

Seasonal changes in social cohesion among males in a same-sex primate group

Pingfen Zhu^{1,2} | Cyril C. Grueter^{3,4} | Paul A. Garber⁵  | Dayong Li⁶ |
Zuofu Xiang⁷ | Baoping Ren¹ | Ming Li^{1,8} 

¹ CAS Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chaoyang District, Beijing, China

² University of Chinese Academy of Sciences, Beijing, China

³ School of Human Sciences, The University of Western Australia, Crawley, Perth, Australia

⁴ Centre for Evolutionary Biology, School of Biological Sciences, The University of Western Australia, Crawley, Perth, Australia

⁵ Department of Anthropology and Program in Ecology and Evolutionary Biology, University of Illinois, Urbana, Illinois

⁶ Key Laboratory of Southwest China Wildlife Resources Conservation [Ministry of Education], China West Normal University, Nanchong, China

⁷ College of Life Science and Technology, Central South University of Forestry and Technology, Changsha, Hunan, China

⁸ Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming, China

Correspondence

Ming Li, CAS Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, 1-5 Beichenxi Road, Chaoyang District, Beijing 100101, China.
Email: lim@ioz.ac.cn

Funding information

Strategic Priority Research Program of the Chinese Academy of Sciences, Grant number: XDA19050202; China Postdoctoral Science Foundation, Grant number: 2017M620906; National Key R&D Program of China, Grant number: 2016YFC0503200; National Natural Science Foundation of China, Grant numbers: 31470459, 31821001

Male-male interactions in mixed-sex groups of social mammals are typically characterized by a mix of hostility and affiliation, as a result of inherent conflicts over mating opportunities, and the costs and benefits of social alliances, co-operative behaviors, and coalitionary defense. In species of nonhuman primates that form all-male groups, it is still unclear how the tradeoffs between the benefits of forming an all-male group and the cost of male-male competition in seeking mating opportunities with females in bisexual groups influence social cohesion in different seasons. Here, we used social network analysis to quantify the impact of reproductive seasonality on social cohesion and clique size of bachelor males residing in an all-male unit (AMU) in wild black-and-white snub-nosed monkeys (*Rhinopithecus bieti*). These primates are strict seasonal breeders and live in a modular social system composed of a number of one-male units (OMUs) and an associated peripheral AMU. We found that the AMU social network had a significantly lower density, centralization, clustering coefficient, and smaller clique size during the mating season compared to the non-mating period. However, aggression among AMU males during both mating and non-mating periods was low. Our results suggest that network structure topology in male same-sex social units is modulated by seasonal changes. Bachelor males engage in two types of competition to gain reproductive success: first, which is analogous to contest competition, in which bachelor males act aggressively and challenge OMU leader males in an attempt to take over an OMU; and second, which is more analogous to scramble competition, in which bachelor males avoid aggressive interactions and instead engage in sneaky copulations with fertile females. Our work adds to an understanding of the maintenance of all-male groups in species that form a multilevel society.

KEYWORDS

bachelor group, male-male competition, multilevel society, *Rhinopithecus bieti*, social network

1 | INTRODUCTION

Male–male relationships in primates and other group-living mammals span the spectrum from antagonism (Clutton-Brock, Guinness, & Albon, 1982; Drews, 1996) to tolerance and bonding (Grueter, 2014; Ostner & Schülke, 2014). This variability is partly contextual and likely related to factors such as kinship, familiarity, and species-specific differences in the ability of males to form long-term same-sex social bonds (van Hooff, 2000). In some primate species (e.g., patas monkeys [*Erythrocebus patas*] (Cords, 2012; Harding & Olson, 1986)), male intrasexual relationships are highly adversarial and intolerant. In other taxa (e.g., chimpanzees [*Pan troglodytes*] (Mitani, 2009), spider monkeys [*Ateles geoffroyi*] (Schaffner, Slater, & Aureli, 2012), Assamese macaques [*Macaca assamensis*] (Schülke, Bhagavatula, Vigilant, & Ostner, 2010), bonnet macaques [*M. radiata*] (Adiseshan, Adiseshan, & Isbell, 2011)), adult males form strong, and persistent social affiliations. Given that many primate species live in stable multimale multifemale groups, a lone male may profit from the presence of additional males – both related and unrelated – through the services they provide, e.g., vigilance, cooperative hunting, resource defense, and cooperative defense of females against rivals inside and outside the group (Bissonnette et al., 2015; Díaz-Muñoz et al., 2014; Ostner & Kappeler, 2004; van Hooff, 2000). In these species, the ability of males to develop behavioral strategies that enable individuals to compete for access to fertile females in ways that are non-aggressive or not socially disruptive (e.g., sneaky copulations, short-term consortships) is critical for maintaining same-sex affiliative bonds and alliances (Garber & Kowalewski, 2011; Sussman & Garber, 2001).

Inter-male competition reaches particularly high levels in societies in which a single male controls access to multiple fertile females, leading to a pronounced skew in male reproductive output (Launhardt, Borries, Hardt, Eppel, & Winkler, 2001). In such a polygynous setting, extra males are largely excluded from breeding groups by resident males and either remain solitary or form all-male groups (Bennett & Sebastian, 1988; Dunbar & Dunbar, 1975; Levréro et al., 2006; Rajpurohit, 1991). These bachelor groups may contain ousted males that have lost their reproductive monopoly (Rajpurohit, Sommer, & Mohnot, 1995), males that are at their reproductive peak (i.e., prime males), as well as young pre-prime males waiting to fully mature and obtain mating opportunities (Qi et al., 2017).

Advantages to males of forming bachelor associations may include a lowered risk of predation if solitary individuals are more vulnerable than sets of individuals (Rubenstein & Hack, 2004; Waterman, 1997), access to social information concerning the location of productive feeding sites, the opportunity to hone social skills (both affiliative and aggressive) required to become the sovereign breeder of an reproductive group (Bercovitch & Berry, 2015; MacFarlane & Coulson, 2009), and in species in which the joint actions of several bachelor males play a critical role in ousting a resident male, the ability to form same-sex social coalitions (Rajpurohit, Chhangani, Rajpurohit, & Mohnot, 2003). All-male groups vary in stability and cohesiveness across species; for example, in Thomas langurs (*Presbytis thomasi*), all-male groups are unstable and characterized by frequent fission and

fusion events (Wich et al., 2007), whereas in mountain gorillas (*Gorilla beringei beringei*) (Robbins, 1995) and African elephants (*Loxodonta africana*) (Chiyo et al., 2011), marginalized males either remain solitary or alternate between a solitary and a same-sex social state. In contrast, gelada (*Theropithecus gelada*) and golden snub-nosed monkey (*Rhinopithecus roxellana*) all-male units (AMUs) are relatively stable and the same set of bachelor males remain together for several years (Dunbar, 1980; Qi et al., 2017).

Data on how individuals in all-male groups allocate social effort and maintain social cohesion are limited. In the absence of competition over access to females, relationships among males in an all-male group are expected to be more tolerant, more affiliative, and less aggressive (Pusey & Packer, 1987; Robbins, 1996) than in the presence of fertile females. In the case of mountain gorillas, males residing in an all-male group were found to spend more time in close proximity (<2 min) during resting (a median of 11.14 vs. 2.97%), and exhibit higher levels of affiliation (physical contact: 0.37 vs. 0.03 times/hr, grooming: 0.22 vs. 0.002 times/hr, play: 0.52 vs. 0.005 times/hr) and homosexuality (male–male mounting or touching of genitals by another male, 0.06 vs. 0 times/hr) than males living in multimale-multifemale groups (Robbins, 1996). In addition, genetic relatedness is reported to have a positive influence on affiliative within-AMU male associations in African elephants and golden snub-nosed monkeys (Chiyo et al., 2011; Qi et al., 2017). Similarly, in several primate species in which males are philopatric (e.g., chimpanzees (Mitani, 2009), spider monkeys (Di Fiore, Link, Schmitt, & Spehar, 2009), and muriquis [*Brachyteles arachnoides*] (Strier, 2000)), group males form strong social alliances, engage in cooperative behavior. In other primate species, such as stump-tailed macaques (*Macaca arctoides*) (Butovskaya & Kozintsev, 1996), Guinea baboons (*Papio papio*) (Patzelt et al., 2014), and black and gold howler monkey (*Alouatta caraya*) (Garber & Kowalewski, 2011), the strength of male–male affiliation was unrelated to kinship.

