



Fission–Fusion Behavior in Yunnan Snub-Nosed Monkeys (*Rhinopithecus bieti*) in Yunnan, China

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Abstract Several species of mammals live in relatively large social groups that temporarily fission or subgroup in response to changes in food availability, predation risk, foraging strategies, and mating competition. Although the dynamics of subgrouping are not well understood, evidence of facultative fission–fusion behavior in species that generally exhibit a highly cohesive group structure may help to clarify the set of ecological and social factors that constrain or affect group size in primates. We here examined patterns of subgrouping in Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) inhabiting the Baimaxueshan National Nature Reserve in Yunnan, China. *Rhinopithecus bieti* lives in a large multilevel society consisting of 6–41 one-male, multifemale units (OMUs) and one all-male unit (AMU). Over a 5-yr period from 2003 through 2008, we tracked a group of >450 *Rhinopithecus bieti*. We recorded the location in the group’s home range where fission and fusion events occurred, the size and number of subgroups, days spent in subgroups, and food availability, and monitored predator sightings. The results indicate that the focal group underwent 12 group fission events, all of which occurred between mid-June and July, and all in the same area of the group’s range. During these fissioning events, the AMU also showed subgrouping behavior. In all cases, the presence of bamboo shoots, an important seasonal component of the snub-nosed monkey diet, appeared to trigger subgrouping behavior. The subgroups reunited in other parts of their range after a period of 2–11 d. We found no evidence that the presence of predators had a direct affect on subgrouping behavior in *Rhinopithecus bieti*, as proposed in previous studies.

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Introduction

Many primate species forage and travel in cohesive social groups that remain stable in size and composition over the course of weeks, months, and in some cases years (Bowler and Bodmer 2009). In contrast, in taxa such as spider monkeys (*Ateles* sp.), chimpanzees (*Pan* sp.), and bonobos (*Pan paniscus*), individuals temporarily aggregate into small parties or subgroups that may change membership several times during the course of a single day (Aureli *et al.* 2008; Di Fiore *et al.* 2011; Stumpf 2011). In the multimale, multifemale social system with fission–fusion (FF) dynamics reported for *Ateles*, parties often consist of individuals of the same sex, and foraging and traveling party size correlate positively with the abundance of preferred, high-value food items in the habitat (Di Fiore *et al.* 2011). In the case of chimpanzee communities, party size appears to be positively influenced by the number of females in estrus and decreases during periods of food scarcity (Anderson *et al.* 2002). Bonobos, in contrast, subgroup into larger sized parties than chimpanzees, and the number of simultaneously estrous females has a less pronounced effect on party size (Stanford 1998). Both chimpanzees and bonobos exhibit an increase in party size at night, and this is believed to represent a response to increased predation risk (Stumpf 2011). A third form of primate social and spatial pattern occurs when a normally large cohesive group splits temporarily into two or more stable subgroups and later reunites after a period of several days (Kummer 1971). The precise social and ecological factors that promote FF behavior in primates that typically form large cohesive groups are not fully understood, but factors such as resource availability and distribution (Dunbar 1988; Ramos-Fernández *et al.* 2006), patch size (Chapman and Chapman 2000), group size and intragroup feeding competition (Asensio *et al.* 2009; Bai *et al.* 1987; Furuya 1969; Henzi *et al.* 1997; Janson and Goldsmith 1995), mating strategies (Stumpf 2011), and predation risk and predator detection (Bai *et al.* 1987; Lehmann *et al.* 2007) all are hypothesized to play a critical role.

Snub-nosed monkeys (*Rhinopithecus* spp.) form some of the largest groups (most >100 individuals) within the Colobinae (Hu *et al.* 1980; Kirkpatrick 1998; Liu *et al.* 2007) and among primates. While many studies have shown that these monkeys live in highly cohesive multilevel social groups composed of several one-male, multifemale and offspring units (OMUs) (*Rhinopithecus bieti*: Kirkpatrick 1998; Ren *et al.* 2008, 2009; Wu 1993; *R. roxellana*: Li *et al.* 2000; Ren *et al.* 2001; Tan *et al.* 2007) and associated all-male units (AMUs), evidence from a few populations of *Rhinopithecus bieti* (Bai *et al.* 1987) and *R. roxellana* (Deng *et al.* 1981; Hu *et al.* 1980; Kirkpatrick *et al.* 1999; Shi *et al.* 1982) indicates that subgroups occasionally form during the day and then later reunite when returning to their common sleeping site (Schaller *et al.* 1985). In the case of *Rhinopithecus roxellana*, researchers have suggested that larger group size among Sichuan populations promotes subgrouping behavior whereas in the smaller Shaanxi populations (<100 individuals; Li *et al.* 2000; Ren *et al.* 2001; Tan *et al.* 2007) subgrouping has not been reported (Kirkpatrick 1998).

