca.* 5°C lower and there is less rainfall (*cf.* Li 1993). Li *et al.* (2000) also hypothesized that *Rhinopithecus roxellana* look for cooler high-elevation places in summer.

**Table VIII** Habitat association and altitudinal distribution of groups of *Rhinopithecus bieti*<sup>a</sup>

Site	Lowest elevation (m)	Highest elevation (m)	Mean elevation (m)	Geographical area	Mainly used forest type	
Wuyapiya	3300	4600	4080	North	Fir	Kirkpatrick <i>et al.</i> 1998
Nauren	3500	4300	ca 4050	North	Fir	Cui 2003
Xiaochangdu	3500	4250	4031	North	Fir	Xiang 2005
Gehuaqing/Samage	2625	4014	3218	Middle	Mixed	This study
Xiangguqing	2700	3700	ca 3200		Mixed	Ding 2003
Fuhe	2800	3400	3105	South	Mixed, fir and deciduous broadleaf	Liu <i>et al.</i> 2004; Liu and Zhao 2004
Jinsichang	3200	3630	3500	South	Mixed <sup>b</sup>	Yang 2003; Ren unpubl.
Longma	2700	3600	3024	South	Mixed	Huo 2005
Zhina	–	–	–	–	Fir and evergreen oak <sup>c</sup>	Xiang <i>et al.</i> 2007
Milaka	–	–	–	–	Fir and evergreen oak <sup>c</sup>	Xiang <i>et al.</i> 2007
Bamei	–	–	–	–	Cypress	Zhong <i>et al.</i> 1998

<sup>a</sup> Elevation data also based on scat findings.

<sup>b</sup> Yang (2000), however, claims that dark conifer forest constitutes the main type at Jinsichang.

<sup>c</sup> Possibly of the sclerophyllous type.

In montane primates, the lower end of their elevational range is often set by human colonization. However, it is still not entirely clear to what degree human presence and activities inside the habitat impinge upon altitudinal range use in *Rhinopithecus bieti*. MacLennan (1999, p. 9) stated that “there appears to be a strong correlation between seasonality of valley use by the monkeys and an absence of human activity in that area, with monkeys apparently using sites just before or just after peak human activity.” However, Kirkpatrick *et al.* (1998) concluded that human activity did not appear to influence the mean altitude of the Wuyapia band, living close to herders yet remaining at high altitudes when human activity >3500 m was minimal. At our site, the evidence is also ambiguous, and no strong effect of human activities on general range use is evident (Grueter *et al.* 2008). Increased anthropogenic pressure in summer may have brought about a consequent upward movement. Contrary to expectations, when human encroachment as a constraining factor was minimal or absent in winter, the group still used fairly high elevations.

That diet is the driving force behind altitude use is manifested in many ways. Leafing or flush of deciduous trees in spring is assumed to have triggered the use of lower elevations. Immature leaves form a dominant constituent of the snub-nosed monkey diet in spring and become available earlier at low than at high elevations (*cf.* Cui 2003; Hu *et al.* 1980; Li *et al.* 2000; Shi *et al.* 1982). The Gehuaqing group covered a wider range of altitudes in spring-summer (when young leaves were available) compared to fall-winter (when young leaves were absent). Moving along an ascending altitudinal gradient during spring-summer ensures fitness gains via a prolonged access to newly emerging foliage of high nutritional quality (Guo 2004; Tan *et al.* 2007; *cf.* Mysterud 1999).

As evidenced by a highly significant correlation between monthly fruit availability and altitudinal distribution of the band, fruiting also has a strong effect on altitude use. In fall, when fruit availability was maximal, the focal group confined their ranging to moderate altitudes where the density of preferred fruits is highest. Even in winter, the band kept foraging at middle altitudes in search of fruits from the preceding fruiting season.

Because one can rule out climate as a general determinant of altitude use, the focal group’s occupancy of relatively high altitudes in winter is likely related to higher concentrations of lichens at higher elevations (*cf.* Kirkpatrick and Gu 1999; Kirkpatrick *et al.* 1998; Shi *et al.* 1982). Cui (2003) further confirmed the relationship between food density and altitudinal ranging, finding more feces at altitudinal zones with dense lichen cover. Our study corroborates the findings: lichens as the major winter food occur at higher densities at higher elevations at Samage (Grueter *et al.*, submitted). The arguments are fundamentally similar to Sugiyama’s (1976) observations of *Semnopithecus schistaceus* remaining at high altitudes in winter owing to greater abundance of conifer-based foods. Likewise, Mehlman (1986) observed that Barbary macaques (*Macaca sylvanus*) stayed at highest altitudes in snowy winter because their main food—fir foliage—occurs at high altitudes.

Harvest of bamboo shoots (*Fargesia* spp.), which represent a seasonally important food source (Ding and Zhao 2004), may also have caused the band to seek higher altitudes in summer. Bamboo shoots as a seasonal key resource also influence range use of Grauer’s gorillas (*Gorilla beringei graueri*) at Mt. Kahuzi,

which show an annual cycle of migration corresponding to the availability of bamboo shoots (Casimir and Butenandt 1973).