However, how the tradeoffs between the benefits of forming an AMU and the cost of male–male competition influence the social cohesion of AMUs across different seasons remains unclear. Here, we examined bachelor male relationships in wild provisioned black-and-white snub-nosed monkeys (*Rhinopithecus bieti*). *R. bieti* is an endangered species of Asian colobine that lives in a large multilevel or modular social organization (Grueter, Li, Ren, Wei, & Li, 2017; Kirkpatrick, Long, Zhong, & Xiao, 1998; Kirkpatrick & Grueter, 2010). The fundamental social unit in this multilevel society is the one-male, multi-female unit (OMU). In this primate species, a number of OMUs coordinate their day-to-day activities and form a larger breeding band composed of ~50–400 individuals (Grueter et al., 2017; Ren, Li, Garber, & Li, 2012). AMU composed of juvenile, subadult, and adult males (some of which are deposed OMU leader males (Ren, Li, He, Qiu, & Li, 2011)) are loosely attached to the breeding band and often follow it at close range (Grueter et al., 2017; Liu, Ding, & Grueter, 2007). Descriptive accounts suggest that relations among bachelor males are principally affiliative and may include homosexual mounting (Grueter, 2009). To attain reproductive success, bachelor males either must displace the resident OMU male through an aggressive OMU takeover (Zhu et al., 2016), sneak copulations with OMU females (Xia, Zhu, Li, &

Ren, 2016), or attract OMU females to join them and form a new OMU (Colmenares, 1992; Pines, Saunders, & Swedell, 2011). In black-and-white snub-nosed monkeys, a single bachelor male typically challenges a resident male, and if successful, expels him and takes over his OMU. Bachelor males engage in highly aggressive conflicts with resident males during takeovers and experience physical injuries (Zhu et al., 2016). To date, bachelor males have not been observed to act collectively to displace resident males (Xia et al., 2016; Zhu et al., 2016). Black and white snub-nosed monkeys are strictly seasonal breeders, with a mating season lasting from July to September (Xia et al., 2016). However, males and females engage in copulations outside this three month (Xia et al., 2016).

In the present study, we used social network analysis to examine changes in bachelor male social interactions during mating and non-mating periods. Given the potential benefits of forming an AMU and the male-male competition for access to fertile females during the mating season, we expected (H1) bachelor males to form affiliative relationships during most of the year but alter these relationships during the mating season by exhibiting lower levels of social cohesion, increased levels of agonism, and smaller clique size as individuals compete to gain access to reproductive females; and (H2) bachelor males who formed stronger affiliative dyads during non-mating periods would engage in less frequent agonism during the mating season.

2 | METHODS

2.1 | Study site and subjects

We studied one provisioned band of black-and-white snub-nosed monkeys at Xiangguqing (99°20' E, 27°30' N) in the Baimaxueshan National Nature Reserve, Yunnan Province, China (for further details, see Li, Ren, Grueter, Li, & Li (2010)). The study band has been provisioned twice daily (approximately 9:00 and 17:00 hr) since May 2008 with lichen, carrots, apples, pumpkin seeds and bamboo shoots provided in a small area (900 m²) within their home range. The diet of our study band consisted largely of natural foods present in their home range (for a detailed description of the origin of the study band and the methods of provisioning see (Li, Ren, Li, Zhang, & Li, 2012; Li, Ren, Li, Zhu, & Li, 2013; Zhu et al., 2016)).

During our study period, from September 2012 to October 2013, the study band consisted of 42–60 individuals belonging to 5–8 OMUs and one AMU. The AMU contained four adult males (PG, BL, LB, and HM), two subadult males (HD and RL), and five juvenile males (ML, LC, XS, LD, and CZ or ML, LC, XS, IP, and IH). Two juveniles, LD and CZ, who were approximately 3 years old, joined the AMU on February 22, 2013 after their OMU had been taken over by a new adult male. These juvenile males disappeared from the AMU on July 6, 2013. IP and IH, who were born in 2012 and therefore approximately 1.5 years old, independently joined the AMU on July 6 and August 25, 2013, respectively, after each resident OMU male was replaced. Since the observations of LD, CZ, IP, and IH did not include both the mating (July–September) and non-mating seasons (October–June), they were not included as subjects.

We observed bachelor males to copulate on nine occasions during our study period, twice during the mating season and seven times during the non-mating period. In addition, four of the nine copulations we observed were between the juvenile bachelor male and the OMU female (four of the remaining five were by adult bachelor males and one were by subadult bachelor males). During one year study, Xia et al. (2016) observed that non-adult bachelor males engaged in four of five copulations with OMU females and an ejaculation occurred when a juvenile bachelor male copulated with a female. Given that it was possible for non-adult males to be sexual competitors, we included data on all adult (PG, BL, LB, and HM), subadult (HD and RL), and juvenile bachelor males (ML, LC, and XS) in all subsequent analyses.

2.2 | Data collection

We were able to identify each individual in the study group based on their hair color, body size, facial features, tail patterns, and other distinctive physical characteristics. We observed the subjects from 9:00 to 17:00 or 19:00 (depending on season and day length) on 292 data collection days. Given difficulties of observing and following the same individual in the dense vegetation and across steep mountainous terrain, we used a focal sampling method (Altmann, 1974) and selected a nearby bachelor male for observation until he was out of view. Focal observation periods lasted from 5 min to 2.75 hr (mean \pm SD: 0.39 \pm 0.45 hr/period). We observed the nine AMU males for a total of 1729.4 hr, with a median 217.4 hr (Q1–Q3: 162–231.7 hr) per individual (Table 1). To reduce the possibility of spurious differences in the cohesion of networks that can be brought about by unequal lengths of observation time among individuals in the two seasons, we subsampled the data set randomly based on the minimum observation time of focal individuals (i.e., 30.42 hr per individual for each season) in R 3.2.3 (<http://www.r-project.org>). We then used this data subset for the following statistical analysis. We recorded male-male grooming interactions, including start time, initiator, recipient, and end time. We scored a new grooming about when (1) grooming direction changed or (2) grooming paused for >1 min. Only grooming bouts of 5 s or longer were included in the analyses and triadic grooming interactions, which accounted for only 0.25% of all grooming bouts were discarded. We also recorded agonistic interactions between males, including behaviors of contact aggression (fighting, biting, and scratching) and non-contact (staring, chasing, threatening, and displacement). We recorded the event as displacement if one male left its position within 1 min of when another male approached (within 2 m).

2.3 | Social network structure

We used grooming rates and grooming duration to construct weighted and directed networks. The network nodes represent individuals, and ties represent the presence of social grooming among pairs (Brent, Lehmann, & Ramos-feranandez, 2011). We used grooming rates and grooming duration to represent the weight of ties. Grooming rates refer to the number of grooming bouts recorded by a particular dyad divided by the time (hours) both individuals were observed. Grooming

TABLE 1 Observation time (in hours) for each male in the all-male unit of black-and-white snub-nosed monkeys at Xiangguqing

| | Age class | Mating season (July–September) | Non-mating season (October–June) | Whole year |
|-------|-----------|-----------------------------------|-------------------------------------|------------|
| PG | Adult | 59.50 | 32.33 | 91.83 |
| BL | Adult | 52.33 | 69.50 | 121.83 |
| LB | Adult | 43.83 | 187.83 | 231.66 |
| HM | Adult | 55.58 | 199.42 | 255 |
| HD | Subadult | 57.25 | 175 | 232.25 |
| RL | Subadult | 43.08 | 148.17 | 191.25 |
| ML | Juvenile | 63.33 | 162.83 | 226.16 |
| LC | Juvenile | 30.42 | 131.58 | 162 |
| XS | Juvenile | 66.67 | 150.75 | 217.42 |
| Total | | 471.99 | 1257.41 | 1729.42 |

duration was computed by dividing the total amount of grooming time (minutes) per dyad by the amount of time the dyad was observed (hours). Since all grooming ties represent social relationships between individuals and might have potential biological significance, we did not filter our networks by removing weak ties (Croft, James, & Krause, 2008a). To quantify and compare different networks, we followed the studies of Lehmann & Boesch (2009) and Brent, MacLarnon, Platt, & Semple (2013) which relied on three commonly used metrics that reflect global network cohesion, i.e., density, centralization, and clustering coefficients. Density is defined as the ratio of the sum of the weights of the edges to the number of possible edges in an entire network (i.e., 72 edges among nine males in our study) and describes the extent of the actual connections between individuals in a group (Hanneman & Riddle, 2005).

Unlike density, which describes the general level of cohesion in a network, centralization describes the extent to which connections are focused around a particular individual, who is defined as the most central individual. Degree-based measures of centralization describe the network as a whole and are calculated as the observed sum of degree centrality differences between the most central node (the node with the highest degree centrality) and other nodes. This value is normalized by the theoretical maximum centralization score (Butts, 2016; Freeman, 1978). Centralization expresses unevenness or variance of the interaction distribution across the overall network, with 0 indicating that all individuals are equally involved in all interactions, and a higher value meaning that a single or a smaller set of individuals are involved in all existing interactions (Freeman, 1978).

Clustering coefficients measure the degree to which nodes in a network tend to cluster together (Croft, James, & Krause, 2008b). We used weighted global clustering coefficient which can be calculated as the total value of triangles divided by the total value of the triplets (Opsahl & Panzarasa, 2009). Triplets include closed triplets, in which all nodes are connected by edges, and open triplets are those in which two of three nodes are connected by edges, forming a “V” (open triplet) (Opsahl & Panzarasa, 2009). The global clustering coefficient can have values between 0 and 1, with 0 meaning that none of a given node's “neighborhoods” (nodes that are directly connected to the node in

question) are connected with each other, and 1 meaning that all of a given node's “neighborhoods” are connected to each other.