To examine the possible effects of large group size on subgrouping behavior in snub-nosed monkeys, we selected the Xiangguqing population of *Rhinopithecus bieti* as our focal group. This group was reported to contain some 366 individuals in 2001 (Ding and Zhao 2004; Li *et al.* 2010; Liu *et al.* 2007). In a previous study of *Rhinopithecus bieti* in the Baimaxueshan Natural Reserve, Bai *et al.* (1987) argued that food distribution and availability did not influence subgrouping behavior. However, recent evidence showed that seasonally preferred foods, such as mountain ash fruits (*Sorbus* spp.), strongly influenced the ranging patterns of *Rhinopithecus bieti* (Grueter *et al.* 2008; 2009a). Bamboo shoots are also considered a preferred food of *Rhinopithecus bieti* (Ding and Zhao 2004; Grueter *et al.* 2009b), so we tested the hypothesis that changes in the availability of bamboo shoots (bamboo shoots are high in fiber, protein, lipids, and minerals such as potassium; Wang *et al.* 2009) have a significant effect on ranging and grouping patterns of *R. bieti* (Zhao *et al.* 2009).

Materials and Methods

Rhinopithecus bieti inhabits high-altitude conifer, evergreen, and bamboo forests in southwestern China. Forested habitats exploited by *Rhinopithecus bieti* range from 3000 to 4700 m in altitude, which is higher than that reported for any other nonhuman primate species (Long *et al.* 1994). At this elevation, 1–2 m of snow covers the ground during 2–4 mo of the year and mean monthly temperature in the winter averages only $0.7 \pm 5.2^\circ\text{C}$ ($N=131$ d; range: -8.3 to 13.6°C ; B. P. Ren, *unpubl. data*).

Focal Group

We conducted this study at Xiangguqing ($99^\circ 18'E$, $27^\circ 36'N$) in the 18,799-km² Baimaxueshan National Nature Reserve in Yunnan, China. Only one group of *Rhinopithecus bieti* inhabits this area. The reserve is characterized by extremely mountainous terrain and contains Yunnan pine (*Pinus yunnanensis*) forest, evergreen broadleaf forest, deciduous broadleaf forest, and coniferous mixed forest including stands of bamboo (*Fargesia* spp.), along with alpine patchy grass meadows and mountain shrublands (Ding and Zhao 2004). The monkeys range from an altitude of 2500 m to >3800 m. We began observing the study group on a daily basis in March 2003. At that time there were 331 monkeys in the group. In May 2008, the group had grown to 480 individuals (B. P. Ren, *unpubl. data*).

We first observed FF behavior in this group in late June and early July 2000, when the group of 210 individuals (Li *et al.* 2010) divided into two distinct subgroups of *ca.* 94 and 110 individuals. These subgroups traveled independently and were separated from each other by a distance of *ca.* 1.5 km. Two teams, each consisting of two or three reserve staff, followed the two subgroups until they merged together several days later. We did not record the particular location within their range where the group fissioned and then joined together, nor the activities of the subgroups while they were apart. Although this group was occasionally observed to fission temporarily over the next few years, we were unable to confirm the part of their range where the group split and merged until we began daily tracking in 2003.

From 2003 through 2008, we followed and monitored by daily direct observation the size of the focal group through accurate counts whenever the group moved or rested on the ground. On occasions when individuals subgrouped, we recorded the number of monkeys in each subgroup and calculated the ratio of smaller subgroup size/larger subgroup size. We also recorded the size of AMUs daily to monitor the transfer of juvenile and subadult males within the group. Using a Garmin® (Uni-Strong, Taiwan) handheld GPS receiver we recorded the spatial locations of feeding sites, midday resting sites, and nighttime sleeping sites. We calculated patterns of home range use and daily path length using ArcView™ 3.3 (ESRI Inc., Redlands, CA). We determined home range area (Fig. 1) using the minimum convex polygon method and daily path length via the three-site straight-line method (Ren *et al.* 2008, 2009). In addition, we analyzed changes in the ranging patterns of the focal group by comparing daily ranging paths taken by the focal group between 2005 and 2008 (Fig. 1).

