

Deciphering the Social Organization and Structure of Wild Yunnan Snub-Nosed Monkeys (*Rhinopithecus bieti*)

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Keywords

Social structure · Grooming · Multilevel society · *Rhinopithecus* · Colobine · China

Abstract

The social organization of natural groups of *Rhinopithecus bieti* (Yunnan snub-nosed monkey) is virtually unknown. We studied the demography and social structure of a free-ranging group at Samage Forest, China, for nearly 2 years. This study confirmed that *R. bieti* exhibits a multilevel social organization of core 1-male units (OMUs) that congregate in a band of >400 members. Even though the band appeared to be unified for the most part, we also witnessed occasional fission-fusion. OMUs were cohesive entities, and their members were spatially and socially isolated from members of other OMUs. Large all-male units associated with the band, and when they closely followed OMUs there was a tendency for elevated male aggression. Within OMUs, females associated preferentially with males and vice versa, resulting in a bisexually bonded society. Contrary to other Asian colobines, *R. bieti* were comparatively social, with grooming occupying 7.3% of the time. Social grooming was primarily a female affair, but males also participated in grooming networks. The integration of males into the social network of the OMU is thought to help to maintain OMU integrity and cohesion with other social units being in close proximity.

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Introduction

Primates as a group display a great variety of social systems [Crook and Gartlan, 1966; Eisenberg et al., 1972; Clutton-Brock and Harvey, 1977; Dunbar, 1988; Grzimek, 2004; Mitani et al., 2012; Mittermeier et al., 2013; Rowe and Myers, 2016], with “social system” encompassing both grouping characteristics and the nature of interindividual relationships [Kappeler and van Schaik, 2002]. The social system of a given species or population results from the combined interactions of individuals [Hinde, 1976]. These are shaped by ecological factors such as the distribution of resources and predation threat [Alexander, 1974; van Schaik, 1983; Terborgh and Janson, 1986; Sterck et al., 1997; Schülke and Ostner, 2012; Clutton-Brock, 2016], social factors such as sexual conflict, moulded by life history [Clutton-Brock and Parker, 1995; van Schaik, 1996; van Schaik and Kappeler, 1997], and perhaps cognitive constraints [Dunbar, 1992].

Among colobines, *Rhinopithecus bieti* (the Yunnan snub-nosed monkey or black-and-white snub-nosed monkey) is an intriguing species with regard to many morphological, ecological, and behavioral features [reviewed in Grueter, 2013]. Among its natural history characteristics not shared by the majority of the colobines are semiterrestriality [Kirkpatrick and Long, 1994], association with subalpine environments [Zhao et al., 1988; Li et al., 2008; Grueter et al., 2012b], a seminomadic ranging style [Kirkpatrick et al., 1998; Grueter et al., 2008; Xiang et al., 2013], a resource base predominantly made up of lichens [Kirkpatrick, 1996; Grueter et al., 2009b], and extremely large groups [Kirkpatrick et al., 1998; Li et al., 2010b]. Originally thought to be organized into multifemale-multimale groups [Li et al., 1982; Bai et al., 1987; Yang, 1988], preliminary field work provided evidence that *R. bieti* societies are organized in small monandrous-polygynous subunits (1-male units or OMUs), which conglomerate into large well-organized and relatively cohesive bands [Kirkpatrick et al., 1998; Liu et al., 2007; Cui et al., 2008]; all-male units (AMUs) are part of these bands as well. This social arrangement with 2 rather fixed layers is referred to as a nested, modular or multilevel social system [Grueter and Zinner, 2004; Grueter and van Schaik, 2010; Kirkpatrick and Grueter, 2010; Grueter et al., 2012a, c, 2017]. Different functional explanations have been proposed for the evolution of these nested societies, e.g. that OMUs come together in order to deter potentially infanticidal and usurping bachelor males [Bleisch and Xie, 1998; Rubenstein and Hack, 2004; Grueter and van Schaik, 2010].

The social behavior of wild *R. bieti* has received relatively scant attention [Kirkpatrick et al., 1998; Li et al., 2010a; for captive groups, see Grueter, 2003; Cui et al., 2014; for provisioned/range-restricted groups, see Zhu et al., 2016], and as such very little is known about the bonding pattern that characterizes natural *R. bieti* social units. Kirkpatrick et al. [1998] found that intraunit aggression was infrequent, and grooming was relatively frequent as compared to other Asian colobines. Moreover, grooming episodes involved both sexes, with an overrepresentation of females.

The collection of data on the size and composition of wild groups of this species is not straightforward because of the extreme size of groups, low levels of habituation, and restricted visibility in the natural environment. Group composition data for *R. bieti* have been derived from eyewitness accounts and video analysis of groups crossing open land [Liu et al., 2007; Cui et al., 2008], quantifying fecal pellets dispersed at sleeping sites [Cui et al., 2006b], and direct scan observations with telescopes of group

members staying in the canopy [Kirkpatrick et al., 1998]. Here we use a relatively large data set stemming from a completely free-ranging and semihabituated group that was followed for a period of 20 months. The study was set up with several objectives:

1. to provide basic demographic data on *R. bieti* group size and composition;
2. to deepen our understanding of the multilevel structure of *R. bieti* societies by determining spatiotemporal distribution of individuals and OMUs in the band;
3. to evaluate the possible existence, time frame, and determinants of fission-fusion events;
4. to better understand the social mechanisms by which OMUs are held together by studying the quality and quantity of social interactions as well as spatial arrangements, such as grooming and proximity, among age-sex classes.