2.4 | Statistical analyses

To examine changes in agonistic behavior, we compared the rate of male–male agonism between mating and non-mating periods using a permutation test in the “perm” package (Fay, 2015). We also divided agonistic behavior into contact aggression and non-contact aggression, and used a permutation test to compare rates of contact and non-contact aggression between mating season and non-mating periods (Fay, 2015). To determine which age dyad combination changed more between mating and non-mating periods in grooming rate, grooming duration, and agonism (contact aggression and non-contact aggression), we used a non-parametric Kruskal–Wallis test to analyze the difference between all six dyad combinations containing adult–adult, adult–subadult, adult–juvenile, subadult–subadult, subadult–juvenile, and juvenile–juvenile, followed by post hoc Dunn tests (Zar, 2010). Dunn tests were used to determine which dyads differ from each other. We performed Dunn tests with the *dunnTest* function in the FSA package, and adjusted *p*-values using the “bh” method to control the false discovery rate (Ogle, 2018).

We used the “statnet” package (Handcock et al., 2016) to calculate density and network centralization, and used the “tnet” package (Opsahl, 2015) to compute global clustering coefficients. These two packages were loaded in R. We compared the network densities between the mating and non-mating season via the “compare-density” test in UCINET 6.0 (Borgatti, Everett, & Freeman, 2002). Since UCINET 6.0 only compares density, we followed Brent et al., (2013) by using “statnet” and “tnet” packages to compare network centralization and global clustering coefficients with a bootstrapping technique. First, for the bootstrap phase, we used the “link reshuffling” procedure with the *rg_reshuffling_w* function of the “tnet” package to reshuffle a weighted network randomly with the same degree distribution (1,000 iterations) (Opsahl, 2009). Then we calculated the centralization of each randomized network with the *centralization* function of “statnet,” using 1,000 iterations (or

calculated global clustering coefficients with the *clustering_w* function, using 1,000 iterations). Finally, we followed the equations of Snijders & Borgatti (1999) for comparing two paired networks to calculate the difference in bootstrap standard error (SEd) for centralization (or clustering coefficients) between the mating and non-mating season networks. We computed a *t*-statistic by dividing the difference of observed values by SEd (for details see Snijders & Borgatti (1999)) and obtained *p*-values. We set the significance threshold at 0.05 for two-tailed tests. We also used “ggplot2” packages (Wickham et al., 2018) to draw violin plots of network centralization and clustering coefficients. Violin plots are rotated kernel density plots, which include means and standard deviations.

To calculate the cliques of a grooming social network, we first transformed the weighted edges to binary values (0/1) as UCINET can not analyze the cliques of a weighted network directly (Liu, 2009). We kept the grooming direction in binary networks, for example in one dyad, if individual A groomed individual B, we valued the edge from A to B as 1. If individual B did not groom individual A, we valued the edge from B to A as 0. Then we used the UCINET path “Network-Subgroups-Cliques” to calculate the cliques present in the AMU, setting the minimum clique size as 3 and setting the Type as strong. A strong clique means that all clique members groomed each other. To calculate correlations between grooming duration or grooming rate during the non-mating periods and various measures of agonism (rate of agonism, rate of contact aggression, and rate of non-contact aggression) during the mating season, we used the quadratic assignment procedure (QAP) with the *qaptest* function in the R package “statnet.” We drew all social network graphs using the software Gephi 0.9.1.

2.5 | Ethical standards

All research methods adhered to Chinese legal requirements and complied with protocols approved by the State Forestry Administration of China and the American Society of Primatologists principles for the ethical treatment of primates.

3 | RESULTS

3.1 | Grooming interactions

The subsampled data set were used in all the following analyses. Each male was involved in grooming interactions (grooming given and grooming received) a median of 0.88 (IQR = 0.60–1.13) times per hour. Grooming accounted for a median of 6.06% (IQR = 4.25–9.00%) of total observation time for each male. The grooming rate for all bachelor males during the mating season was lower than during non-mating period (permutation test: $Z = -3.17$, $p < 0.05$, mating: median = 0, IQR = 0–0.09; non-mating: median = 0.11, IQR = 0.03–0.26). Similarly, the grooming duration of all males during the mating season was lower than during non-mating period (permutation test: $Z = -2.81$, $p < 0.05$, mating: median = 0, IQR = 0–0.42; non-mating: median = 0.44, IQR = 0.07–1.26).

We also compared rates of grooming across mating and non-mating periods for all six dyad combinations containing adult–adult, adult–subadult, adult–juvenile, subadult–subadult, subadult–juvenile, and juvenile–juvenile bachelor males. We found a significant difference between these six dyad combinations (Kruskal–Wallis: $\chi^2 = 23.62$, $df = 5$, $p < 0.05$), with adult–adult male dyads showing smaller changes in grooming rates than adult–juvenile male dyads (Dunn test: $Z = -2.41$, $p < 0.05$), subadult–juvenile male dyads (Dunn test: $Z = -2.52$, $p < 0.05$) and juvenile–juvenile male dyads (Dunn test: $Z = -2.72$, $p < 0.05$). Adult–subadult male dyads were found to exhibit smaller changes in grooming rates than adult–juvenile male dyads (Dunn test: $Z = -3.47$, $p < 0.05$), subadult–juvenile male dyads (Dunn test: $Z = -3.39$, $p < 0.05$) and juvenile–juvenile male dyads (Dunn test: $Z = -3.40$, $p < 0.05$). There also was a significant difference between the six dyad combinations in changes in grooming duration during mating vs. non-mating periods (Kruskal–Wallis: $\chi^2 = 28.17$, $df = 5$, $p < 0.05$), with adult–adult male dyads showing smaller differences than adult–juvenile male dyads (Dunn test: $Z = -2.75$, $p < 0.05$), juvenile–juvenile male dyads (Dunn test: $Z = -2.87$, $p < 0.05$) and subadult–juvenile male dyads (Dunn test: $Z = -2.49$, $p < 0.05$). Adult–subadult male dyads were found to exhibit a smaller difference in grooming duration between mating and non-mating periods than did adult–juvenile male dyads (Dunn test: $Z = -3.91$, $p < 0.05$), and subadult–subadult male dyads (Dunn test: $Z = -2.39$, $p < 0.05$), subadult–juvenile male dyads (Dunn test: $Z = -3.42$, $p < 0.05$) and juvenile–juvenile male dyads (Dunn test: $Z = -3.61$, $p < 0.05$).

3.2 | Agonistic interactions

Agonistic interactions for each male occurred at a median rate of 0.21 (IQR = 0.16–0.36) times per hour. Overall, male–male agonistic interactions were characterized by the absence of direct physical contact (89.36%) and principally involved avoidance or displacement. Only 10.6% involved contact aggression (overall rate of contact aggression was 0.03 events per individual male per hour). The agonistic rate among all AMU males was not significantly different between the mating season and the non-mating period (permutation test: $Z = -1.27$, $p = 0.20$, mating: median = 0, IQR = 0–0.03; non-mating: median = 0, IQR = 0–0.07). There also were no differences in the rate of agonistic interactions during mating and non-mating periods by six dyad combination (Kruskal–Wallis: $\chi^2 = 3.25$, $df = 5$, $p = 0.66$). Without considering the direction of agonistic behavior, the total number of male dyads was 36 ($N = 36$). Only 25% ($n = 9$) of male dyads showed an increase in the rate of agonistic behavior during the mating season compared with the non-mating period. Of these, 2.78% ($n = 1$) were adult male–subadult male dyads, 16.67% ($n = 6$) adult male–juvenile male dyads and 5.56% ($n = 2$) subadult male–juvenile male dyads.

Although in H1, we expected an increase in rates of aggression during the mating season compared to the non-mating period, this was not the case. Rates of contact aggression (fighting) among all AMU males were lower during the mating season than during the non-mating period (permutation test: $Z = -2.59$, $p < 0.05$, mating: median = 0, IQR = 0–0, range: 0–0.03; non-mating: median = 0,

IQR = 0–0.002, range: 0–0.11; Figure 1a). The change in rates of contact aggression between mating and non-mating periods was not significantly different among the six dyad combinations (Kruskal–Wallis: $\chi^2 = 1.17$, $df = 5$, $p = 0.95$). Only one of the 36 male dyads exhibited an increase in the rate of contact aggression during the mating season compared with the non-mating period. This dyad was composed of subadult male–juvenile male.