Vegetation Data Collection and Diet

We recorded food species and plant parts eaten by *Rhinopithecus bieti* by direct observation using scan sampling (Altmann 1974). Given difficulties in following the monkeys across steep rocky slopes on extremely mountainous terrain, group scans varied in length from 1 to 15 min. During each group scan we recorded all observed feeding behavior, but acknowledge that some food species and plant parts consumed by the monkeys were likely missed due to limitations in visibility. Therefore, we categorized foods consumed by the focal group as staple (>80%), common (5–79%), and rare (<5%) based on a mean ratio of the number of times each plant species was eaten divided by the number of feeding records of that plant species. In total we collected 17,345 feeding scans from March 2003 to April 2008.

In addition, to determine dietary preferences for particular staple foods such as lichen (*Usnea longissima*) and bamboo shoots (*Fargesia yunnanensis*), we provided each of these foods to the monkeys on 20 d (08:30–17:00 h) as they moved on the ground across a commonly used travel route located in an area of treeless grassland. We placed equal amounts of lichen and bamboo shoots (1.5 kg) along the path. The provisioned area measured *ca.* 2 m×3 m and could accommodate only one OMU at a time (*ca.* 10 individuals). We used this research design to ensure that we could observe feeding behavior at the provisioned site directly, recording whether a particular food type was fed on first, and whether individuals consumed all or most of one food type before consuming the remaining food type. We assumed that the resource consumed first and consumed most was preferred over the remaining resource.

To determine whether the presence of bamboo shoots had an effect on group fissioning, we investigated the floristic composition of two sites, each located at the intersection of one of the group's major travel routes, and each 200 m²: the bamboo site and a comparison site (Fig. 1). The elevation of the comparison site was 3345 m, similar to the bamboo site (3370 m), so we assumed that the two sites maintained similar levels of plant diversity.

Ding and Zhao (2004) described vegetation in the study area in detail. We sampled bamboo productivity (*Fargesia* spp.) by identifying one 20 m×20 m plot on each of the four branches of the main travel path used by the monkeys when moving through

