



Grooming Strategy of the Female Yunnan Snub-Nosed Monkeys (*Rhinopithecus bieti*)

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ABSTRACT

Grooming behaviours have a functional role, keeping animals clean. However, the social dimension of grooming has attracted more attention in research. According to biological market theory, grooming can be traded as currency for other commodities or exchanged for reciprocal grooming. Based on this theory we can roughly rank females, according to the reciprocity index of grooming. Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) are a polygynous species, and the female individuals have to compete for access to a single male in their unit to get pregnant. We collected data on grooming in the mating and birthing seasons. We suggest that females directed more grooming to males in the mating season than in the birthing season, especially 'non-mother' females. After the mating season, female individuals redirected their attention to focus on babies in the birthing season, and correspondingly the proportion of grooming given to babies was higher than in the mating season. For 'mother' females, there was no significant difference in the grooming given to males between the two seasons. Another remarkable phenomenon was that *R. bieti* individuals groomed the anogenital area more frequently before the mating season than on the two other periods, and compared with the birthing season, the rate of grooming on the anogenital region was also higher in the mating season. In conclusion, females made use of grooming as a currency to exchange for valuable resources, and during the mating season grooming was traded for copulation. Meanwhile, grooming is essential to maintain a complex social network for the female *R. bieti*.

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XW, DZ, WX, XY and DL wrote the manuscript. DZ, DL, WX and JH collected field data. DL and AK revised the manuscript.

Key words

Yunnan snub-nosed monkeys, *Rhinopithecus bieti*, Social grooming, Mating season

INTRODUCTION

Grooming, a widespread behaviour among primates, is especially important for establishing complex social networks (Akinyi *et al.*, 2013; Perez and Veà, 2002). Grooming patterns conform with the hygienic function hypothesis, suggesting that primates need to spend time grooming in order to remove ectoparasites, skin flakes, and debris (Perez and Veà, 2002; Barton, 1985). This is essential for recipients of grooming, as a grooming dyad

can reach areas of the body each individual monkey cannot on its own. Grooming is also assumed to serve social functions, including bonding, tension reduction, and facilitation of group cohesion (Chiarello, 1995; Dunbar, 1991; De *et al.*, 1989; Masataka *et al.*, 2018; Nakamichi *et al.*, 2020; Terry, 1970; Maestripieri, 1993). Grooming can be conceptualized as a strategic social tool or tradable currency exchanged for a number of benefits: reciprocal grooming from the recipient (Arnold *et al.*, 2003; Barrett *et al.*, 1999; Packer, 1977), further support in agonistic encounters (Koyama *et al.*, 2006; Schino, 2007, 2011), and access to limited resources such as mates (Barelli *et al.*, 2011; Gumert, 2007), infants (Gumert, 2007; Barrett *et al.*, 2002; Yu *et al.*, 2013), and food (Leinfelder *et al.*, 2001).

Research on social bonding in nonhuman primates is an important field in the study of primate behaviour. The concept of social class in nonhumans was utilized in a study of social group structure to explain individuals' resource priorities (Wilson, 2000), a social hierarchy can be described in light of individuals' variable ability to

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obtain limited resources controlled by or within a group. Previous research on female bonding has concentrated on adult individuals. For instance, Seyfarth (1976) found that grooming in female baboons is actively directed by low-level individuals towards high-level ones after conflict. Studies of bonnet macaques suggests that the frequency of grooming exchange between same-sex individuals is higher than between males and females, though the direction and distribution of grooming in same-sex dyads and triads is variable (Nakamichi *et al.*, 2020; Simonds, 1974).

Studies conducted on the genus *Rhinopithecus* (snub-nosed monkeys) have shown that while high-ranking females often receive grooming from low-level females, they seldom reciprocate (Wei *et al.*, 2012). Biological market theory predicts that when resources are monopolised, dominant individuals use greater access to limited resources as an asset, prompting others without such special access to try to outbid each other by increasing their rate of grooming the dominant individuals (Barrett *et al.*, 1999). Alternatively, when dominance relations are weak, grooming will not be exchanged for other rank-related benefits, instead, grooming will be reciprocally exchanged. This is because under conditions of low resource competition, dominant individuals have fewer commodities to offer (Wei *et al.*, 2012). When grooming is the only currency to exchange, the best groomers will be more attractive social partners (Barrett *et al.*, 1999). Moreover, any given dyad's grooming interactions will have higher reciprocity when dominance relations are relaxed (Barrett *et al.*, 2002).

Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) is an endangered primate that the total populations are just over 3000 individuals (Wang *et al.*, 2022). *R. bieti* lives at the highest altitudes of monkey, and their geographic distribution is restricted to the Hengduan Mountains of northwest Yunnan Province and south-eastern Tibet, China (Xia *et al.*, 2020). They that displays a multilevel social structure comprised of flexible aggregations of two basic units: One-male units (OMUs) and typically all-male unit (AMU) (Li *et al.*, 2014). Their polygynous mating arrangement inevitably results in resource competition, particularly for mating rights. Within the mixed-sex OMUs, access to breeding males is a limited resource for females. Females use grooming to develop a good relationship with the OMU's resident male to increase their mating frequency (Wei *et al.*, 2012). The more females within an OMU, the more intense the sexual competition (Xia *et al.*, 2020). As a result, patterns of grooming exchange can be used to understand the community structure of *R. bieti*. In this study, we present detailed information on social grooming among the females in *R. bieti*. We attempt to

the deeper understand social grooming function, while revealing social grooming strategies for the resource exchange and the maintenance of social network among the females Yunnan snub-nosed monkeys.

MATERIALS AND METHODS

Study site and subjects

This study was conducted in the Xiangguqing region of the southern tip of Baimaxueshan National Nature Reserve, Yunnan province, China. The study area covered about 90 km² (Li *et al.*, 2010). Because of its special geography and complex natural environment, the area has various types of vegetation, including variable forest types with patchy distribution and a core of well-preserved old-growth forest. Annual rainfall is 1370.7 mm, and the mean annual temperature is 9.8°C (Li *et al.*, 2010).

The focal group was comprised of about 80 individuals divided into five OMUs and one AMU. This group is habituated to human presence, and their regular activities are not impacted by human observation (Xia *et al.*, 2020). Therefore, we were able to observe the monkeys at close range. This allowed individual identification by means of prominent physical features such as facial characteristics, body size, crown hair pattern, pelage color, scars, and physical disabilities (Xia *et al.*, 2020). Observations from four OMUs, denoted by their resident males (DGZ, DS, HL, and DB), were chosen for further analysis (Table I). The other OMU was excluded due to a small sample size.

Table I. The composition of four one male units in this study.

Age class	DGZ	DB	DS	HL
Adult female	3	3	2	3
Sub-adult		1	1	
Juvenile	6	1	1	2
Infant		3	1	3
Mother female	3	3*	1*	3*

* indicates that the females give birth to an infant during the birthing season of 2014, other mothers gave birth the year before. One individual in the DGZ unit gave birth in the birthing season of 2014. The other two females gave birth in the birthing season of 2013. Theoretically, they should have been in oestrus, mated and given birth in 2014, but they were not in heat, so we classified them as mother females. In the results presented below, 'babies' refers to both infants and juveniles.

Data collection

Behavioural observations were conducted during the mating season (September to November) in 2013, the birth season (February to April) in 2014, and again August in 2014, defined as the pre-mating season. Observations were

recorded 2124 grooming dyads over a total of 840 hours in 168 days. The occurrence of grooming among 4 resident males in OMUs (excluding those in the AMU) and 11 females (only adult females in this text) was continuously recorded via all-occurrence sampling and focal animal sampling (Altmann, 1974). We attempted to allot observation time equally across each individual observed according to observation condition of the individuals. When a single grooming bout paused for more than 10s, or when the giver and receiver swapped roles, it was recorded as a completed grooming bout. We did not include samples where individuals could not be identified due to distance or visual obstruction.

Data analysis

We aggregated the number of times it was groomed in all grooming bouts to calculate the rate of grooming in this region across all three periods.

A chi-square test was used to examine differences among female grooming of males, other females, and babies within their OMUs in the mating and birthing seasons. A chi-square test was also performed to determine whether differences existed in the rate of grooming of resident males and babies in these two seasons by 'mother' females and 'non-mother' females. Similarly, we tested the same groups to compare the difference in the grooming rate of particular body areas, including the anogenital area, in the mating season and birth seasons.

While we initially planned to rank the females within every OMU based on the direction and number of occurrences of aggressive and submissive behaviours, we did not record a sufficient number of aggressive behaviours. As the experimental group has been provisioned for a long time, and their habitat is in good condition, the monkeys display high tolerance between individuals. We calculated a reciprocity index R instead to determine whether the duration and direction of grooming were approximately equal in grooming dyads (Wei *et al.*, 2012; Payne *et al.*, 2003). Based on the R -index, we were able to roughly order the females.

$$R = \frac{G_{AB} - G_{BA}}{G_{AR} + G_{RA}}$$

G_{AB} is the amount of grooming from individual A directed to individual B, and G_{BA} is the amount of grooming by individual B of individual A. The R -index ranges from -1 to 1. A positive number indicates that individual A gave more grooming than was received, while a value of 1 represents complete grooming altruism (no grooming received). Negative values indicate that individual B gave more grooming than was received, with -1 indicating that A never groomed B in return. A value of 0 represents complete reciprocity.