The rate of staring, chasing, threatening, and displacement, which we define as non-contact or milder forms of aggression than fighting, among all AMU males also was not significantly different between mating and non-mating periods (permutation test: $Z = -1.17$, $p = 0.24$, mating: median = 0, IQR = 0–0.007; non-mating: median = 0, IQR = 0–0.06; Figure 1b). There were no differences when we compared the six dyad combination in the rate of non-contact agonistic behavior between mating and non-mating periods (Kruskal–Wallis: $\chi^2 = 2.43$, $df = 5$, $p = 0.79$), and only 15.28% of male dyads exhibited an increase in the rate of these aggressive behaviors during the mating season compared with the non-mating period. Male dyads (total number: $N = 36$) that exhibited increased non-contact aggression were composed of adult male–subadult male (5.56%, $n = 2$), adult male–juvenile male (16.67%, $n = 6$), subadult male–juvenile male (5.56%, $n = 2$), and juvenile male–juvenile male (2.78%, $n = 1$).

3.3 | Network cohesion

Based on bootstrap analyses, the grooming rate networks of all AMU males exhibited a lower density during the mating season (0.07) than the non-mating season (0.20) ($t = -2.13$, $df = 4999$, $p < 0.05$) (Figure 2). The difference of density in grooming duration networks between the mating (0.31) and non-mating seasons (0.95), however, was not significant ($t = -1.82$, $df = 4999$, $p = 0.07$), suggesting that grooming rate and grooming duration may represent different measures of social bonding to bachelor male snub-nosed monkeys. We did find significant differences between the mating season and non-mating season in network centralization among all nine individuals (grooming rates: mating = 0.04, non-mating = 0.23, $t = -4.04$, $df = 999$, $p < 0.001$; grooming duration: mating = 0.25, non-mating = 1.26, $t = -3.94$, $df = 999$, $p < 0.001$; Figure 3), with a lower level of centralization during the mating season. Network clustering coefficients were lower

during the mating season compared to the non-mating season, for both grooming rates (mating = 0.49, non-mating = 0.74, $t = -6.10$, $df = 999$, $p < 0.001$) and grooming duration (mating = 0.51, non-mating = 0.73, $t = -4.92$, $df = 999$, $p < 0.001$; Figure 4). These results based on network density, centralization, and clustering coefficients provide partial support for H1. Although agonism did not increase during the mating season, bachelor exhibited reduced rates of social cohesion during periods of increased mating opportunities.

3.4 | Cliques

Three cliques were detected in the grooming rate network during the mating season. These were {HM, ML, and XS}, {BL, ML, and XS}, and {PG, ML, and XS}. Clique membership overlapped, and the most shared members were juvenile ML and XS (3/3 times). The same set of individual relationships were found in our analysis of grooming duration networks during the mating season. During the non-mating period, we identified ten cliques based on grooming rate or grooming duration networks. These were {BL, HM, RL, ML, and LC}, {BL, LB, HM, and RL}, {BL, HM, ML, LC, and XS}, {BL, LB, HM, and XS}, {HM, HD, RL, ML, and LC}, {LB, HM, HD, and RL}, {HM, HD, ML, LC, and XS}, {LB, HM, HD, and XS}, {PG, RL, and LC}, and {PG, LC, and XS}. The most strongly shared clique members were adult male HM (10/10 times), followed by juvenile LC (6/10 times), and then subadult male RL and juvenile XS (5/10 times). Moreover, clique size was larger during the non-mating period than during the mating season (Wilcoxon rank sum test: $W = 3$, $p < 0.05$; mating season: median = 3, IQR = 3–3; non-mating period: median = 4, IQR = 4–5). Two of three cliques present during the mating season were maintained during non-mating periods indicating that several bachelor males remained clique partners throughout the year.

3.5 | Affiliative interactions do not predict agonism

To understand whether two males who groomed frequently during the non-mating period engaged in a less frequent agonism during the mating season, we analyzed the correlation between grooming rate/duration (during the non-mating season) and overall agonistic behavior (contact aggression and non-contact aggression during the mating season). The results indicated no evidence of a correlation (Table 2),

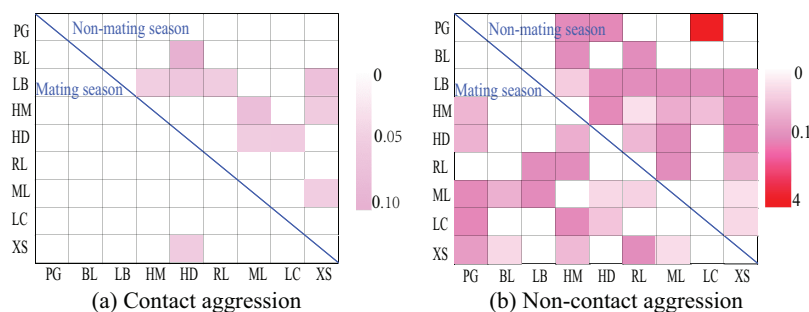


FIGURE 1 The heatmaps of contact aggression (a) and non-contact aggression (b) among all males in AMU of black-and-white snub-nosed monkeys. Bottom-left corner of the yellow diagonal represents aggressions during the mating season while the top right corner of the yellow diagonal represents aggression during the non-mating period. A darker pink shows a higher aggressive rate

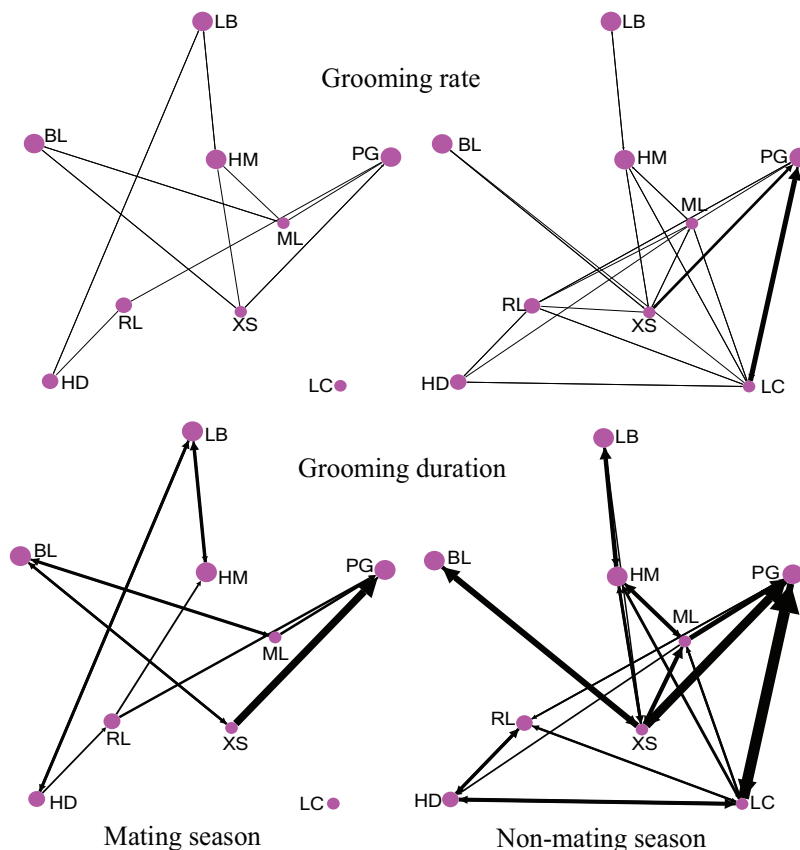


FIGURE 2 The social structure of an all-male unit of black-and-white snub-nosed monkeys during the mating and non-mating season. The network is based on grooming rate and grooming duration. Only the edges whose weights above the average are showed. Filled pink circles represent males, where there size of circles reflects the three age-class. The largest circles represent adult males, the second largest circles represent subadult males, and the smallest circles represent juvenile males. Arrows show the direction of grooming. The thickness of lines represents the weighting of interactions, where a thicker line indicates a more frequent or a stronger interaction

and therefore, more affiliative dyadic social interactions between bachelor males during the non-mating periods were not a strong predictor of a reduction of agonistic interactions between these same bachelor males during the mating season. Therefore H2 was not supported.