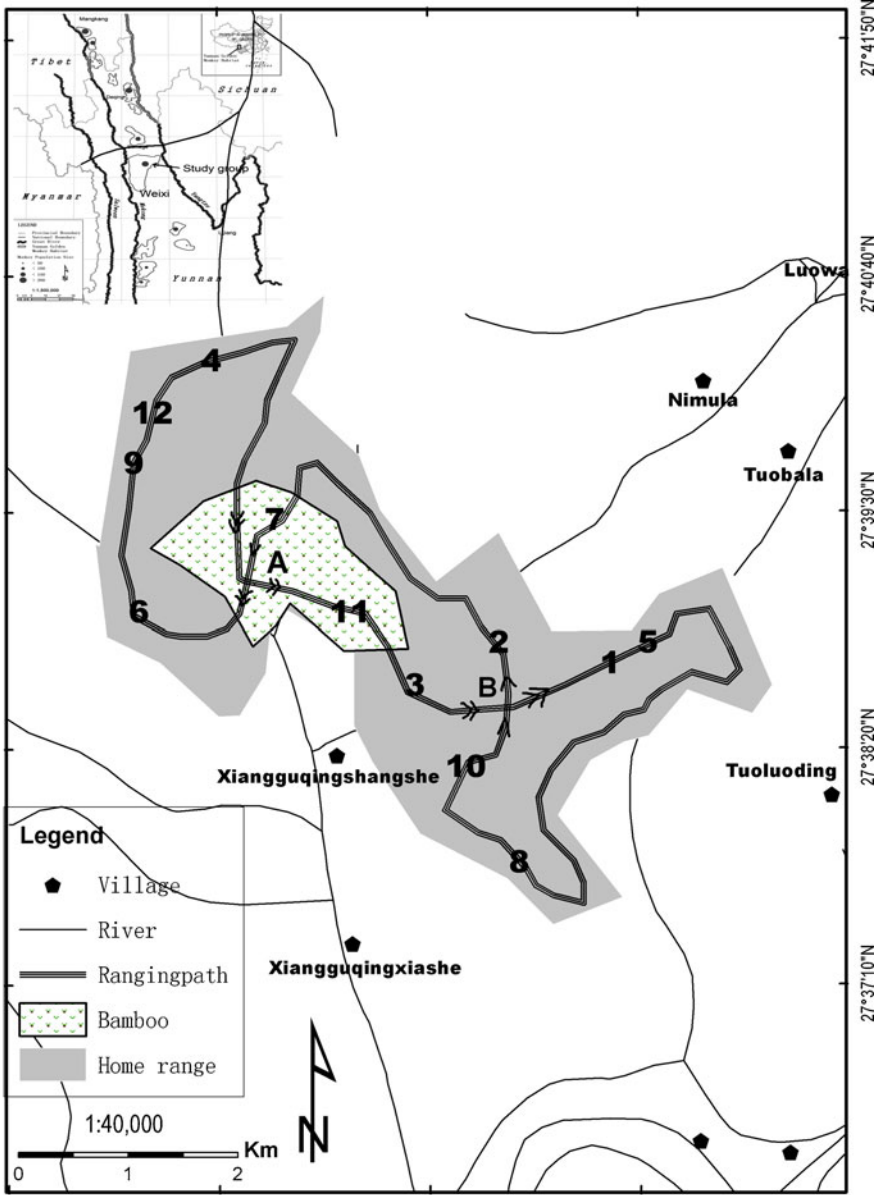


Fig. 1 Home range and travel paths used by the Xiangguqing group of *Rhinopithecus bieti* between 2006 and 2007. A indicates the site of group fissioning and B the comparison site. Both sites were located at the intersection of a major travel path habitually used by the study group. Arrows mark travel directions of the original group and subgroups (double arrows at site A) along traditional ranging paths. Arabic numbers indicate the location of the fusion sites where the two subgroups merged.

the bamboo area (Fig. 1) plus an additional 20 m×20 m plot at the precise location where group fissioning occurred (Fig. 2a). We noted the slope, aspect, number of trees and shrubs, and the diameter at breast height (DBH, in cm) and height (m) of the

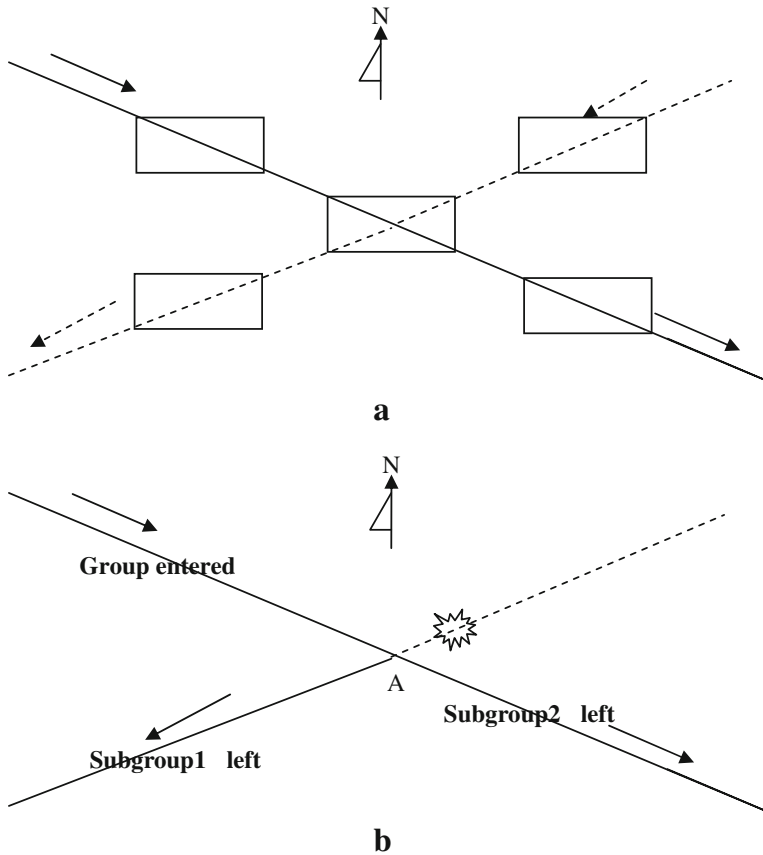


Fig. 2 **a** Directions traveled by the Xiangguqing group of *Rhinopithecus bieti* along its main travel routes at the fission site (A). We sampled five plots (rectangles) along these travel routes and at the intersection point. **b** The direction of travel taken by the entire focal group, and each subgroup after fissioning at site A. Subgroup 1 left the area and traveled southwest. Subgroup 2 left the area and traveled southeast, the same direction traveled before group fissioning. The starburst indicates that neither the original group nor either subgroup traveled along that route (compared with the same path in **a**).

most dominant trees in each plot. We also selected five 1 m×1 m areas within each plot to determine the number of bamboo plants, height (m), basal diameter (mm), and number of bamboo shoots. These five bamboo areas were located at the center and the four corners of each 20 m×20 m plot. We monitored the bamboo areas every 3 d in June and July during each of the 5 yr of our study ($N=10$ samples per area×5 areas×5 plots=250 samples per year). Given that the monkeys consumed only young bamboo shoots (<50 cm in height), we excluded older shoots (>50 cm in height) as a food resource. Bamboo shoots of *Fargesia* grow 0–50 cm in height in *ca.* 5 d, at which point the monkeys ceased eating them. On all days during which the focal group passed through the bamboo site, we counted the number of bamboo shoots <50 cm in height and used this as a measure of bamboo shoot availability to the focal group.