Methods

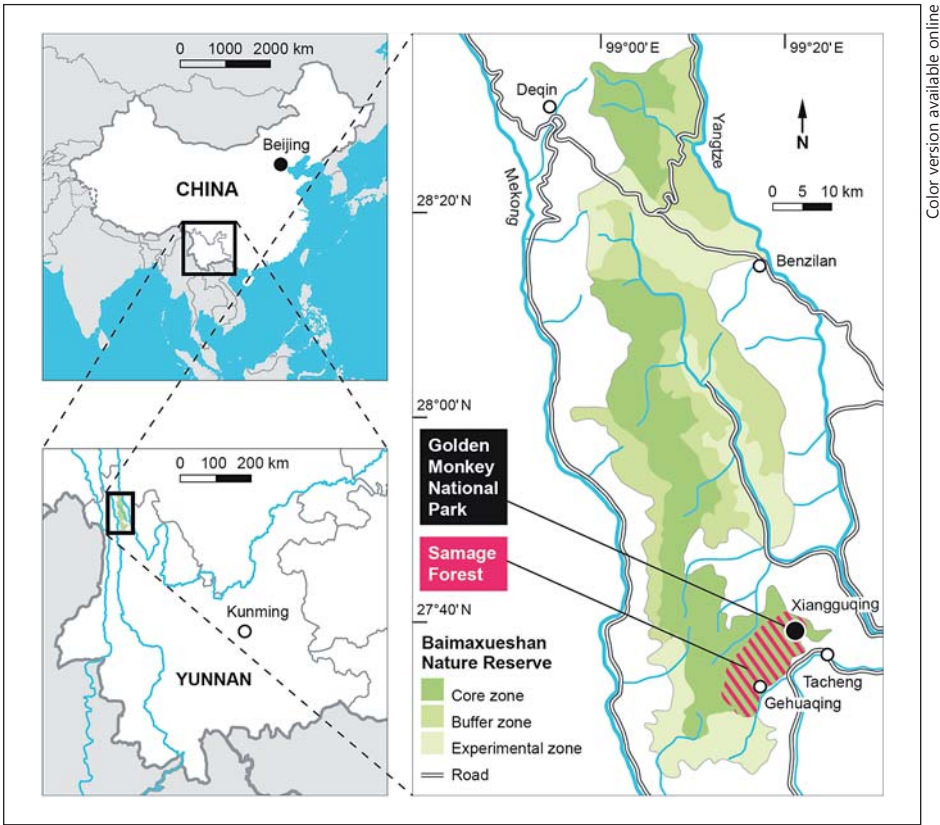
Study Site

The study site, Samage, is located at 27°34' N, 99°17' E in Baimaxueshan National Nature Reserve, Yunnan, PR China (Fig. 1). The area is dominated by steep mountain slopes and narrow ravines covered with a mosaic of mostly temperate vegetation types: mixed coniferous and deciduous-broadleaf forest (at 2,900–3,600 m), subalpine George's fir forest (3,500–4,000 m), montane sclerophyllous oak forests (3,200–3,500 m), subtropical evergreen-broadleaf forest (2,500–3,000 m), Yunnan pine forest (2,500–3,100 m), alpine scrublands (3,700–4,100 m), as well as cattle pastures at various elevations. The habitat of *R. bieti* at this locality ranges from 2,600 to 4,000 m and includes all major vegetation types, but predominantly mixed forest. The area is demarcated to the north by the border between the counties of Weixi and Deqin. Parts of the Samage Forest have been selectively logged, and human encroachment in the form of livestock grazing and harvest of forest products is widespread. The site experiences extreme seasonal variation in precipitation and temperature. Monthly temperatures at base camp ranged from a mean of 6.6°C in January 2007 to a mean of 21.5°C in July 2006, and monthly amounts of precipitation (rain or snow) from 0 mm in January 2006/2007 to 275 mm in August 2007. The seasons are divided as such: spring (March to May), summer (June to August), fall (September to November), and winter (December to February). A more detailed ecological description of the site is given in Grueter et al. [2009b], Grueter [2015], and Li et al. [2008].

Data Collection

During the 20-month study period (September 2005 to May 2006; August 2006 to November 2006; January 2007 to July 2007), we located the semihabituated¹ focal band (the Gehuaqing band) on 315 days, with a total contact time of 1,444 h. We collected behavioral data on 116 days. The number of scan-based visual contact hours was 456 during which we obtained 19,146 individual activity records. Using a high-performance spotting scope (Kowa® TSN 820, 20–60× zoom), we usually conducted behavioral observations from rocky outcrops, ridges, or hillsides. These distant observations ensured that the animals were unaware of the observer's presence and allowed us to obtain a better overview of the spatial configuration of the group members and see into forest patches that were difficult to reach on foot. However, group members occasionally accepted us to stay within 10–30 m to them. Taken as a whole, distances to the location of the monkey group ranged from 10 to 1,500 m (mean: 240 ± 211 m; median: 200 m). Rarely a given OMU could be reidentified, and only very few individuals could be repeatedly recognized by conspicuous traits, e.g. a split lip, a damaged eye, or a missing limb.

¹ Unlike the nearby group at Xiangguqing, this one has never been the subject of human management initiatives such as provisioning and range confinement.



Color version available online

Fig. 1. Location of the study site (Samage Forest) at the southern end of Baimaxueshan National Nature Reserve in Yunnan, China. Map by K. Meisterhans.

We collected systematic behavioral data on the focal group via scan sampling [Altmann, 1974; Morrison et al., 1998]. We took scans of all visible animals at 15- or 30-min intervals and dictated them into a tape recorder. Group members were often spread out over large distances (mean: 130 ± 110 m; median: 90 m) in the forest and across forest strata, precluding data collection on all members of the group during a single scan. Animals on the ground were frequently overlooked during scans due to poor visibility. If a large number of monkeys (usually >20) was in view, we chose 30-min scans; if only a small number (usually <20) was visible, we did 15-min scans. Scans needed to be completed at least 5 min before the beginning of the next scan. Every scan included information on date, time and weather conditions. For every subject being scanned, we recorded age, sex, and activity (rest, groom, move, play, feed, vigilance, cling, aggressive, and miscellaneous). “Active allogrooming” refers to grooming given and “passive allogrooming” refers to grooming received. For definitions of activity categories, see Grueter [2009]. We also recorded the distance to the nearest neighbor (in arm’s lengths), age-sex class of the nearest neighbor, and recorded all animals occupying the same tree. Whenever an AMU was spotted, we recorded its position in relation to the most peripheral OMUs, i.e. whether they were peripheral (>500 m), close to (200–500 m), or inside the band (<200 m). We scored both sexual and aggressive behavior, including display behavior on an all-occurrence basis. Since aggressive behavior was difficult to record visually, we also used auditory cues, i.e. the characteristic male aggressive calls, as an indicator of an aggressive event involving a male.

Age-sex classes were divided into the following categories: adult male, adult female, sub-adult male, juvenile (approx. 1–4 years), and infant (<1 year). Subadult females were not differentiated, but included in the category “juvenile.” An individual was recorded as “unclassified” if its age-sex class could not be determined. Subadult males in snub-nosed monkeys are sometimes falsely identified as adult females [Bleisch et al., 1993]. We thus used the category “SAMOF” (sub-adult male or female) for cases where it was not possible to determine the sex of an animal whose body size was close to or bigger than that of an adult female, but was not accompanied by an infant. Males were positively categorized from genital anatomy. Other morphobehavioral criteria used to distinguish the age-sex classes in *R. bieti* are listed in Grueter [2009]. Because the birth season is March/April (see below), the youngest animals were categorized as infants until February; after that, they were treated as yearling juveniles.

The density of the forest canopy and underbrush coupled with the semiterrestrial lifestyle of the monkeys prevented us from obtaining reliable group counts during scan sessions. Occasionally, however, we had the opportunity of observing the band crossing an open area (gully or a ridge) at rather close range (<100 m), allowing us to obtain an accurate count of all members of the group. One such group progression (November 12, 2006) was also videotaped, but not completely. Fission-fusion was studied by more or less simultaneously following 2 group parts and taking GPS coordinates. For details on how we sampled geographical positions of the group, see Grueter et al. [2008].

Data Analysis

We used scan records to generate summary data on time spent in proximity to others for each age-sex class, distance and identity of the nearest noninfant neighbor, time spent grooming, identities of groomer and groomee, and demographic composition of the band. We excluded unclassified individuals from calculations of age-sex composition. All individuals recorded as “adult female or large juvenile” ($n = 22$) were likely adult females of smaller stature and were treated as adult females for demographic analyses. Data on OMU size and composition are not provided because we had no a priori criterion for differentiating among OMUs, and because rarely all suspected OMU members were visible to the observers due to thick foliage occluding clear lines of sight.

We analyzed the group progression video footage showing a part of the group crossing a gully on screen. We recorded the time intervals between successively passing individuals. Time intervals reflect proximities and were used to detect social boundaries between age-sex classes. We used a 1-sample run test [Siegel and Castellan, 1988] to ascertain whether the arrangement of males and females in the moving column was random.

We used χ^2 goodness-of-fit tests to determine which age-sex classes (excluding infants) were nearest neighbors more often than expected (the expected percentage was determined from the composition of the study band) and which age-sex classes showed higher frequencies of grooming than expected (expected frequencies were based on the relative representation of different age-sex classes in the band). We analyzed seasonal rates of aggression by 1-way ANOVA. Prior to conducting the ANOVA, we checked the data for homogeneity of variances using Levene’s test and for normal distribution using a 1-sample Kolmogorov-Smirnov test. We ran analyses in JMP 7.0.2 (SAS Inc.) and SPSS 16.0. All probabilities reported are for 2-tailed tests. Statistics were considered significant at $p < 0.05$.