4 | DISCUSSION

Despite the existence of male-only associations in some species of primates and other mammals, little is known concerning the underlying behavioral interactions and partner relationships that enable bachelor

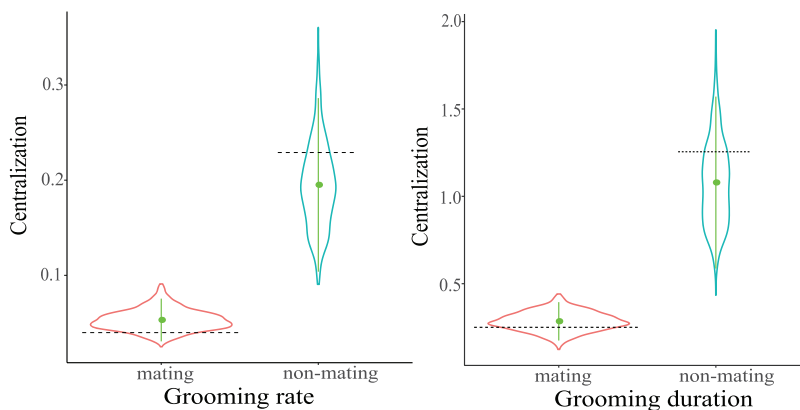


FIGURE 3 Violin plots of the network centralization of the all-male unit during the mating and non-mating season based on grooming rate and grooming duration. The points and lines in the violin plot represent means and standard deviations of 1,000 randomized networks, respectively. The dashed lines represent the observed value of network centralization

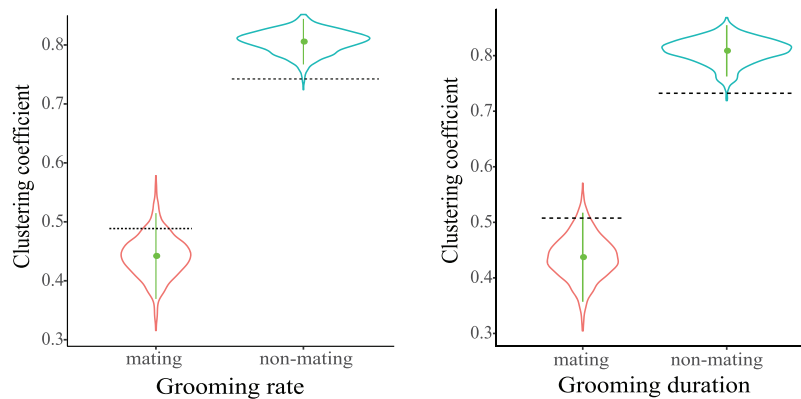


FIGURE 4 Violin plots of the clustering coefficients of the all-male unit during the mating and non-mating season based on grooming rate and grooming duration. The points and lines in the violin plot represent means and standard deviations of 1,000 randomized networks, respectively. The dashed lines represent the observed value of network centralization

males to both reside together in a cohesive social unit, and to compete for opportunities to fertile females. The present study on black-and-white snub-nosed monkeys has provided detailed insights into the social interactions of a primate species in which OMU leader males are intolerant of juvenile, subadult, and adult males, whereas bachelor males form an AMU that is characterized by intrasexual tolerance, low rates of contact aggression, and remains relatively cohesive throughout the year.

Theories of primate sexual selection, especially among species characterized by polygyny, argue that during the breeding season or in the presence of fertile females, male intrasexual aggression and intolerance are expected to escalate, as males compete to monopolize access to reproductively active and nonshareable females (Lawler, Richard, & Riley, 2005; Muller & Emery Thompson, 2012; Ohsawa, Inoue, & Takenaka, 1993; Richard, 1992). Males also may engage in sexual coercion, patrolling behavior, and mate guarding to limit the opportunities of fertile females to mate with other resident males, lone males, or males from neighboring groups (Wrangham & Muller, 2009).

In this study, we examined social interactions among bachelor male black and white snub-nosed monkeys who reside in an AMU. Snub-nosed monkeys are unique among Asian langurs in forming a multilevel society. The snub-nosed monkey multilevel society is argued to have evolved by the fusion of several independent OMUs into a cohesive breeding band that is shadowed by one or more AMU (Grueter et al., 2010; Qi et al., 2014). In most other species of Asian langurs, the leader male of a single OMU defends a territory and his OMU from neighboring OMUs, solitary bachelor males, or members of

an AMU (Sterck, 2012; Yeager & Kool, 2000). In the case of snub-nosed monkeys, although bachelor males may live together for several years, and in some cases are close relatives (Qi et al., 2017), it is rare for bachelor males to act collectively to attempt to take over an OMU.

We found that although bachelor male networks and dyadic interactions during the mating season were less cohesive and cliques were smaller compared to non-mating periods, during the mating season bachelor male black and white snub-nosed monkeys did not engage in more frequent aggression than during non-mating periods. Combining the findings of male aggressions in this study with a previous study of male takeovers (Zhu et al., 2016), we suggested two types of behavioral strategies to gain reproductive success used by bachelor male black-and-white snub-nosed monkeys. One, which is analogous to contest competition, is characterized by high levels of aggression and high risk of physical injury. This occurs when individual bachelor males attempt to takeover females and expel its current leader male. During successful male takeovers, 40% (10/25) of antagonistic interactions between challenging males and resident males was contact aggression (Zhu et al., 2016). The second strategy, which is more similar to scramble competition, is for individual bachelor males to shadow OMUs in an attempt to engage in sneaky or hidden copulations with fertile and nonfertile resident females. This latter strategy is typically associated with low levels of intrasexual contact aggression either between leader males and bachelor males or between competing bachelor males as these sneaky copulations do not occur in the presence of multiple males. Given that seven of nine

TABLE 2 The correlation between grooming duration/rate during the non-mating season and agonism/contact/non-contact rate during the mating season

| | Grooming rate_nonmating | | Grooming duration_nonmating | |
|--------------------------------------|-------------------------|----------|-----------------------------|----------|
| | <i>r</i> | <i>p</i> | <i>r</i> | <i>p</i> |
| Agonism_mating season | 0.10 | 0.14 | 0.09 | 0.17 |
| Contact aggression_mating season | -0.04 | 0.45 | -0.04 | 0.45 |
| Non-contact aggression_mating season | 0.11 | 0.14 | 0.09 | 0.16 |

bachelor male copulations occurred during periods when females were unlikely to be fertile, it remains unclear whether this strategy is best understood as an attempt by a bachelor male to form a sociosexual bond with a future mating partner or an attempt to attract that female to leave the OMU of her current leader male. Studies of golden snub-nosed monkeys indicate that new OMU can form when one or more adult females join a bachelor male (Qi et al., 2014). These transfers appear voluntary and rarely involve forms of sexual coercion or harassment (Qi et al., 2014). Both types of bachelor male reproductive strategies function to maintain AMU cohesion and affiliative relationships throughout the year as there is little behavioral evidence of direct reproductive competition involved in severe aggressions among bachelor males.

A similar pattern of tolerant and affiliative social relationships is reported among bachelor male mona monkeys (*Cercopithecus mona*) (Glenn, Matsuda, & Bensen, 2002) and bachelor male western lowland gorillas (*Gorilla Gorilla gorilla*) (Stoinski, Kuhar, Lukas, & Maple, 2004) that form an AMU. For example, in mona monkeys, bachelor male grooming and sitting together were frequent, and several pairs of bachelor males formed stable associations for more than one year (Glenn et al., 2002).

Bachelor male social relationships in black and white snub-nosed monkeys may be explained in terms of the fitness benefits males receive by forming an AMU. High affiliation and low male–male agonistic interactions provide bachelor males with a “buffer zone” in which they can develop and practice social skills such as dominance, fighting, and bonding, which are needed not only to takeover an OMU, but also to attract and keep OMU females (Steenbeek, Sterck, De Vries, & Van Hooff, 2000; Zhu et al., 2016). In golden snub-nosed monkeys, leader males act cooperatively to expel intruder males from attempting to take over an OMU (Xiang et al., 2014). To date, leader male black-and-white snub-nosed monkeys have not been reported to act cooperatively against intruder males, and bachelor males have not been observed to form coalitions in an attempt to mate guard or exert sexual coercion over OMU females (Xia et al., 2016; Zhu et al., 2016). Moreover, some degree of male intrasexual tolerance is required in all snub-nosed monkeys species given that the evolution of their multilevel society is best understood as the fusion or aggregation of several independent OMUs and bachelor males into a large and cohesive band (Grueter et al., 2010; Qi et al., 2014). A second potential benefit of male bonding and AMU formation is access to ecological information. Black and white snub-nosed monkeys exploit a home range of >10 km² that is characterized by hyper dispersed food resources (Grueter et al., 2008; Ren, Li, Long, Wu, & Wei, 2009). In forming an AMU with deposed males who have lost their OMUs, younger males and prime males might benefit from shared knowledge regarding the availability and distribution of productive feeding sites (Bercovitch & Berry, 2015). A third potential benefit of AMU formation is a reduction in physiological stress. The social buffering hypothesis predicts that reliable and affiliative social bonds can buffer against the adverse effects of increased physiological stress by modulating the reactivity of the hypothalamic-pituitary-adrenal axis (Hennessy, Kaiser, & Sachser, 2009; Wittig et al., 2016). For example in Barbary

macaques (*Macaca sylvanus*), Young, et al. (2014) found that male Barbary macaques who maintained stronger social bonds (as measured by composite sociality index of grooming, body contact, male-infant-male triadic interactions and proximity) were characterized lower fecal glucocorticoid metabolite levels (an indication of reduced physiological stress) compared to males who did not maintain these social bonds. Finally, it also is possible that since AMUs are composed of males of different age categories (e.g., adult, subadult, and juvenile) different individuals benefit in different ways.