We set up five 20 m×20 m sample plots at the comparison site B (Fig. 2a), and recorded the slope, aspect, number of trees and shrubs, and the DBH (cm) and height (m) of the most dominant trees as in the bamboo site A. However, we did not

establish bamboo plots at the comparison site as bamboo did not grow in this part of the group's home range.

Because lichen, especially *Usnea longissima*, is a common nonseasonal food source for the monkeys during most of the year (Ding and Zhao 2004; Grueter *et al.* 2009a; Kirkpatrick 1998), we evaluated the lichen-load on each measured tree (DBH >8 cm) in all sample plots as per Grueter *et al.* (2009b).

Finally, we have monitored the presence of predators at our field site since 2003. This was accomplished by *ad libitum* recording (Altmann 1974) of all researcher-observed predator sightings, monkey predator alarm calls, and other predator-response behaviors of the monkeys.

Statistical Analysis

We calculated tree species diversity in the plots at the two sites using the Shannon–Wiener index (Krebs 1999):

$$H = - \sum [P_i \times \ln(P_i)]$$

where P_i = the proportion of each tree species in the sample.

We also used the following formula to determine the annual bamboo regrowth rate:

$$r = \frac{\text{no. of first year bamboo plants}}{\text{no. of } >1\text{-yr-old bamboo plants} + \text{no. of first-year bamboo plants}}$$

in the 1 m × 1 m bamboo areas

where “first-year bamboo plants” refers to young bamboo shoots >50 cm in height that the monkeys had fed on during that year, and “>1-yr-old bamboo plants” refers to live bamboo plants that survived for >1 yr.

We performed all statistical tests using SPSS® 15.0 for Windows (SPSS Inc., Chicago, IL). We used a Mann–Whitney U test to detect differences in tree species diversity between the bamboo site and the comparison site. We used a Kolmogorov–Smirnov one-sample test to compare plant species diversity at the bamboo site with plant species diversity at the other four 20 m × 20 m vegetation plots. We used χ^2 tests to compare the frequencies at which the subgroups reunited in the bamboo forest compared to other areas of their home range and to evaluate variation in subgroup size. All analyses were two-tailed, with the significance level set at 0.05. We present data in the form of mean ± SD.

Results

Food and Food Preference in June and July

During June and July in 2003–2008, we identified >32 food species eaten (Table 1) by members of our focal group at the bamboo and comparison sites (Fig. 1). Overall, the main plant parts consumed were leaves, flowers, fruits, lichens, and bamboo shoots. Thirteen plant species were categorized as staple foods and these accounted for 83.6% of total feeding records. In particular, bamboo shoots (*Fargesia* spp.) were consumed on 28 of 177 observations days during June and July from 2005 to 2007,

Table 1 Foods and food preferences of the Xiangguqing group of *Rhinopithecus bieti* in June and July

Food species	Parts eaten	Preference rank
<i>Usnea longissima</i>	All parts	I
<i>Schisandra rubriflora</i>	Flowers and fruits	II
<i>Aquilegia rockii</i>	Leaves and tenderstems	I
<i>Cimicifuga foetida</i>	Acrial part	I
<i>Clematis</i> spp.	Leaves and flowers	I
<i>Impatiens delavayi</i>	Acrial part	II
<i>Ribes glaciale</i>	Leaves and flowers	I
<i>Ribes longeracemosum</i>	Leaves and flowers	III
<i>Deutzia glomeruliflora</i>	Leaves	III
<i>Cotoneaster microphyllus</i>	Leaves and fruits	II
<i>Pyrus pseudopashia</i>	Leaves and flowers	II
<i>Sorbus</i> spp.	Leaves and flowers	I
<i>Spiraea lichiangensi</i>	Leaves and flowers	II
<i>Populus bonatii</i>	Leaves and flowers	II
<i>Salix radinostachya</i>	Leaves and flowers	III
<i>Pilea fasciata</i>	Leaves	I
<i>Euonymus frigidus</i>	Leaves and flowers	II
<i>Euonymus tingens</i>	Leaves and flowers	I
<i>Ilex delavayi</i>	Leaves and flowers	I
<i>Acer davidii</i>	Leaves	II
<i>Acer</i> spp.	Leaves	III
<i>Acanthopanax evodiaefolius</i>	Leaves	I
<i>Lyonia ovalifolia</i>	Leaves	III
<i>Rhododendron yunnanesis</i>	Leaves and flowers	II
<i>Rhododendron</i> spp.	Flowers	III
<i>Dipelta yunnanesis</i>	Leaves and fruits	II
<i>Lonicera hispida</i>	Leaves and fruits	I
<i>Viburnum</i> spp.	Leaves and fruits	II
<i>Smilacina</i> spp.	Acrial part	I
<i>Trillium tschonokii</i>	Acrial part	II
<i>Smilax menispermoidea</i>	Leaves	II
<i>Fargesia</i> spp.	Leaves and bamboo shoots	I (Bamboo shoots), II (leaves)