Results

Group Size and Composition

Based on the observation of a whole group progression on June 17, 2007, the total group count was 407 individuals. Due to the high possibility of having missed some individuals taking a different travel path, this is a minimum estimate. The adult male-female ratio was 1:2.2 (Table 1). When we restricted the demography estimates to the putative reproductive population [Kirkpatrick and Gu, 1999] and excluded 17

Table 1. Demography of the Gehuaqing group of *R. bieti* at Samage, as estimated from a group census on June 17, 2007

Males	63 (46)
Females	138
Juveniles	132
Infants	42
SAMOFs	21
Unknown	11
<hr/>	
Total	407
<hr/>	
<i>Ratios</i>	
M:F	1:2.2 (3.0)
I:AF	1:3.3

SAMOF, subadult male or female; I, infant; AF, adult female. In parentheses, excluding putative nonreproductive all-male unit males.

males that presumably were part of bachelor units, the sex ratio then became even more female biased (1:3.0). The ratio of infants to adult females was 1:3.3. As a complementary measure to this group count, we determined sex ratios based on the frequency distribution of age-sex classes in scans ($n_{\text{mal}} = 2,516$, $n_{\text{fem}} = 4,539$, $n_{\text{juv}} = 4,379$, $n_{\text{inf}} = 1,443$). The male-female ratio was 1:1.8, and the ratio of infants to adult females was 1:3.2. The estimate derived from the group progression is likely more accurate than the scan-based one since adult males were consistently more conspicuous and more easily detected than females.

OMUs are the core units of the *R. bieti* society; they were composed of 1 male, an assumed average of 3 adult females (based on the putative reproductive population-based sex ratio) and a not quantified number of adolescents. OMUs also appeared to sometimes monopolize trees that were in fruit. Units appeared to tolerate each other's presence/space, but adult members of different units typically did not interact. When members of different units came to within a few meters of each other, aggressive gestures and vocalizations were common. Rarely all OMU members were clearly visible in trees, and an unambiguous differentiation among OMUs was not possible. We have only a few cases of more than 1 male ($n = 18$; 1.14% of tree scans), but several females, staying in the same tree during resting periods (AMUs excluded; $n = 166$; 10.51%); therefore, OMUs seem to be cohesive units that stay together in only 1 single tree and keep a spatial distance from other units (Fig. 2). Derived from the number of individuals staying in the same tree, the largest OMU had 17 members (1 male, 8 females, 5 infants, and 3 juveniles).

AMUs or bachelor units are another element within the *R. bieti* society. There were 3 kinds of AMUs, adult-male units, subadult-male units, and mixed adult-subadult units. Subadult-male units were made up mostly of large male juveniles and subadult males. The size of AMUs varied over time (mean 4.99, SD 3.43; range 2–17; median 4). The largest AMU with 17 members (observed on June 17, 2007) was composed of 4 adults, 8 subadults, and 5 juveniles. One suspected AMU had 33 members (a few individuals could not be reliably sexed). On a few occasions, we saw pairs or lone males wandering around separately from the focal band, at distances >1 km.



Color version available online

Fig. 2. An OMU with an adult male, adult female, older juvenile, female with infant, younger juvenile and unidentified individual (from right to left). OMU members tended to stay closely together while resting. Photo by J. Weingarten.

AMU males showed affiliative behavior towards each other; they occasionally groomed and mounted one another. AMU members often exhibited stereotyped displays; they rushed through the canopy, stopped abruptly and then remained in a semi-crouching position for a few seconds before rising (“jumping and freezing”). The function of these displays remained unclear. AMUs were seen on 62 days, i.e. 53% of all observation days. We recorded the position of AMUs in relation to the most peripheral OMUs, i.e. whether they were peripheral (>500 m), close to (200–500 m), or inside the group (<200 m). AMUs were peripheral on 3% of the observation days, close to the OMUs on 37% of the days, and in the center of the band within reach of the OMUs on 14% of the days. On 47% of the days on which we did not see the AMUs, they may have been peripheral.

It was unclear how *R. bieti* initiated and coordinated group movement and how they reached travel direction consensus, but their rate of vocalizing constantly increased before moving. All OMUs used the same travel path and sometimes formed parallel walking columns (sometimes a single column moving terrestrially). On 2 occasions, we saw a single male moving in front and one in the rear, “temporally separated” from the band by up to a few minutes. By plotting the time intervals between sequentially passing adult and subadult males using the video footage taken on November 12, 2006, it became evident that there were clear temporal gaps between males (Fig. 3). Males were more clumped only at the periphery, representing the AMUs that led the progressions. After excluding the AMU males ($n = 15$), we used a 1-sample run test to determine whether the arrangement of males and females in the moving column was random (in-

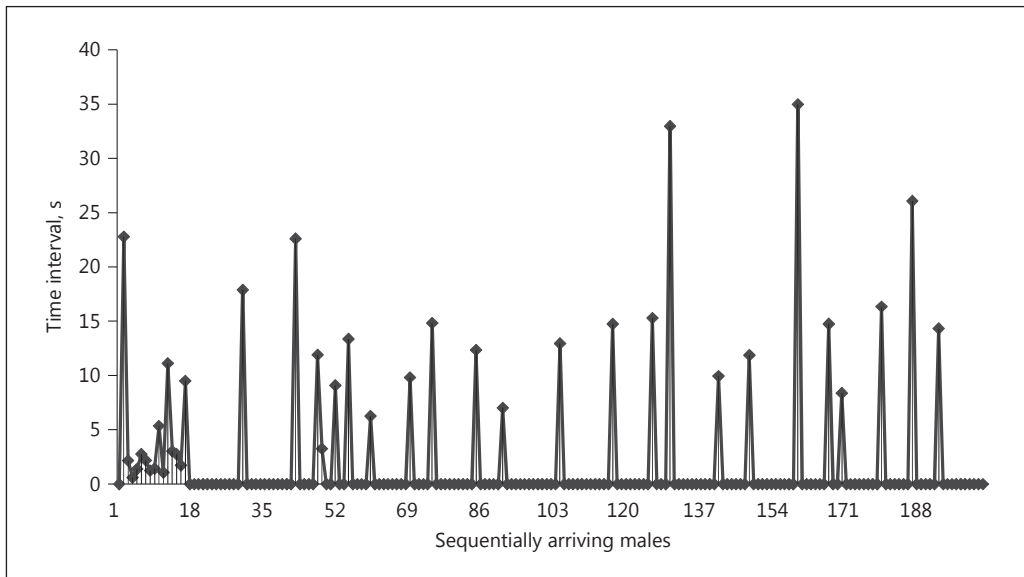


Fig. 3. Time interval between arriving adult and subadult males (based on the video footage of a partial group progression on November 12, 2006). The diamonds on the *x* axis refer to females and juveniles. The raised diamonds refer to males, and the first grouping of these represents an AMU.

fants and juveniles were not considered in this analysis because infants did not usually walk independently and juveniles were associated with both OMUs and AMUs). The order was not random – r (number of runs) = 46; $n_{\text{mal}} = 23$, $n_{\text{fem}} = 86$, $z = 2.38$, $p = 0.014$, 2-tailed – with the large number indicating that adult males were overdispersed.