Our results indicate although male social cohesion during the mating season in black and white snub-nosed monkeys was reduced compared to the non-mating period, bachelor males maintain affiliation throughout the year. This may reflect a trade-off between behaviors associated with short-term reproductive competition in response to mating opportunities and the longer-term importance of reestablishing social alliances required for AMU cohesion, stability, predator protection, and territorial maintenance. Although data indicating that bachelor males are able to successfully sire offspring in black-and-white snub-nosed monkeys are limited (Xia et al., 2016), research on the closely related golden snub-nosed monkey shows that 6.5% of observed copulations involved males other than the OMU leader male, and that these occurred mainly at the beginning of the mating season (Guo, Ji, Li, Chang, & Li, 2010). In addition, genetic studies confirmed that in golden snub-nosed monkeys, 57% (12 of 21) of immature individuals were sired by extra-unit males (Guo et al., 2010). Thus, although during the mating season increased time spent searching for opportunities to challenge resident males or pursue sneaky copulations with OMU females is expected to result in a less connected AMU social network, it appears to reflect a set of effective reproductive strategies enabling some bachelor males to sire offspring with only minor disruptions in social cohesion.


In this study, we examined intrasexual social bonds and reproductive strategies among adult, subadult, and juvenile male *R. bieti* who form a cohesive AMU. In future, we plan to examine the set of strategies used by bachelor males to takeover an OMU, and the degree to which bachelor male social alliances and kinship ties effect individual reproductive strategies. Our understating of the social network dynamics of bachelor groups also would be enhanced by investigating the influence of individual attributes (e.g., age, kinship, and rank) on the social network topology, and the degree to which social networks vary across years.

On a broader scale, exploring the processes and factors generating variation in the topology of social structure is essential for understanding the causes and consequences of sociality (Andrew, Hanser, & McHugh, 2009; Ilany & Akcay, 2016). Our work has identified the dynamics of AMU cohesion and affiliation during mating and non-mating periods. Given the strength and ubiquity of male–male bonds in several primate species, including human societies past and present (Bailey & Aunger, 1990; Foley, 1989; Grueter, 2014; Rodseth & Novak, 2000) studying the dynamics of social interactions of bachelor males in non-human primates provides a comparative framework for assessing the costs and benefits of male intrasexual social alliances and cooperation.

ACKNOWLEDGMENTS

This study was supported by Strategic Priority Research Program of the Chinese Academy of Sciences (XDA19050202), National Natural Science Foundation of China (grant No. 31470459), National Key R&D Program of China (2016YFC0503200), and China Postdoctoral Science Foundation (grant No. 2017M620906). We thank Baimaxueshan Nature Reserve for permission to undertake the research on Xiangguqing. We are grateful to Mr Xinmin He, Tai Zhong, and Lizhong Yu for help with data collection in the field. We thank Lauren J. N. Brent, Carter T. Butts, and Damien R. Farine for helpful suggestions on social network analysis. Paul A. Garber thanks Chrissie, Sara, and Jenni for their support and guidance.

ORCID

Paul A. Garber  <http://orcid.org/0000-0003-0053-8356>

Ming Li  <http://orcid.org/0000-0001-5689-6270>

REFERENCES

- Adishesan, A., Adishesan, T., & Isbell, L. A. (2011). Affiliative relationships and reciprocity among adult male bonnet macaques (*Macaca radiata*) at Arunachala Hill, India. *American Journal of Primatology*, 73(11), 1107–1113. <https://doi.org/10.1002/ajp.20987>
- Altmann, J. (1974). Observational study of behavior-sampling methods. *Behaviour*, 49(3), 227–267. https://doi.org/10.1163/156853974_x00534
- Andrew, S., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: New insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology*, 63, 975–998. <https://doi.org/10.1007/s00265-009-0725-6>
- Bailey, R. C., & Aunger, R. (1990). Humans as primates: The social relationships of Efe pygmy men in comparative perspective. *International Journal of Primatology*, 11(2), 127–146. <https://doi.org/10.1007/BF02192785>
- Bennett, E. L., & Sebastian, A. C. (1988). Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest in Sarawak. *International Journal of Primatology*, 9(3), 233–255. <https://doi.org/10.1007/bf02737402>
- Bercovitch, F. B., & Berry, P. S. M. (2015). The composition and function of all-male herds of Thornicroft's giraffe, *Giraffa camelopardalis thornicrofti*, in Zambia. *African Journal of Ecology*, 53(2), 167–174. <https://doi.org/10.1111/aje.12169>
- Bissonnette, A., Perry, S., Barrett, L., Mitani, J. C., Flinn, M., Gavrilets, S., & de Waal, F. B. M. (2015). Coalitions in theory and reality: A review of pertinent variables and processes. *Behaviour*, 152(1), 1–56. <https://doi.org/10.1163/1568539x-00003241>
- Borgatti, S. P., Everett, M. G., & Freeman, L. C. (2002). Ucinet for Windows: software for social network analysis. Harvard, MA: Analytic Technologies.
- Brent, L. J. N., Lehmann, J., & Ramos-fernanandez, G. (2011). Social network analysis in the study of nonhuman primates: A historical perspective. *American Journal of Primatology*, 73, 1–11. <https://doi.org/10.1002/ajp.20949>
- Brent, L. J. N., MacLarnon, A., Platt, M. L., & Semple, S. (2013). Seasonal changes in the structure of rhesus macaque social networks. *Behavioral Ecology and Sociobiology*, 67(3), 349–359. <https://doi.org/10.1007/s00265-012-1455-8>
- Butovskaya, M. L., & Kozintsev, A. G. (1996). Gender-related factors affecting primate social behavior: Grooming, rank, age, and kinship in heterosexual and all-male groups of *Stumptail macaques*. *American Journal of Physical Anthropology*, 101(1), 39–54.
- Butts, C. T. (2016). Package 'sna': Tools for social network analysis. R package, version 2.4. <https://CRAN.R-project.org/package=sna>.
- Chiyu, P. I., Archie, E. A., Hollister-Smith, J. A., Lee, P. C., Poole, J. H., Moss, C. J., & Alberts, S. C. (2011). Association patterns of African elephants in all-male groups: The role of age and genetic relatedness. *Animal Behaviour*, 81(6), 1093–1099. <https://doi.org/10.1016/j.anbehav.2011.02.013>
- Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red deer: Behavior and ecology of two sexes*. Chicago: The University of Chicago Press.
- Colmenares, F. (1992). Clans and harems in a colony of hamadryas and hybrid baboons: Male kinship, familiarity and the formation of brother-teams. *Behaviour*, 121(1), 61–94. https://doi.org/10.1163/156853992_x00444
- Cords, M. (2012). The behavior, ecology, and social evolution of cercopithecine monkeys. In J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *The evolution of primate societies* (pp. 91–112). Chicago and London: The University of Chicago Press.
- Croft, D. P., James, R., & Krause, J. (2008a). Visual exploration. In D. P. Croft, R. James, & J. Krause (Eds.), *Exploring animal social networks* (pp. 54–61). UK: Princeton University Press.
- Croft, D. P., James, R., & Krause, J. (2008b). Node-based measures. In D. P. Croft, R. James, & J. Krause (Eds.), *Exploring animal social networks* (pp. 65–87). UK: Princeton University Press.
- Di Fiore, A., Link, A., Schmitt, C. A., & Spehar, S. N. (2009). Dispersal patterns in sympatric woolly and spider monkeys: Integrating molecular and observational data. *Behaviour*, 146(4), 437–470. https://doi.org/10.1163/156853909_x426345
- Díaz-Muñoz, S. L., DuVal, E. H., Krakauer, A. H., & Lacey, E. A. (2014). Cooperating to compete: Altruism, sexual selection and causes of male reproductive cooperation. *Animal Behaviour*, 88, 67–78. <https://doi.org/10.1016/j.anbehav.2013.11.008>
- Drews, C. (1996). Contexts and patterns of injuries in free-ranging male baboons (*Papio cynocephalus*). *Behaviour*, 133(5), 443–474. https://doi.org/10.1163/156853996_x00530
- Dunbar, R., & Dunbar, P. (1975). *Social dynamics of gelada baboons*. Basel: Karger.
- Dunbar, R. I. M. (1980). Demographic and life history variables of a population of gelada baboons (*Theropithecus gelada*). *Journal of Animal Ecology*, 49(2), 485–506. <https://doi.org/10.2307/4259>
- Fay, M. (2015). Package 'perm': Exact or asymptotic permutation tests. R Package, version 1.0–0.0. <https://CRAN.R-project.org/package=perm>.
- Foley, R. A. (1989). The evolution of hominid social behaviour. In V. Standen, & R. A. Foley (Eds.), *Comparative socioecology* (pp. 473–494). Oxford: Blackwell Scientific Publications.
- Freeman, L. C. (1978). Centrality in social networks conceptual clarification. *Social Networks*, 1(3), 215–239. [https://doi.org/10.1016/0378-8733\(78\)90021-7](https://doi.org/10.1016/0378-8733(78)90021-7)
- Garber, P. A., & Kowalewski, M. K. (2011). Collective action and male affiliation in howler monkeys (*Alouatta caraya*). In R. W. Sussman, & C. R. Cloninger (Eds.), *Origins of altruism and cooperation [Developments in primatology: Progress and prospects]* (pp. 145–165). New York: Springer.
- Glenn, M. E., Matsuda, R., & Bensen, K. J. (2002). Unique behavior of the mona monkey (*Cercopithecus mona*): All-male groups and copulation calls. In M. E. Glenn, & M. Cords (Eds.), *The guenons: Diversity and adaptation in African monkeys* (pp. 133–145). Boston: Kluwer Academic/Plenum Publishers.
- Grueter, C. C. (2009). Determinants of modular societies in snub-nosed monkeys (*Rhinopithecus bieti*) and other Asian colobines. University of Zurich (unpublished doctoral dissertation).
- Grueter, C. C. (2014). Primate model offers insights into male bonding in complex societies. *Proceedings of the National Academy of Sciences*, 111(41), 14645–14646. <https://doi.org/10.1073/pnas.1416140111>