I=staple (>80%); II=common (5–80%); III=rare (<5%)

Food species with the same preferred rank in the same genus are combined with genus name plus spp.; otherwise they are listed individually

and accounted for 7.4% of feeding records during this 2-mo period. Monkeys consumed lichen (*Usnea longissima*) on every observation day, accounting for 65% of feeding records.

In our provisioning experiment, we found that *Rhinopithecus bieti* preferred bamboo shoots to lichen. Bamboo shoots were selected first and consumed

completely before individuals began feeding on lichen 98.2% (107/109) of the time. In only 1.8% of our sample did the monkeys consume lichen before feeding on bamboo shoots.

Group FF Events Between 2003 and 2008

The group traveled, fed, foraged, and rested as a cohesive entity during the majority of the study period (>11 mo/yr). We recorded 12 fission events, 11 of which also included fissioning of the AMU (Table II). On one occasion in July 2003, the AMU did not split when the large bisexual group divided into two social units (Table III). Group fissions occurred in June and July during each year of the 5-yr study period and the group always split into two subgroups. Subgroup size varied significantly (χ^2 test: $\chi^2=56.672$, $df=11$, $P<0.001$, two-tailed) but the mean was 199 ± 63 ($N=24$, range: 104–300 individuals). Subgroups contained 14 ± 5 ($N=24$) OMUs and one AMU, except in July 2003, when one subgroup did not have an AMU associated with it (Table III). During all fission events, we termed the larger subgroup subgroup 1 and the smaller subgroup subgroup 2 (Fig. 2). The larger subgroup contained 258 ± 47 ($N=12$) individuals and the smaller subgroup contained 147 ± 29 ($N=12$) individuals.

All group fission event occurred at the same location in the group's home range (bamboo site, Fig. 1), with each of the two subgroups moving off in opposite directions, taking a different but habitually used travel route. Both subgroups fed together on bamboo shoots in the same bamboo area before fissioning. We did not observe any conspicuous increase in aggression or other noticeable change in behavior among group members before fissioning events.

The mean time spent in subgroups was 6 ± 3 d ($N=12$, range: 2–11 d). Time spent in subgroups ranged from 2 to 11 d (one-sample t -test: $t=8.075$, $df=11$, $P<0.001$) (Table II). Although fission events always occurred at the same site, fusion events

Table II Fission–fusion events in the Xiangguqing group of *Rhinopithecus bieti* from 2003 to 2008

Case	Fission date	Fission site	Subgroup size	Ratio of subgroup sizes	Split AMUs	Ratio of sub-AMU size	Time spent in subgroup (days)	Fusion site
1	6/11/2003	A	152, 179	0.85	22, 2	0.09	5	No bamboo
2	7/22/2003	A	134, 197	0.68	0, 23	0	8	No bamboo
3	6/12/2004	A	160, 200	0.80	23, 6	0.26	6	No bamboo
4	7/26/2004	A	107, 253	0.42	4, 25	0.16	11	No bamboo
5	6/14/2005	A	104, 291	0.34	27, 7	0.26	3	No bamboo
6	7/15/2005	A	110, 285	0.39	5, 29	0.17	8	No bamboo
7	6/14/2006	A	190, 230	0.83	7, 34	0.21	2	Bamboo
8	6/20/2006	A	154, 266	0.58	28, 13	0.46	7	No bamboo
9	7/14/2006	A	148, 272	0.54	5, 36	0.14	9	No bamboo
10	6/20/2007	A	150, 300	0.50	36, 7	0.19	5	No bamboo
11	7/3/2007	A	176, 274	0.64	9, 32	0.28	4	Bamboo
12	7/17/2007	A	194, 256	0.76	10, 33	0.30	5	No bamboo

Table III All-male transfers between subgroups of the Xiangguqing group of *Rhinopithecus bieti* during the study period