We used SPSS 20.0 to analyse the data, setting the significance level to 0.05. All tests were 2-tailed.

RESULTS

Differences in grooming for female Rhinopithecus bieti in different seasons

There was only slight variation in the proportion of female-female grooming across the two periods. In contrast, the fluctuation between the mating and the birth season in rates of female-male and female-baby grooming was significant for both. Females spent more time grooming the resident male in the mating season than in the birth season ($\chi^2=8.40$, $df=1$, $p<0.01$). Babies received more grooming in the birth season than in the mating season ($\chi^2=8.97$, $df=1$, $p<0.01$) (Fig. 1).

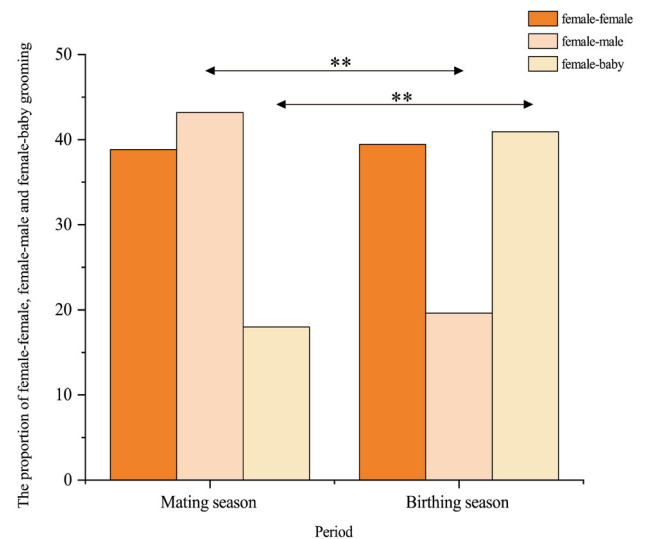


Fig. 1. The proportion of grooming time directed to females, males, and babies by females in the mating and birthing seasons (**indicates $p<0.01$).

The mean duration time of grooming on the anogenital area was higher before the mating season (Mean \pm SE: 78.6 \pm 7.2 sec) than during mating season (Mean \pm SE: 44.8 \pm 2.8 sec) and the birth season (Mean \pm SE: 38.9 \pm 4.3 sec). In a grooming bout, this area is not always considered, or could be groomed more than once. There were significant differences across the three periods ($\chi^2=41.27$, $df=2$, $p<0.01$). The results show that the rate of grooming pre-mating season was higher than during the mating season ($\chi^2=11.56$, $df=1$, $p<0.01$) and the birth season ($\chi^2=38.29$, $df=1$, $p<0.01$). Additionally, the rate of grooming was higher in the mating season than in the birth season ($\chi^2=9.8$, $df=1$, $p<0.01$) (Fig. 2).

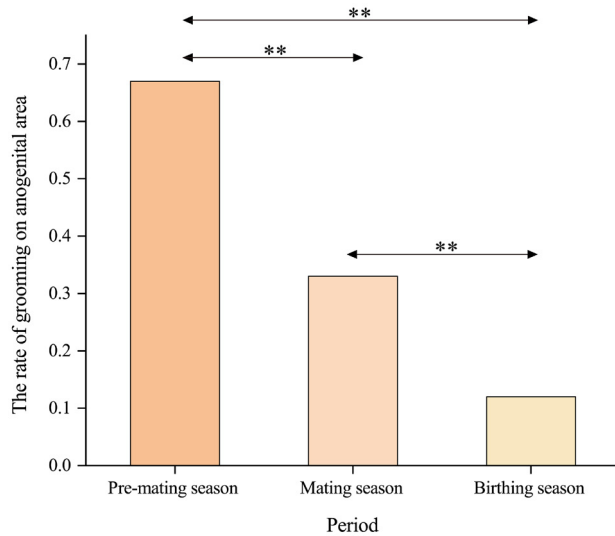


Fig. 2. The rate of grooming on the anogenital area across the three different periods. (**indicates $p < 0.01$).

Differences in grooming between mothers and non-mother adult females

The mean duration of grooming bouts that mothers with dependent offspring directed towards the resident male during the mating season (Mean \pm SE: 28.1 \pm 17.7 min) was slightly longer than in the birth season (Mean \pm SE: 17.9 \pm 5.3 min), but this difference was not statistically significant ($\chi^2=1.19$, $df=1$, $p>0.05$). In contrast, the average duration of grooming bouts directed towards resident males by adult females without dependent offspring during the mating season (Mean \pm SE: 44.6 \pm 15.6 min) was considerably longer than in the birth season (Mean \pm SE: 20.1 \pm 6.1 min), and this seasonal difference was statistically significant ($\chi^2=7.04$, $df=1$, $p<0.01$). In addition, within the mating season there was a statistically significant difference in the rates that adult females groomed resident males, with females lacking dependent offspring directing grooming towards males more often than mothers ($\chi^2=14.4$, $df=1$, $p<0.01$). However, there was no significant difference in the rate of grooming by females with and without dependent offspring during the birth season ($\chi^2=0.04$, $df=1$, $p>0.05$) (Fig. 3).