Fission-Fusion

The focal band of *R. bieti* appeared relatively stable and unified, although it sometimes broke up briefly for several hours probably as a result of logistics of travel, food distribution, or human disturbance. For example, local cattle herders occasionally cut off the group's way, resulting in one part staying on one side of the ridge and the other on the other side. The subgroups usually assembled again in the evening. Only once were we able to document a medium-term group fission: we observed 2 splinter groups of several OMUs traveling separated from each other for roughly 4 weeks in late winter, separated by a maximum of >5 km (Fig. 4).

Spatial and Social Behavior

We saw adult females in proximity (<1 arm's length) with another unit member on 31% of all scans, males on 21%, juveniles on 20%, and infants on 61%. This analysis was restricted to OMUs and to times when the animals were not moving. The actual values are likely higher because it was sometimes difficult to see whether a scanned animal was in fact in body contact with another one when rest-huddling. This bias is inherent and affects all age-sex classes equally.

Different age-sex classes varied in their nearest neighbor and proximity relations. As measured by the identity of the nearest neighbor, males had females as nearest neighbors much more often than expected, and other males and juveniles much less often ($\chi^2 = 284.542$, $df = 2$, $p < 0.001$). Females had other females as nearest neighbors about as often as expected, males more often and juveniles less often ($\chi^2 = 510.510$, $df = 2$, $p < 0.001$). Juveniles had females as nearest neighbors less often than expected, other juveniles and males more often ($\chi^2 = 14.563$, $df = 2$, $p = 0.001$) (Fig. 5a).

When considering the identity of the animal in proximity, results are similar (Fig. 5b). Males were in proximity mostly with females (80%) and very rarely with other males (1%). Females showed proximity with all age-sex classes at comparable frequencies. The nearest neighbor and proximity diagrams look very similar for females and males, but differ for juveniles: while other juveniles were most often nearest neighbors of juveniles (44%), it was most often females who stayed in proximity with juveniles (61%).

R. bieti spent 6.7% of their diurnal activity budget in allogrooming. After excluding SAMOF and infants from the χ^2 analyses, the observed frequencies of active

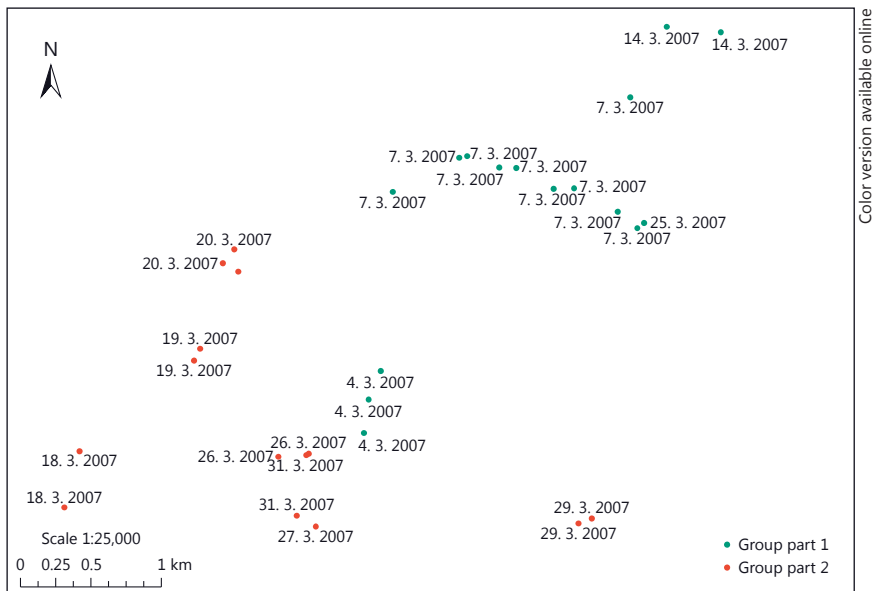
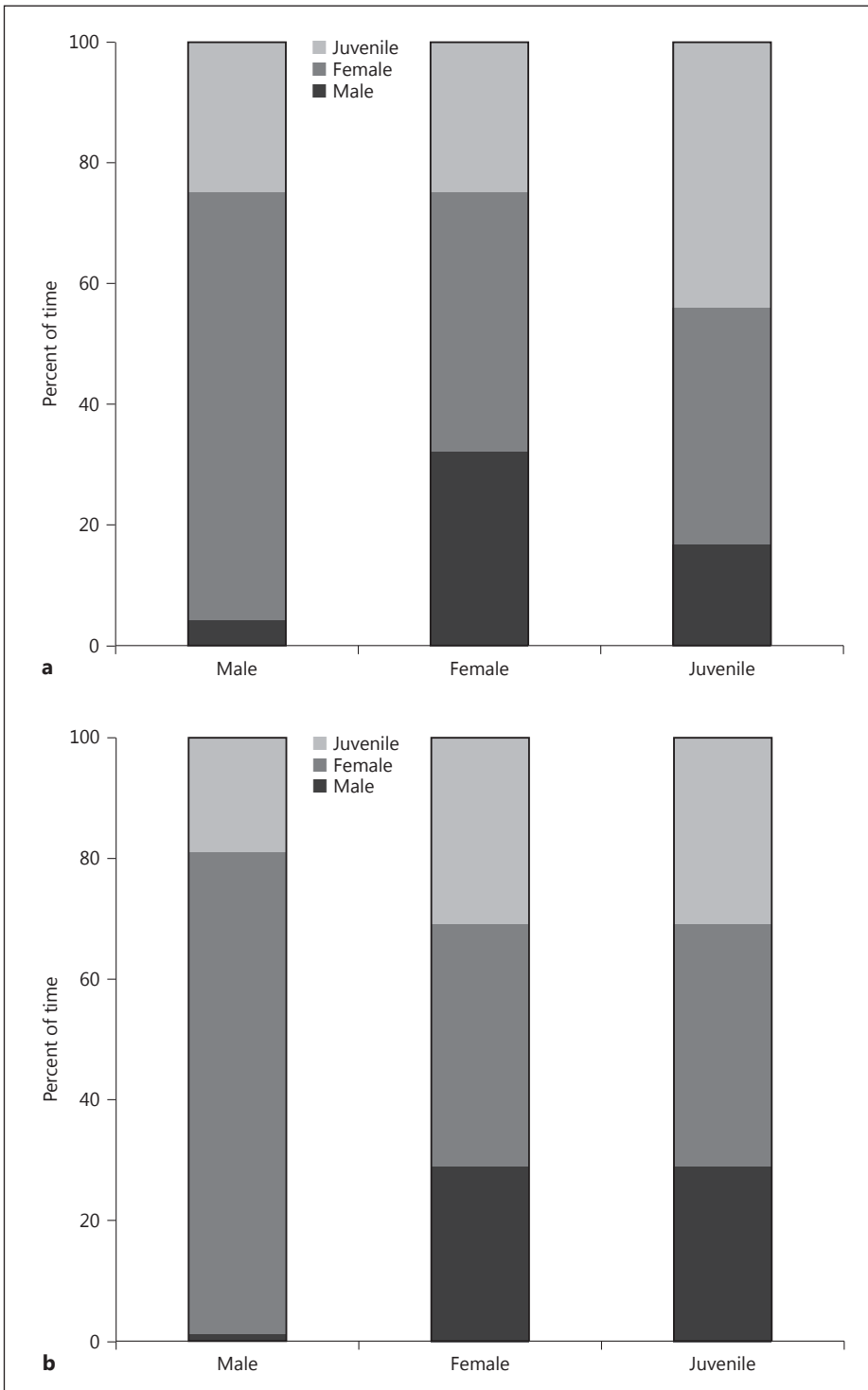


Fig. 4. A fission event of the study group in March 2007. The red points indicate the locations of one splinter group, and the green points the locations of the other (color refers to the online version only). The dates (day/month/year) on which the location records were obtained are also given.