Case	Transfer date	Sizes of all-male bands	Merged date	Sizes of sub-AMU
1	6/15/2003	3 AMs	2003.6.18	19, 5
2	7/28/2003	7 (4 AMs, 3 SMs)	2003.8.13	16, 7
3	6/17/2004	2 AMs	2004. 7.5	23, 6
4	7/31/2004	4 (3 AMs, 1 J)	2004.8.22	21, 5
5	7/20/2005	5 (3 AMs, 1 SM, 1 J)	2005. 8.11	10, 24
6	6/26/2006	2 AMs	2006. 7.15	26, 15
7	7/23/2006	6 (3 AMs, 2 SMs, 1 J)	2006.8. 7	30,11
8	6/24/2007	3 AMs	2007. 6. 26	33, 10

AM=adult males; SM=subadult males; J=juveniles

occurred at different site within the group's home range (Fig. 1). Subgroups reunited more often at sites outside the bamboo forest than inside the bamboo forest (χ^2 test: $\chi^2=5.33$, $df=1$, $P=0.021$).

The AMU also showed FF behavior when the whole group split and merged (Table III). Mean AMU subgroup size was 18 ± 12 individuals, and varied markedly across fission events (χ^2 test: $\chi^2=69.8$, $df=11$, $P<0.001$, two-tailed). The AMU subgroups that traveled with larger subgroups (mean: 29 ± 5 individuals) was larger than the AMU subgroup that traveled with smaller subgroups (mean: 6 ± 3 individuals) (one-sample t -test: $t=16.934$, $df=22$, $P<0.001$).

Finally, in late April 2008, the group was fissioned permanently into two independent groups of 134 and 346 monkeys.

Evidence of Predation Risk

Between March 2003 and April 2008, we followed the focal group on 1567 d, with *ca.* 7981 h of observation. On no occasion did we observe the presence of a predator in the vicinity of the focal group, hear a predator alarm call or see a monkey act in a manner suggesting that a predator had been sighted. Therefore, we conclude the FF events we recorded were not affected by changes in perceived predation risk.

The Fission Site

The site where the group consistently fissioned was located on a ridge (3370 m) flanked by bamboo forests (Fig. 1). We sampled a total of 79 trees in five plots at this site. The dominant tree species were *Tsuga dumosa* (38%) and *Rhododendron yunnanense* (21.5%). Other trees present included *Quercus pannosa*, *Sorbus prattii*, *Larix potaninii* var. *macrocarpa*, and *Eleutherococcus evodiaefolius*. The lichen load at this site was very low (<1.2%). The Shannon–Wiener diversity index of the plot located on the travel route used by the monkeys when the group fissioned was 1.66, and did not differ significantly from the other four 20 m \times 20 m vegetation plots at the fission site (Kolmogorov–Smirnov one-sample test: $Z=0.427$, $N=5$, $P=0.993$).

The bamboo forest measured *ca.* 3.4 km² (Fig. 1), with *Fargesia yunnanensis* providing the majority (93%) of bamboo shoots consumed by the focal group during June and July of each year. The annual bamboo regrowth rate was 5.7% ($N=5$, range: 1.1–6.3%). Monkeys preferred bamboo shoots (mean=17.3 ± 4.6 cm high, $N=365$, range: 9–44 cm) to all other food items, including the lichen *Usnea longissima*, in this part of their range. After the group passed through the fission site, 90.5% of the bamboo shoots along the ranging path (10–60 m breadth) were depleted. When group fission occurred, the bamboo shoots in three of the plots (double arrows at the fission site in Fig. 1) at the fission site were nearly depleted while bamboo shoots in the fourth plot (single arrow in Fig. 1) had not been consumed at all.

The Comparison Site

We sampled 108 trees belonging to 16 species at the comparison site. The Shannon–Wiener diversity index here was 2.05 ($>H'$ at the fission site) and did not differ significantly from the other four plots (Kolmogorov–Smirnov one-sample test: $Z=0.408$, $N=5$, $P=0.996$). This forested area was dominated by *Tsuga dumosa* (24%) and *Rhododendron rubiginosum* (22%), and the shrub layer was dominated by *Lyonia ovalifolia* (16%) and *Enkianthus deflexus* (13%). Other tree species present included *Acer hookeri*, *Quercus pannosa*, *Euonymus tingsens*, *Eleutherococcus evodiaefolius*, *Pinus armandii*, and *Taxus yunnanensis*. The lichen load at the comparison site was 6.3%, higher than that at the fission site (<1.2%).