### What Constitutes the Natural Habitat of *Rhinopithecus bieti*?

An understanding of a species' extant habitat requirements is incomplete without considering palaeobiogeographic events and the history of anthropogenic habitat alteration. Environmental fluctuations during the Quaternary period are assumed to have influenced the distribution and habitat association of snub-nosed monkeys (Jablonski 1993; Kirkpatrick 1998). For example, the termination of the glacial periods in the Holocene brought about vegetation changes along an elevational gradient. Fir forest subsequently became restricted to mountain ridges, and the reduction in fir forest reduced the range of *Rhinopithecus bieti*. Anthropogenic forces (population explosion, deforestation, cultivation) in recent and historic times have led to large-scale destruction of suitable habitat at medium elevations and extinction of some populations of *Rhinopithecus bieti*. This is corroborated by the fact that historical records document populations of *Rhinopithecus bieti* farther south than their current distribution. The historic distribution of Chinese snub-nosed monkeys in general also included lowlands in several provinces and has become gradually confined to the highlands through the combined effects of habitat destruction and hunting (Li *et al.* 2002a, b, 2003).

Researchers initially considered *Rhinopithecus bieti* to be a characteristic species of the high-elevation fir forest ecosystem. Even recent reviews proclaim that *Rhinopithecus bieti* is "definitely associated with fir forest" (Li *et al.* 2003, p. 38). However, researchers subsequently found that the taxon in fact exhibits a greater diversity and flexibility with regard to habitat affiliation. Similarly, early observations of Barbary macaques living in several habitats in the Mediterranean climatic zone of North Africa suggested that they were cedar forest specialists (Taub 1977). However, a reexamination of data on distribution and abundance refuted the idea of cedar forests constituting their preferred habitat and instead revealed that their primary occurrence there is an artifact produced by elimination from other forest types due to historic anthropogenic forest destruction (Fa 1984).

The fact that an array of discrete vegetation types occurs within the home range of the more or less free-ranging group of *Rhinopithecus bieti* at Samage provides a good opportunity to investigate habitat association patterns. Our findings that cold temperate fir forest is largely avoided by *Rhinopithecus bieti* provides strong evidence that milder mixed forest may represent their characteristic habitat and that high dependence on fir forest as shown by some groups living in the far north may be at least partly a consequence of past human habitat modification.

Habitat association and altitudinal distribution of most known groups of *Rhinopithecus bieti* are provided in Table VIII. Fir forest typifies for the most part the habitat in Tibet and other localities in the north, whereas more mixed forests are found in more southern regions. Mixed forest occurs at localities in the north as well, but may differ from the mixed forest at more southern localities by being less nutritionally valuable and having a different species composition.

## Implications for Management and Conservation

If animals select habitat and habitat-specific resources disproportionate to their availability, it is commonly concluded that the habitat or resource is of relatively higher quality and enhances fitness, i.e., survival or fecundity. Thus, researchers often use data on habitat selectivity to manage supposedly important habitats for the target population. However, frequent use may not correlate with habitat quality and suitability and fitness (Garshelis 2000; Hobbs and Hanley 1990; Jones 2001). Correspondingly, infrequent use may not indicate lack of suitability. Garshelis (2000, p. 150) noted that “a habitat may be used infrequently because it serves little value, because its value can be extracted in a short amount of time, because it is not readily available, or because access is constrained by threats (social pressures, competition, predation) or physical barriers.” Thus one can better view infrequently used habitats as ones of relatively little value instead of being unsuitable. For example, the monkeys may use sclerophyllous oak forest less because it is not readily available at Samage. They might use even cool temperate fir forest slightly more often if it were not semi-isolated due to man-made barriers, i.e., grazing land. The value of pine forest and evergreen broadleaf forest can be extracted in a short amount of time because they serve mainly as transit habitats (both) and watering places (evergreen broadleaf forest only).

All forest types at Samage show signs of human alteration, mainly in the form of past and present selective wood extraction for commercial and subsistence purposes. The forest types least affected are sclerophyllous oak and fir forests. The lower areas of the pine forest zone close to the agricultural fields are the main source of firewood and construction material and hence the target of intensive tree cutting. The snub-nosed monkeys never used the buffer zone.

Even though Baimaxueshan Nature Reserve was primarily set up to promote protection of the snub-nosed monkeys, the heterogenous habitat with interspersed grazing land implies that large areas of the reserve do not represent monkey habitat. Though *Rhinopithecus bieti* is semiterrestrial (Xiang 2005) and researchers have occasionally observed individuals going to open areas (Kirkpatrick 1996), we have no location record for open areas. Hence clear-cutting is assumed to have a fatal effect by rendering the areas uninhabitable to the monkeys.

The overwhelming preference for mixed forest by *Rhinopithecus bieti* underscores the significance of ensuring protection of this type not only at Samage, but also at other sites where black-and-white snub-nosed monkeys occur and where some type of habitat manipulation is proposed. Evergreen broadleaf, pine and fir forests do not represent prime snub-nosed monkey habitat, but nevertheless provide vital forest corridors that must be preserved at all costs to maintain connection between forest patches.

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