Fig. 5. a Identity of nearest neighbors: the (observed) percentage of time for which an individual of a particular age-sex class was nearest to the subject. **b** Identity of animal in close proximity (<1 arm's length).

(For figure see next page.)



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Table 2. Grooming dyads ($n = 449$) within *R. bieti* OMUs

Groomer	Groomee						total	percent
	AM	AF	J	I	SAMOF			
AM	0	34	2	0	3	39	9	
AF	68	87	89	58	0	302	67	
J	26	39	21	6	6	98	22	
I	0	1	0	0	0	1	0	
SAMOF	6	0	0	0	3	9	2	
Total	100	161	112	64	12	449	100	
Percent	22	36	25	14	3	100		

AM, adult male; AF, adult female; J, juvenile; I, infant; SAMOF, subadult male or female. Grooming episodes within AMUs are not considered here.

allogrooming differed significantly from the expected ones based on the relative representation of these age-sex classes in the group ($\chi^2 = 112.478$, $df = 2$, $p < 0.001$), i.e. males and juveniles groomed less than expected and females more than expected (Table 2). The observed frequencies of passive allogrooming also differed significantly from the expected ones ($\chi^2 = 50.180$, $p < 0.001$, $df = 2$), i.e. females were groomed about as often as expected, while males were groomed more than expected and juveniles less than expected (Table 2). Females groomed other females, males and juveniles at about equal frequencies whereas males groomed mostly females. Females received grooming by all age-sex classes, but most often by other females. Males received grooming predominantly by females. Grooming bouts often lasted several minutes, though the sampling regime did not allow us to record actual durations.

Juveniles at times provided alloparental care to infants (holding, grooming, or carrying them). Males were very tolerant of infants, but usually did not engage in active caretaking/babysitting.

We witnessed only 4 copulations in approximately 500 h of direct observations, with 1 in August, 2 in October and 1 in December. We observed newborn infants from March to April, in both 2006 and 2007. With a gestation length of about 7 months [He et al., 2001], conception is assumed to occur in August-September, coinciding with more frequent copulating.

We compared the number of aggressive events involving males among seasons and found that hourly aggression rates involving males differed significantly among the 4 seasons (ANOVA, $F = 4.149$, $p = 0.010$, $df = 1$) (Fig. 6), with the highest rates in summer and fall, i.e. during the mating season. However, no statistical difference in male aggression frequencies between the “mating season” and “nonmating season” was found (ANOVA, $F = 0.004$, $p = 0.954$, $df = 1$). Summer and fall are also the time of high availability of fruit, a contestable resource [Grueter et al., 2009a]. We checked for a correlation between frequencies of male aggression and monthly fruit availability: for the first study year, the correlation was significant ($r_s = 0.632$, $p = 0.050$, $n = 10$ months); for the second study year, the correlation was nearly significant ($r_s =$

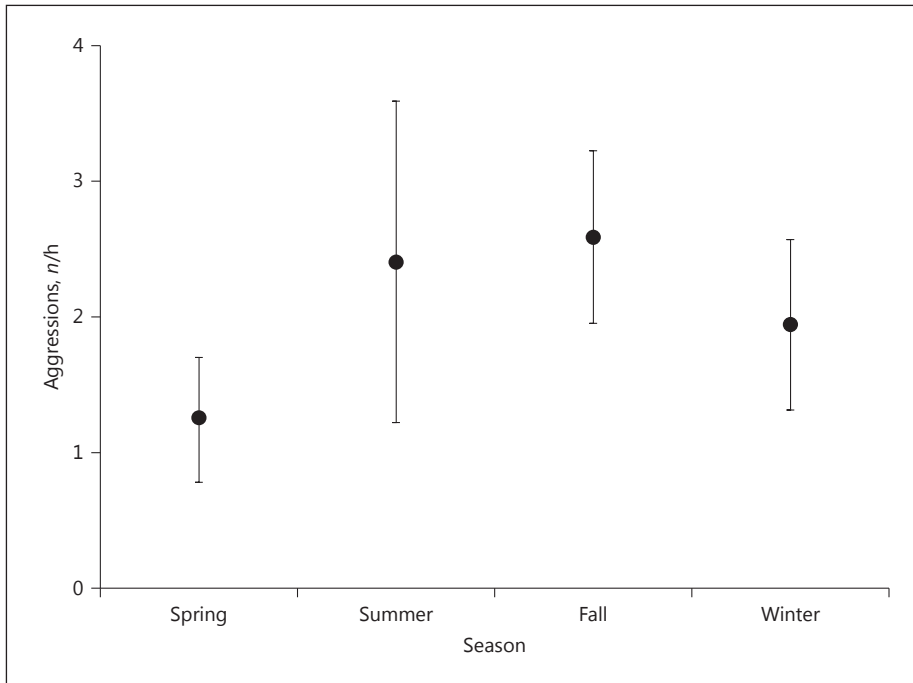


Fig. 6. Male aggression frequencies (number of aggressive vocal events involving males per hour) compared among seasons (spring = March to May, summer = June to August, fall = September to November, and winter = December to February). The means are represented by filled circles, and the whiskers indicate the 95% confidence interval for the mean.

0.560, $p = 0.073$, $n = 11$ months). Finally, we investigated whether there was a statistical influence of bachelor presence on male aggression rates, with an ambiguous outcome. For the first study year, there was a highly significant correlation between monthly male aggression frequencies and the percentage of band contact days on which AMUs were seen ($r_s = 0.828$, $p = 0.003$, $n = 10$ months), but not for the second year ($r_s = 0.051$, $p = 0.897$, $n = 9$ months). If we lump all 19 months together for which these data are available, there is a trend toward a positive relationship between the 2 variables ($r_s = 0.431$, $p = 0.065$, $n = 19$ months).

Discussion

Overall Group Composition and Sociospatial Organization

Our study group of *R. bieti* was formerly estimated to comprise about 200 individuals, probably based on information given by local rangers [Ding et al., 2003; Xiao et al., 2003]. It took us a year and a half of field research to work out its approximate size, which is more than twice the original estimate. This discrepancy in group size may at least partly reflect an upward trend in population size. Groups of more than

200 have been reported in only a small number of primate taxa: Guinea baboons (*Papio papio*) [Sharman, 1981], drills (*Mandrillus leucophaeus*) [Wild et al., 2005], mandrills (*Mandrillus sphinx*) [Abernethy et al., 2002], Angolan black-and-white colobus (*Colobus angolensis*) [Fashing et al., 2007; Miller A., pers. commun.], hamadryas baboons (*Papio hamadryas*) [Kummer, 1984], and geladas (*Theropithecus gelada*) [Dunbar and Dunbar, 1975]. Most of these are subdivided into smaller modules, indicating that such huge group sizes may be incompatible with multimale-multifemale social organization (although the societal structure of some species is data deficient) [Grueter and Zinner, 2004].