Discussion

Our focal group contained >450 individuals (in 2007) and was characterized by facultative FF behavior two to three times each year. Between 2003 and 2008, these group fissioning events occurred only during June and July, a time of the year when bamboo shoots, a high protein resource (bamboo shoots of *Fargesia yunnanensis* can contain up to 32.4% protein; Wang *et al.* 2009) were an important component of the diet. This also coincided with the end of the birth season, when some 40–50 females were nursing young offspring. Lactation is the most energetically costly phase of primate reproduction (NRC 2003), and in several primate species lactating females increase their foraging time and nutritional requirements significantly (Lee 1996). Thus, it is possible that fissioning events in *Rhinopithecus bieti* at our field site were strongly affected by changes in female nutritional demands and the distribution and availability of high-quality food resources.

During subgrouping events, the large single group split into two smaller groups (average: 258 and 147 individuals) that foraged apart for 2–11 d. Fissioning occurred in a part of the group's home range where the density of lichen, a year-round dietary staple, was low and the availability of new bamboo shoots was decreasing dramatically. Young bamboo shoots distributed along the group's habitual ranging path (10–60 m breadth) were 90.5% depleted when fission occurred. Thus, flexibility in grouping patterns may allow *Rhinopithecus bieti* to live in large groups when resources are abundant, and to adjust foraging group size by fissioning into smaller social units during periods when food supply is more variable. This is similar to the

situation of *Rhinopithecus roxellana*, in which food supply also appears to play a critical role in group stability (Hu *et al.* 1980; Kirkpatrick 1998), with subgrouping reported to occur during food limited periods in the winter (Deng *et al.* 1981).

Snub-nosed monkeys are thought to follow the same set of travel paths across their home range consistently (Bai *et al.* 1987; Deng *et al.* 1981; Hu *et al.* 1980; Kirkpatrick *et al.* 1999). This is likely to reflect features of habitat topography, and patterns of tree growth and regeneration on steep mountain slopes and rocky terrain. In the present study, we found that the group moved unidirectionally along particular ranging path in its home range (Fig. 1). Previous studies of *Rhinopithecus* have shown that when group fission occurred, subgroups moved along the same route and in the same direction as that of the original group, and subsequently merged later that same day (*R. roxellana*: Deng *et al.* 1981; Hu *et al.* 1980; Kirkpatrick *et al.* 1999; *R. bieti*: Bai *et al.* 1987). In our study, all fissioning events occurred at one specific site in an area of bamboo forest. A decrease in the availability of bamboo shoots in this traditional feeding area appeared to trigger subgrouping behavior, with each subgroup leaving the area by traveling in opposite directions. The subgroups did not reunite for several days. Our long-term data also confirmed that the two subgroups always moved unidirectionally along traditionally used travel paths (Fig. 1), and thus avoided coexploiting the same set of feeding patches before reuniting.

Increased group size is expected to result in increased opportunities for feeding competition, aggression, and subgrouping, especially among females (Janson and Goldsmith 1995), and in many primate species, new groups form by the fissioning of a large established group into two smaller units (Furuya 1969; Henzi *et al.* 1997; Sussman and Garber 2011). New group formation in Chinese snub-nosed monkeys also appears to occur through a prolonged process in which an extremely large group permanently splits into two smaller groups. For example, a group of *Rhinopithecus roxellana* separated permanently into two groups of >90 individuals each and the groups remained in their original home ranges and isolated from each other (Li *et al.* 2000; Tan *et al.* 2007; Zhang *et al.* 2006). However, the process of fissioning and new group formation remain unclear. Although our focal group contained >200 individuals for ≥ 8 yr, and >450 individuals in 2007, it did not fission permanently until April, 2008. At this stage it was artificially split into two isolated groups by the reserve management for three reasons: 1) the focal group was the largest of the 13 extant natural groups of *Rhinopithecus bieti* but its home range was thought too small to support it long term (>3 yr); 2) the smaller subgroup left in the original home range was used to test feasibility of enclosing a monkey group in a confined area by aiding provision; and 3) the nature reserve proposed a test of *ex situ* conservation of the large group and to monitor its exploration of a new home range.

Overall our data support the contention that *Rhinopithecus bieti* live in a large, highly cohesive multilevel society, but maintain the behavioral flexibility to subgroup when high-quality resources, such as bamboo shoots, are limited. Even groups of >450 *Rhinopithecus bieti* feed and forage as a cohesive social unit throughout most of the year. However, at the end of the birth season (March–June), when a large percentage of adult females are lactating and supplying the nutritional needs of their young offspring, subgrouping occurs. A critical question that emerges from this research is how *Rhinopithecus bieti* solve the problems of locating sufficient resources to sustain such a large social group while inhabiting an extremely harsh high-

altitude environment? We plan to continue this research to examine further questions of snub-nosed monkey feeding ecology, diet, and to identify physiological and behavioral traits that assist these primates in adapting to a high-altitude environment.

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