- Grueter, C. C., Li, D. Y., Ren, B. P., Wei, F. W., & Li, M. (2017). Deciphering the social organization and structure of wild Yunnan snub-nosed monkeys (*Rhinopithecus bieti*). *Folia Primatologica*, 88(4), 358–383. <https://doi.org/10.1159/000480503>
- Grueter, C. C., Li, D. Y., van Schaik, C. P., Ren, B. P., Long, Y. C., & Wei, F. W. (2008). Ranging of *Rhinopithecus bieti* in the samage forest, China. I. characteristics of range use. *International Journal of Primatology*, 29(5), 1121–1145. <https://doi.org/10.1007/s10764-008-9299-9>
- Grueter, C. C., & van Schaik, C. P. (2010). Evolutionary determinants of modular societies in colobines. *Behavioral Ecology*, 21(1), 63–71. <https://doi.org/10.1093/beheco/arp149>
- Guo, S. T., Ji, W. H., Li, M., Chang, H. L., & Li, B. G. (2010). The mating system of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*). *American Journal of Primatology*, 72(1), 25–32. <https://doi.org/10.1002/ajp.20747>
- Handcock, M. S., Hunter, D. R., Butts, C. T., Goodreau, S. M., Krivitsky, P. N., Bender-deMoll, S., & Morris, M. (2016). Package 'statnet': Software tools for the statistical analysis of network data. R package, version 2016.9. <https://CRAN.R-project.org/package=statnet>
- Hanneman, R. A., & Riddle, M. (2005). *Introduction to social network methods*. USA: University of California Riverside.
- Harding, R. S. O., & Olson, D. K. (1986). Patterns of mating among male patas monkeys (*Erythrocebus patas*) in Kenya. *American Journal of Primatology*, 11(4), 343–358. <https://doi.org/10.1002/ajp.1350110405>
- Hennessy, M. B., Kaiser, S., & Sachser, N. (2009). Social buffering of the stress response: Diversity, mechanisms, and functions. *Frontiers in Neuroendocrinology*, 30(4), 470–482. <https://doi.org/10.1016/j.yfrne.2009.06.001>
- Ilany, A., & Akcay, E. (2016). Social inheritance can explain the structure of animal social networks. *Nature Communications*, 7, 12084. <https://doi.org/10.1038/ncomms12084>
- Kirkpatrick, R. C., & Grueter, C. C. (2010). Snub-nosed monkeys: Multilevel societies across varied environments. *Evolutionary Anthropology*, 19(3), 98–113. <https://doi.org/10.1002/evan.20259>
- Kirkpatrick, R. C., Long, Y., Zhong, T., & Xiao, L. (1998). Social organization and range use in the Yunnan snub-nosed monkey *Rhinopithecus bieti*. *International Journal of Primatology*, 19(1), 13–51. <https://doi.org/10.1023/A:1020302809584>
- Launhardt, K., Borries, C., Hardt, C., Epplen, J. T., & Winkler, P. (2001). Paternity analysis of alternative male reproductive routes among the langurs (*Semnopithecus entellus*) of Ramnagar. *Animal Behaviour*, 61, 53–64. <https://doi.org/10.1006/anbe.2000.1590>
- Lawler, R. R., Richard, A. F., & Riley, M. A. (2005). Intrasexual selection in Verreaux's sifaka (*Propithecus verreauxi verreauxi*). *Journal of Human Evolution*, 48(3), 259–277. <https://doi.org/10.1016/j.jhevol.2004.11.005>
- Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: The nature of social bonds in West African female chimpanzees *Pan troglodytes*. *Animal Behaviour*, 77(2), 377–387. <https://doi.org/10.1016/j.anbehav.2008.09.038>
- Levréro, F., Gatti, S., Menard, N., Petit, E., Caillaud, D., & Gautier-Hion, A. (2006). Living in nonbreeding groups: An alternative strategy for maturing gorillas. *American Journal of Primatology*, 68(3), 275–291. <https://doi.org/10.1002/ajp.20223>
- Li, D. Y., Ren, B. P., Grueter, C. C., Li, B. G., & Li, M. (2010). Nocturnal sleeping habits of the Yunnan snub-nosed monkey in Xiangguqing, China. *American Journal of Primatology*, 72(12), 1092–1099. <https://doi.org/10.1002/ajp.20871>
- Li, T. F., Ren, B. P., Li, D. Y., Zhang, Y. B., & Li, M. (2012). Maternal responses to dead infants in Yunnan snub-nosed monkey (*Rhinopithecus bieti*) in the Baimaxueshan Nature Reserve, Yunnan, China. *Primates*, 53(2), 127–132. <https://doi.org/10.1007/s10329-012-0293-7>
- Li, T. F., Ren, B. P., Li, D. Y., Zhu, P. F., & Li, M. (2013). Mothering style and infant behavioral development in Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) in China. *International Journal of Primatology*, 34(4), 681–695. <https://doi.org/10.1007/s10764-013-9687-7>
- Liu, J. (2009). *Lectures on whole network approach: a practical guide to UCINET*. Shanghai: Polytechnic Press.
- Liu, Z., Ding, W., & Grueter, C. (2007). Preliminary date on the social organization of black and white snub-nosed monkeys *Rhinopithecus bieti* at Tacheng, China. *Acta Theriologica Sinica*, 27(2), 120–122.
- MacFarlane, A. M., & Coulson, G. (2009). Boys will be boys: Social affinity among males drives social segregation in western grey kangaroos. *Journal of Zoology*, 277(1), 37–44. <https://doi.org/10.1111/j.1469-7998.2008.00508.x>
- Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, 77(3), 633–640. <https://doi.org/10.1016/j.anbehav.2008.11.021>
- Muller, M. N., & Emery Thompson, M. (2012). Mating, parenting, and male reproductive strategies. In J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *The evolution of primate societies* (pp. 387–411). Chicago and London: University of Chicago Press.
- Ogle, D. (2018). Package 'FSA': Simple fisheries stock assessment methods. R package, version 0.8.20. <https://CRAN.R-project.org/package=FSA>
- Ohsawa, H., Inoue, M., & Takenaka, O. (1993). Mating strategy and reproductive success of male patas monkeys (*Erythrocebus patas*). *Primates*, 34(4), 533–544. <https://doi.org/10.1007/bf02382664>
- Opsahl, T. (2009). Structure and evolution of weighted networks. Queen Mary, University of London (unpublished doctoral dissertation).
- Opsahl, T. (2015). Package 'tnet': Software for analysis of weighted, two-mode, and longitudinal networks. R package, version 3.0.14. <https://CRAN.R-project.org/package=tnet>
- Opsahl, T., & Panzarasa, P. (2009). Clustering in weighted networks. *Social Networks*, 31(2), 155–163. <https://doi.org/10.1016/j.socnet.2009.02.002>
- Ostner, J., & Kappeler, P. M. (2004). Male life history and the unusual adult sex ratios of redfronted lemur, *Eulemur fulvusrufus*, groups. *Animal Behaviour*, 67, 249–259. <https://doi.org/10.1016/j.anbehav.2003.05.012>
- Ostner, J., & Schülke, O. (2014). The evolution of social bonds in primate males. *Behaviour*, 151(7), 871–906. <https://doi.org/10.1163/1568539x-00003191>
- Patzelt, A., Kopp, G. H., Ndao, I., Kalbitzer, U., Zinner, D., & Fischer, J. (2014). Male tolerance and male-male bonds in a multilevel primate society. *Proceedings of the National Academy of Sciences of the United States of America*, 111(41), 14740–14745. <https://doi.org/10.1073/pnas.1405811111>
- Pines, M., Saunders, J., & Swedell, L. (2011). Alternative routes to the leader male role in a multi-level society: Follower vs. solitary male strategies and outcomes in Hamadryas baboons. *American Journal of Primatology*, 73(7), 679–691. <https://doi.org/10.1002/ajp.20951>
- Pusey, A. E., & Packer, C. (1987). Dispersal and philopatry. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 250–266). Chicago: University of Chicago Press.
- Qi, X. G., Garber, P. A., Ji, W., Huang, Z. P., Huang, K., Zhang, P., & Zhang, P. (2014). Satellite telemetry and social modeling offer new insights into the origin of primate multilevel societies. *Nature Communications*, 5, 5296. <https://doi.org/10.1038/ncomms6296>
- Qi, X. G., Huang, K., Fang, G., Grueter, C. C., Dunn, D. W., Li, Y.-L., & Li, B. G. (2017). Male cooperation for breeding opportunities contributes to the evolution of multilevel societies. *Proceedings of the Royal Society B-Biological Sciences*, 284(1863), 20171480. <https://doi.org/10.1098/rspb.2017.1480>
- Rajpurohit, L. S. (1991). Resident male replacement, formation of a new male band and paternal behavior in *Presbytis entellus*. *Folia Primatologica*, 57(3), 159–164.
- Rajpurohit, L. S., Chhangani, A. K., Rajpurohit, R. S., & Mohnot, S. M. (2003). Observation of a sudden resident-male replacement in a unimale bisexual troop of Hanuman Langurs, *Semnopithecus entellus*, around Jodhpur (India). *Folia Primatologica*, 74(2), 85–87. <https://doi.org/10.1159/000070002>