Previous researchers of *R. bieti* societies have mistakenly considered an aggregation of independent OMUs as 1 big multimale-multifemale group [Ma et al. 1989]. Our research has provided several lines of evidence indicating that groups are organized in a modular fashion with distinct social clusters (OMUs) embedded within a band. First, an analysis of the marching formation of the band revealed that there were visible spatial gaps between males, and males were evenly distributed across the whole band (with the exception of the peripheral AMU males). If it was a multimale-multifemale group, we would expect the spacing of the males to be more random. Second, because in only 1% of the observations the nearest neighbor of a focal male was another male, it is clear that we are not dealing here with a classical multimale-multifemale group, but with a multilevel society of discrete core OMUs united in bands. Third, using spatial distance as an indicator of social unit boundaries, we found that OMUs occupied fixed spaces, and unit members maintained close proximity while resting. Individual trees seem to act as natural barriers separating OMUs, with 1 OMU usually occupying a single tree or occasionally 2 adjacent trees with overlapping crowns [see also Ren et al., 1998; Qi et al., 2004; Cui et al., 2006a; Li et al., 2010a]. In only 1% of the tree scans was there more than 1 male staying in the same tree during resting periods (AMUs excluded), which supports our prediction that this species forms multilevel societies. In another study, only once was there more than 1 adult male seen in the same tree with females [Kirkpatrick, 1996]. Based on the empirical evidence that OMUs are well delineated spatially (especially obvious when resting) and more interactions occur within this social entity than between (see below), a useful criterion for allocating individuals to units would be to consider all animals within a tree as grouped, i.e. belonging to the same OMU. This recalls ecological patch theory which defines a patch as an area of food concentration, such as a single tree, separated from other patches by areas with little or no food [Astrom et al., 1990; Snaith and Chapman, 2005].

The multitiered system of the *R. bieti* population at Samage appears to be basically similar to that found in other populations of *R. bieti* [Kirkpatrick et al., 1998; Cui et al., 2008] and other members of the genus *Rhinopithecus* (*R. roxellana* [Ren et al., 1998; Zhang et al., 2006; Qi et al., 2014]; *R. brelichi* [Bleisch and Xie, 1998]; *R. avunculus* [Boonratana and Le, 1998]) and bears some resemblance to the system of proboscis monkeys [Yeager, 1991; Murai et al., 2007]. All these studies reported spatially and socially distinct OMUs that frequently or permanently stay in close proximity with other such units. On the surface, the *R. bieti* social system can also be considered as analogous to that found in geladas [Dunbar and Dunbar, 1975; Kawai et al., 1983; Grueter and Zinner, 2004] and hamadryas baboons [Kummer, 1968; Grueter and Zinner, 2004; Swedell, 2006] where in both cases a multilevel society based on OMUs has been described. However, the latter 2 species differ fundamentally in many characteristics of

their finer social structure such as dispersal patterns, grooming networks and OMU-building strategies [Kummer, 1968; Dunbar and Dunbar, 1975; Kawai et al., 1983; Grueter and Zinner, 2004; Swedell, 2006]. Moreover, the number of tiers recognized in the multilevel systems of hamadryas and geladas exceeds 2 [e.g. Kummer, 1968; Dunbar and Dunbar, 1975; Schreier and Swedell, 2012; Snyder-Mackler et al., 2012]. Recently Qi et al. [2014] have analyzed association patterns among social components in an *R. roxellana* society and identified transient grouping levels above the band.

Our demographic findings of the Samage band are largely in accordance with the Wuyapiya band [Kirkpatrick et al., 1998]. The Wuyapiya band was composed of 15–18 OMUs, with the largest putative OMU having 14–16 individuals, of which 5–6 were females. The Nanren group, which is likely the Wuyapiya group at a later point in time, was composed of 17–29 OMUs (depending on the year of assessment and number of units sampled), with OMUs having an average size of 7.1–9.7 members of which 3.8–5.1 were adult females [Cui et al., 2008]. The most conclusive count of the Tacheng group with 24 reproductive units revealed that OMUs had an average of 11.3 members and 4.7 females [Liu et al., 2007]. The Bamei group comprised 14 reproductive/bisexual units; these units were comparatively smaller with an average of 5 individuals and 2.8 females [Cui et al., 2008]. Overall, the population-based sex ratio of *R. bieti* is around 1 male to 3 females (Table 3) at most sites, but OMU-based ratios are usually higher (up to 5 females). This difference in sex ratio is likely due to an inclusion of some males associated with AMUs in the population-based estimate.

In line with Kirkpatrick et al. [1998] and Cui et al. [2008], the relatively high ratio of adult females per infant (among the highest for Asian colobines [Kirkpatrick, 2011]) in this population suggests a low birth rate (low female fecundity) or high infant mortality. Assuming an even sex ratio at birth, the surplus of females (even after controlling for AMU males) may be due to earlier maturation of females [Ohsawa and Dunbar, 1984] or higher mortality among males [Rajpurohit and Sommer, 1991].

Previous studies reported the existence of the occasional monogamous units and multimale units in *R. bieti* [Xiang, 2005; Liu et al., 2007; Cui et al., 2008]. However, we were unable to provide unequivocal evidence with regard to the existence of such units. On a few occasions, we saw 2 males in 1 tree accompanied by a cluster of females, which could be a multimale unit. However, when 2 males were spatially separated within the tree (e.g. 1 male in the upper canopy, 1 in the lower canopy), they could have belonged to 2 independent OMUs. We had the impression that if a tree was very tall, a second unit could have settled in the lower canopy. Given the high number of supposedly non-AMU males in the focal band (46), it is to be expected that a few units contained additional males.

In some primate populations, group size is positively correlated with habitat quality [Dunbar, 1987; Struhsaker, 2000], supposedly because primates can maintain higher reproductive rates in high-quality habitats [Dunbar, 1987]. Depending on the altitude and latitude, *R. bieti* populations occur either in predominantly mixed forest or predominantly coniferous forest. Based on the data given in Table 3, the mean group size is not different between the 2 habitats (Mann-Whitney U, $U_{5,6} = 6$, $p = 0.099$). Using altitude as a proxy for productivity, there is also no significant correlation between band size and altitude ($r_s = 0.342$, $p = 0.452$, $n = 7$). One possible reason for the absence of an effect of habitat quality on group size is that hunting and forest destruction/compression have been particularly severe in some of the southern areas with mixed forest, thus leading to smaller group sizes despite productive habitat.

Table 3. Size, composition, and habitat association for several natural bands of *R. bieti*

Study site	Main habitat	Mean altitude, m	Band size	Adult sex ratio (M:F)	Reference
Samge (Gehuaqing)	Mixed (deciduous and conifer)	3,218	407	1:3.0 ^d	This study, Li et al. [2008]
Xiangguqing ^a (Tacheng)	Mixed	3,200	366	1:3.3 ^d (1:4.7 ^b)	Liu et al. [2007]
Wuyapiya ^b	Conifer	4,080	175	1:3.1 ^d	Kirkpatrick et al. [1998]
Bamei	Conifer	–	73	1:2.8 ^c	Cui et al. [2008]
Nanren ^b	Conifer	–	225	1:3.8 ^c	Cui et al. [2008]
Jinsichang	Mixed	3,500	180	1:3.4 ^d	Ren et al. [2008], Yang [2000]
Fuheshan	Mixed	3,105	80	–	Liu et al. [2004]
Xiaochangdu	Conifer	4,031	>210	1:2.2 ^d	Xiang [2005]
Zhina	Conifer	–	Ca 50	–	Xiang et al. [2007]
Milaka	Conifer	–	Ca 50	–	Xiang et al. [2007]
Longmashan	Mixed	3,024	>80	–	Huo [2005]
Shiba	Mixed	–	200	1:2.5 ^c	Wan et al. [2013]
Lasha	Mixed	–	130	–	Li et al. [2014]

^a Prior to being artificially split and provisioned for tourism. ^b This might be the same band of *R. bieti*. ^c OMU-based estimates. ^d Population-based sex ratios.