- Rajpurohit, L. S., Sommer, V., & Mohnot, S. M. (1995). Wanderers between harems and bachelor bands: Male Hanuman langurs (*Presbytis entellus*) at Jodhpur in Rajasthan. *Behaviour*, 132, 255–299. <https://doi.org/10.1163/156853995x00739>
- Ren, B. P., Li, D. Y., Garber, P. A., & Li, M. (2012). Fission-fusion behavior in Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) in Yunnan, China. *International Journal of Primatology*, 33(5), 1096–1109. <https://doi.org/10.1007/s10764-012-9586-3>
- Ren, B. P., Li, D. Y., He, X. M., Qiu, J. H., & Li, M. (2011). Female resistance to invading males increases infanticide in Langurs. *PLoS ONE*, 6(4), e18971. <https://doi.org/10.1371/journal.pone.0018971>
- Ren, B. P., Li, M., Long, Y. C., Wu, R. D., & Wei, F. W. (2009). Home range and seasonality of Yunnan snub-nosed monkeys. *Integrative Zoology*, 4(2), 162–171. <https://doi.org/10.1111/j.1749-4877.2009.00153.x>
- Richard, A. F. (1992). Aggressive competition between males, female-controlled polygyny and sexual monomorphism in a Malagasy primate, *Propithecus verreauxi*. *Journal of Human Evolution*, 22(4-5), 395–406. [https://doi.org/10.1016/0047-2484\(92\)90067-j](https://doi.org/10.1016/0047-2484(92)90067-j)
- Robbins, M. M. (1995). A demographic analysis of male life history and social structure of mountain gorillas. *Behaviour*, 132, 21–47. [https://doi.org/10.1016/0047-2484\(92\)90067-j10.1163/156853995x00261](https://doi.org/10.1016/0047-2484(92)90067-j10.1163/156853995x00261)
- Robbins, M. M. (1996). Male-male interactions in heterosexual and all-male wild mountain gorilla groups. *Ethology*, 102(11), 942–965. [https://doi.org/10.1016/0047-2484\(92\)90067-j10.1111/j.1439-0310.1996.tb01172.x](https://doi.org/10.1016/0047-2484(92)90067-j10.1111/j.1439-0310.1996.tb01172.x)
- Rodseth, L., & Novak, S. A. (2000). The social modes of men: Toward an ecological model of human male relationships. *Human Nature-an Interdisciplinary Biosocial Perspective*, 11(4), 335–366. [https://doi.org/10.1016/0047-2484\(92\)90067-j10.1007/s12110-000-1007-1](https://doi.org/10.1016/0047-2484(92)90067-j10.1007/s12110-000-1007-1)
- Rubenstein, D. I., & Hack, M. (2004). Natural and sexual selection and the evolution of multi-level societies: Insights from zebras with comparisons to primates. In P. Kappeler, & C. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 266–279). New York: Cambridge University Press.
- Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, 20(24), 2207–2210. <https://doi.org/10.1016/j.cub.2010.10.058>
- Schaffner, C. M., Slater, K. Y., & Aureli, F. (2012). Age related variation in male-male relationships in wild spider monkeys (*Ateles geoffroyi yucatanensis*). *Primates*, 53(1), 49–56. <https://doi.org/10.1007/s10329-011-0271-5>
- Snijders, T. A., & Borgatti, S. P. (1999). Non-parametric standard errors and tests for network statistics. *Connections*, 22(2), 161–170.
- Steenbeek, R., Sterck, E. H. M., De Vries, H., & Van Hooff J. (2000). Costs and benefits of the one-male, age-graded, and all-male phases in wild Thomas's langur groups. In P. M. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 130–145). United Kingdom: Cambridge University Press.
- Sterck, E. H. M. (2012). The behavioral ecology of colobine monkeys. In J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *The evolution of primate societies* (pp. 65–90). Chicago and London: University of Chicago Press.
- Stoinski, T. S., Kuhar, C. W., Lukas, K. E., & Maple, T. L. (2004). Social dynamics of captive western lowland gorillas living in all-male groups. *Behaviour*, 141, 169–195. <https://doi.org/10.1163/156853904322890807>
- Strier, K. B. (2000). Population viabilities and conservation implications for muriquis (*Brachyteles arachnoides*) in Brazil's Atlantic Forest. *Biotropica*, 32(4B), 903–913.
- Sussman, R. W., & Garber, P. A. (2011). Cooperation, collective action, and competition in primate social interactions. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. Bearder, & R. Stumpf (Eds.), *Primates in perspective* (pp. 587–599). New York: Oxford University Press.
- van Hooff, J. (2000). Relationships among non-human primate males: A deductive framework. In P. M. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 183–191). Cambridge: Cambridge University Press.
- Waterman, J. M. (1997). Why do male cape ground squirrels live in groups? *Animal Behaviour*, 53, 809–817. <https://doi.org/10.1006/anbe.1996.0346>
- Wich, S. A., Steenbeek, R., Sterck, E. H. M., Korstjens, A. H., Willems, E. P., & Van Schaik, C. P. (2007). Demography and life history of Thomas Langurs (*Presbytis thomasi*). *American Journal of Primatology*, 69(6), 641–651. <https://doi.org/10.1002/ajp.20386>
- Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., ... RStudio. (2018). Package 'ggplot2': Create elegant data visualisations using the grammar of graphics. R package, version 3.0.0. <https://CRAN.R-project.org/package=ggplot2>.
- Wittig, R. M., Crockford, C., Weltring, A., Langergraber, K. E., Deschner, T., & Zuberbühler, K. (2016). Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nature Communications*, 7, 8. <https://doi.org/10.1038/ncomms13361>
- Wrangham, R. W., & Muller, M. N. (2009). Sexual coercion in humans and other primates: The road ahead. In M. N. Muller, & R. W. Wrangham (Eds.), *Sexual coercion in primates and humans: An evolutionary perspective on male aggression against females* (pp. 451–468). Cambridge and London: Harvard University Press.
- Xia, F., Zhu, P., Li, M., & Ren, B. (2016). Mating behavior of yunnan snub-nosed monkeys (*Rhinopithecus bieti*) at xiangguqing in baimaxueshan national nature reserve, yunnan, China. *Acta Theriologica Sinica*, 36(1), 1–14.
- Xiang, Z. F., Yang, B. H., Yu, Y., Yao, H., Grueter, C. C., Garber, P. A., & Li, M. (2014). Males collectively defend their one-male units against bachelor males in a multi-level primate society. *American Journal of Primatology*, 76(7), 609–617. <https://doi.org/10.1002/ajp.22254>
- Yeager, C. P., & Kool, K. (2000). The behavioral ecology of Asian colobines. In P. F. Whitehead, & C. J. Jolly (Eds.), *Old world monkeys* (pp. 496–521). United Kingdom: Cambridge University Press.
- Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2014). Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. *Proceedings of the National Academy of Sciences of the United States of America*, 111(51), 18195–18200. <https://doi.org/10.1073/pnas.1411450111>
- Zar, J. H. (2010). *Biostatistical analysis*. 5th edition. Upper Saddle River, New Jersey: Prentice Hall.
- Zhu, P., Ren, B., Garber, P. A., Xia, F., Grueter, C. C., & Li, M. (2016). Aiming low: A resident male's rank predicts takeover success by challenging males in Yunnan snub-nosed monkeys. *American Journal of Primatology*, 78(9), 974–982. <https://doi.org/10.1002/ajp.22567>

How to cite this article: Zhu P, Grueter CC, Garber PA, et al. Seasonal changes in social cohesion among males in a same-sex primate group. *Am J Primatol*. 2018;80:e22914. <https://doi.org/10.1002/ajp.22914>