All-Male Units

AMUs are universally associated with *Rhinopithecus* multilevel societies [Grueter and Zinner, 2004; Grueter et al., 2012b; Qi et al., 2014; Zhu et al., 2016]. When population density and feeding costs associated with group living are low (as is the case with most *Rhinopithecus* populations), surplus males probably fare best when joining together instead of drifting away by themselves. It remains unclear, though, whether they form alliances and in so doing gain strength and improve their chances of success during a group takeover, as reported for hanuman langurs [Hrdy, 1977] and other primates [reviewed in Teichroeb and Jack, 2017]. While males of different units never engage in sociopositive behavior [Kirkpatrick et al., 1998; this study], amicable interactions exist among AMU members, due to the absence of females and mating competition.

All-male groups were encountered on many occasions, and they tended to lag behind or walk in front of the bisexual band, often at a certain distance [see also Liu et al., 2007; for *R. brelichi*, see Bleisch et al., 1993]. Even though they seem to be socially and spatially rather peripheralized, AMUs were sometimes seen in the center of the bisexual band [Kirkpatrick and Gu, 1999; this study]. This closeness may enhance the AMU males' familiarity with the males and females of the reproductive units and may facilitate a possible later takeover attempt. Indeed, Zhu et al. [2016] have recently demonstrated that prior to launching a successful coup bachelor males engage in low-risk, low-aggression encounters with harem males during which they may assess their opponents' resource-holding potential. This may be a similar situation as reported for zebras, where AMUs stay close to breeding units and can thereby learn how to behave toward females to later initiate and maintain bonds with them. These are social skills that can only be learned when consistently being within reach of the reproductive units, and these skills are needed for successful transition from nonbreeder to breeder [Rubenstein and Hack, 2004].

The few solitary males encountered were probably postreproductive males whereas most juvenile and subadult males as well as full-grown males found in bachelor groups were probably prereproductive [see also Bleisch and Xie, 1998; Kirkpatrick et al., 1998; Ren et al., 2000]. However, Ren et al. [2011] describe a case of an overthrown *R. bieti* OMU male seeking refuge in the AMU. The almost exclusive association of subadult males with AMUs indicates male-biased dispersal [Sicotte and MacIntosh, 2004; Liu et al., 2007]. Since most bands of *R. bieti* live in a fragmented habitat with limited possibilities for contacts with other bands, most bachelor males probably follow their natal band, as found in geladas [Dunbar, 1980].

Fission-Fusion

Fission-fusion refers to fluctuations in group size and number of units. Based on the time scale, we distinguish between small-scale/short-term (hours) and large-scale/long-term (days, weeks, months) fission-fusion. Small-scale fissioning, i.e. temporarily dividing into "subbands" and staying at a distance of several 100 m, was documented on several occasions and seems to have been triggered by human disturbance, travel logistics, and spatial distribution of food items [see also Kirkpatrick, 1995; Kirkpatrick et al., 1998]. Large-scale fissioning remains a poorly documented and poorly understood phenomenon in *Rhinopithecus*. There is anecdotal evidence of fission-fusion on a seasonal basis in *R. roxellana* [Schaller et al., 1985] and *R. brelichi* [Bleisch et al., 1993; Yang et al., 2002]. Others documented more erratic patterns of fission-

fusion [Kirkpatrick and Gu, 1999; Kirkpatrick et al., 1999; Zhang et al., 2006]. Theoretically one might expect that fission is related to the mating season, i.e. less band cohesion in the breeding season (late summer/early fall), as suggested by Kirkpatrick [1996]. However, we documented 1 long-term group split in winter which can be viewed as a strategy to increase the efficiency of resource use in times of overall food paucity [Grueter et al., 2009b]. If this interpretation is correct, it may have been elicited by the increasingly patchy distribution of valued food resources such as winter fruits [sensu Anderson, 1981; White and Abernethy, 2008]. An intriguing recent finding is that all recorded band fissions at the Xiangguqing site occurred in June and July, the bamboo shoot growth season [Ren et al., 2012]. In particular, it was a decrease in the availability of bamboo shoots that appeared to trigger subgrouping behavior, which suggests that fissions were due to the avoidance of food competition. Fission-fusion may well have happened more often at our study site, but confirmation is lacking.

Interunit Social Interactions

OMUs are usually within view of other neighboring OMUs. As long as units keep a spatial distance from one another, interunit relations are rather neutral and indifferent. Overt aggression, however, ensues when interunit distance becomes too small [Kirkpatrick et al., 1998; see also Zhang et al., 2006; this study]. Absence of constant and escalated aggression among OMU holders may be explained with the familiarity hypothesis, which posits that familiarity between the contestants influences encounter intensity [Ydenberg et al., 1988]. So we would expect more familiar opponents to evoke less intense encounters [sensu Wich and Sterck, 2007]. Moreover, OMU leaders may well react differently to other OMU leaders compared to nonreproductive bachelors, consistent with the threat hypothesis, which posits that the potential threat of the opponent explains variation in the intensity of the encounter [Getty, 1987]. A group of western gorillas (*Gorilla gorilla*) at Lossi normally responded to lone males by fleeing or displaying, whereas it was frequently tolerant and even indifferent in its meetings with other groups [Bermejo, 2004]. AMU males are expected to pose a larger threat and show a higher propensity for takeover attempts and possibly infanticidal attacks [Steenbeek, 2000; Xiang and Grueter, 2007]. We are far from an understanding of intermale relations in *R. bieti*, and disentangling the nature and context of intermale aggression is challenging given low visibility and extremely large groupings. The higher rate of male aggression during fall may be related to the mating season [Kirkpatrick et al., 1998] or agonistic incursions by bachelors [Laws and Vonder Haar Laws, 1984; Cords, 1988; Jack and Pavelka, 1997] or simply a result of contesting for access to the most valued food item, fruits. Indeed, in this study, there was a positive correlation between the frequency of male aggression and monthly availability of fruit. We also had the impression that large, potentially dominant OMUs monopolized fruiting trees, implying that there is a dominance rank order among OMUs, as has recently been reported for a semi-free-ranging group of *R. bieti* [Zhu et al., 2016] and for *R. roxellana* [Zhang et al., 2008b]. We found partial support for the hypothesis that male aggression is elevated when AMUs are present. “Mating season” did not have an influence on frequencies of male aggression.

While social interactions seem to be confined to within OMUs [Kirkpatrick et al., 1998; see also Zhang et al., 2006; this study], sexual interactions may well occur beyond the OMU boundary. *R. bieti* males seem to have much larger testes than other species that show a single male mating system, implying that the breeding system

has a promiscuous or (polygynandrous) component [Grueter and Zinner, 2004]. We were unable to detect extraunit matings due to lack of individual recognition, but precisely such have been recorded in semiprovisioned groups of the closely related *R. roxellana* [Zhao et al., 2005; Xiang et al., 2014]. On the other hand, the low copulation rates documented in this study show that males have more or less a reproductive monopoly in their OMUs.

Intraunit Social Interactions

Asian colobines are renowned for their low levels of social interaction [Newton and Dunbar, 1994; Yeager and Kool, 2000]. As measured by grooming, Asian colobines are an unsocial group. Some species, such as *Trachypithecus johnii*, *Presbytis rubicunda*, *P. siamensis*, and *P. potenziani*, are characterized by an almost total lack of social grooming [Poirier, 1970; Bennett, 1983; Davies, 1984; Sangchantr, 2004]. *R. bieti* are relatively social, however, with grooming occupying about 7.3% of the time. This compares well to the 6.1% grooming reported by Kirkpatrick et al. [1998].

Data on spatial relations and directionality and frequency of grooming allowed us to make preliminary inferences about social affinities and the mechanism that holds the OMUs in this species together. This was done under the following assumptions: (1) grooming frequency among particular age-sex classes is a good predictor of social bond formation [Dunbar, 1991], and (2) closeness to a neighbor is an indicator of positive affiliation [White and Chapman, 1994]. This latter assumption seems realistic since proximity should signify the opportunity for positive interactions and the willingness to tolerate some negative effects of proximity, such as increased feeding competition [White and Chapman, 1994] or disease transmission.

In Asian colobines in general, social grooming is primarily the province of females [Kirkpatrick, 2011]. Our data confirm for *R. bieti* that females spent much time grooming socially, which suggests relatively strong interfemale social relationships [Kirkpatrick et al., 1998]. However, consistent with Kirkpatrick et al. [1998], we found that males also participate in grooming. The amount of grooming activity by males implies that *R. bieti* males are relatively social and affiliative with females when compared with males of other colobines [e.g. Bennett, 1983; Megantara, 1989; Boonratana, 1993; Fuentes, 1994]. Grooming is often viewed as the “cement that maintains social relationships” [Dunbar, 1991], and the cohesion produced by male participation in grooming may help to maintain OMU integrity in the midst of a crowded neighborhood with many other units (both bachelor and reproductive) in close proximity.

Male social disintegration, as typically reported for Asian colobines, is also manifested in greater spatial distances between males and other members of the unit [Davies, 1984; van Schaik and Hörstermann, 1994; Kirkpatrick, 2011]. Contrary to this paradigm and in keeping with Kirkpatrick et al. [1998], *R. bieti* males seem to be highly integrated into the social network of an OMU. While controlling for the proportional representation of age-sex classes in the population, we found that females kept close contact primarily with males and males avoided other males almost totally and primarily sought contact with females. The relatively strong social incorporation of *R. bieti* males living in a modular system may be related to the need of male protection against rivals from the loosely associated bachelor groups and other harems. The typically high levels of association in modular societies have the potential to generate conflicts; we would thus expect conciliatory frequencies to be very high since reconciliation is a strategy to preserve social relationships and reinforce unit cohesion, all

of which could be jeopardized by conflicts [Kummer, 1978; de Waal, 1993]. Indeed conciliatory tendencies are high in both captive and wild *Rhinopithecus* (*R. bieti*: 55% [Grueter, 2004]; *R. roxellana* 43% [Ren et al., 1991], 58% [Zhang et al., 2010]), but also in 1 species of Asian colobines living in single OMUs, *Trachypithecus obscurus*: 46% [Arnold and Barton, 2001]. Another means by which unit cohesion can be maintained is by uttering contact calls [Li et al., 1982; Kirkpatrick, 1996; Ren et al., 2000]. When traveling in such busy social environs, nonstop vocalizing was common during this study [Grueter, pers. observation].

Primate social systems have conventionally been divided into male-bonded and female-bonded societies. Most colobine societies resemble the female-bonded pattern although female relationships may be subtle and infrequent as compared to many cercopithecines [Newton and Dunbar, 1994]. Recent evidence has gradually refuted the existence of pure male-bonded societies in primates by demonstrating that intrasexual relations are less strictly sex-biased. As an example, chimpanzees and hamadryas baboons have traditionally been placed near the male-bonded end of the spectrum [Kummer, 1968; Goodall, 1986], but more recent research has shown that females (at least in some populations) do frequently associate with one another and participate in sociopositive interactions [Swedell, 2002; Lehmann and Boesch, 2008]. As indicated by grooming relationships and spatial association in *R. bieti*, it seems that the OMUs are held together neither through strong female bonds (as in geladas [Dunbar, 1983]) nor through aggressive male herding (as in hamadryas baboons [Kummer, 1990]), but through bisexual ties: males sustain the allegiance of females through frequent socializing and females have tight bonds with other females. Male policing of female conflicts without the use of overt aggression, as has been observed in captive and wild groups [Grueter, 2004; see also Ren et al., 1991], may help to stabilize unit cohesion. Males and females have also been observed to cooperatively engage in interunit aggressive interactions, both in captive *R. bieti* [Grueter, 2003] and semiwild *R. roxellana* [Zhang et al., 2008b]. In *R. roxellana*, females have also been observed jointly attacking and chasing off their leader male [Ren et al., 2000; Zhang et al., 2006], which is an indication of cohesion among them. Female *R. roxellana* also commonly engage in social interactions with one another [Ren et al., 2000; Zhang et al., 2008a]. Social interactions may also be used strategically by individuals to obtain return benefits (sometimes in a different currency) and thus reflect the importance of the return benefit which can vary seasonally. For instance, sociopositive interactions among female *R. roxellana* increase in frequency in the birth season, which may facilitate access to other females' infants; in the mating season, however, females prioritize males as grooming partners, presumably because these investments will pay off in terms of sexual access to the male [Wei et al., 2012; Yu et al., 2013].

The currently available empirical body of work on dispersal in *R. bieti* is limited but the observation that most or all subadult males are associated with bachelor units provides support for male-biased dispersal [Liu et al., 2007]. A system of male-biased dispersal has also been confirmed in *R. roxellana* [Yao et al., 2011; Chang et al., 2014]. However, it has also been demonstrated that females undertake both small- and large-scale dispersal in *R. roxellana* [Zhang et al., 2006, 2008a; Zhao et al., 2008; Qi et al., 2009; Guo et al., 2014], and there are anecdotal reports of female transfers following the takeover of an OMU leader in *R. bieti* [Ren et al., 2011]. Female dispersal is likely facilitated by the familiarity with and closeness of other units in modular societies [Zhang et al., 2008a]. The temporal fluctuation in unit membership as a result of

emigration and immigration can only be assessed via a long-term study following a focal unit, something that is enormously challenging under wild conditions.

According to the socioecological models [Wrangham, 1980; van Schaik, 1989; Isbell, 1991; Sterck et al., 1997], many aspects of female social behavior depend on the distribution and defendability of food resources. Data on within-unit dominance relationships among *R. bieti* females are sparse, but it appears that they exhibit a relaxed and egalitarian system with a weak dominance hierarchy [Cui et al., 2014]. This egalitarianism is likely the result of diminished *within-unit* feeding competition [Struhaker and Leland, 1987; Newton and Dunbar, 1994; Yeager and Kirkpatrick, 1998], as patches usually seem to provide sufficient resources for a single *R. bieti* unit [Grueter et al., 2009a]. To what extent *between-unit* competition [Grueter et al., 2009a] has an influence on female coalitionary relationships remains uninvestigated. The fact that they feed on both widely dispersed foods (lichen) with low usurpability and clumped foods (fruits, sprouts) with monopolization potential [Zhang et al., 2008b; Grueter et al., 2009a] makes such an assessment complex.

Conclusions

This study has enhanced our understanding of the social organization and structure of Yunnan snub-nosed monkeys. We confirmed that they exhibit a nested social organization with cohesive “harems” united in semi-stable bands and transient AMUs at the periphery. A network of seemingly strong bisexual bonds promotes harem stability within the band. By primate standards, this species is characterized by unusually large groups (with the study group/band numbering >400). Strict conservation measures (continued enforcement of logging ban, habitat restoration, anti-poaching activities, etc.) are needed to prevent these bands from disbanding and disappearing.

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Statement of Ethics

This research was noninvasive and abided by the legal requirements in the People’s Republic of China.

Disclosure Statement

The authors declare no conflicts of interest.

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