Female competition within the one-male unit

We ranked the females in each OMU in order of ascending R -index values: BYD>JH>JY>XH (DB's unit), BM>XM>DYB (DGZ's unit), BB>XH>BM (HL's unit), and PL>ML>YL (DS's unit) (Table II). These ranks may not necessarily reflect true dominant/subordinate relationships, as a female with a high R -index could simply be a good groomer, encouraging other individuals to initiate more grooming bouts with her to exchange grooming services.

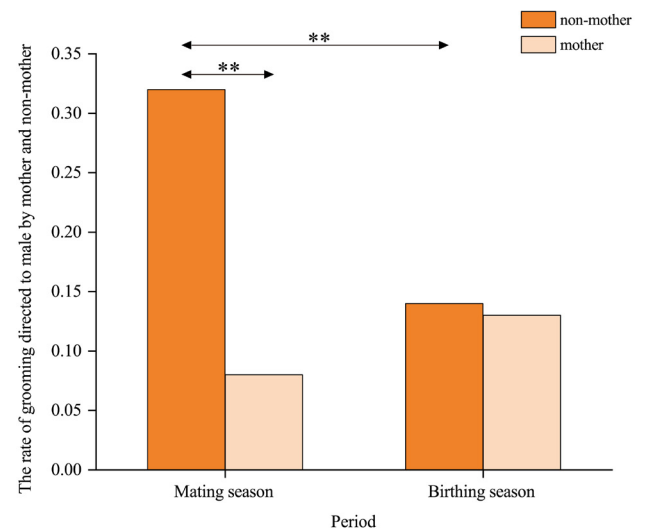


Fig. 3. The rate of grooming directed to males by mother females and non-mother females. (**indicates $p < 0.01$).

The resident male preferentially grooms one or two females within the OMU. In three out of the four focal OMUs (The left arm of resident male DS was broken off, and few data on grooming behavior from DS to females), the differences in the time the male spends grooming his unit's females were statistically significant (DB unit: $\chi^2=68.0$, $df=3$, $p<0.01$, DGZ unit: $\chi^2=70.97$, $df=2$, $p<0.01$, HL unit: $\chi^2=69.14$, $df=2$, $p<0.01$) (Fig. 4). This provides further evidence that females must compete for the attention of their OMU's resident male.

Table II. The R -index of every female grooming dyad in the four units during the mating season.

DB	R	DGZ	R	HL	R	DS	R
BYD-JH	-0.7351	XM-BM	0.1579	BB-XH	-0.3317	YL-ML	0.0090
BYD-JY	-0.4476	XM-DYB	-0.0925	BB-BM	-0.6847	YL-PL	0.4671
BYD-XH	-0.2675	BM-DYB	-0.5032	XH-BM	-0.0122	ML-PL	0.1292
JH-JY	-0.2548						
JH-XH	-0.3318						
JY-XH	-0.2037						

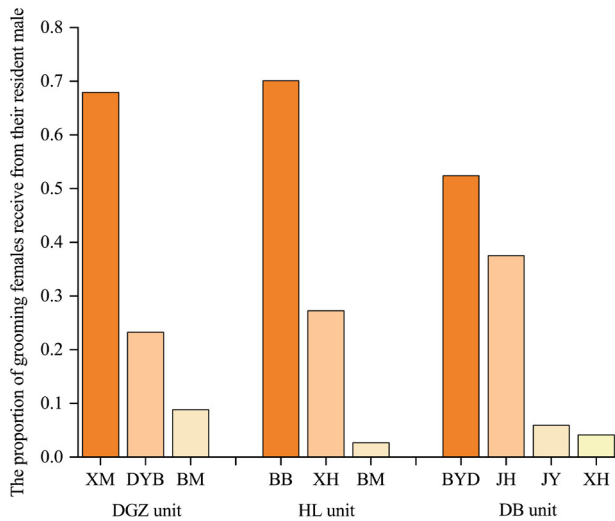


Fig. 4. The proportion of grooming females receive from their resident male in three units. (DB unit, DGZ unit, HL unit).

DISCUSSION

Following Zhang et al. (2014), we divided the monkey's body into ten areas. The null hypothesis with regards to grooming function is that the part that is groomed should be stochastic. However, grooming skews towards the areas individuals cannot easily reach on their own (Borries, 1992; Ghiglieri, 1984; Reichard and Sommer, 1994). The anogenital area is one of these. According to the hygienic function hypothesis, individuals need to cooperate in order to keep it clean. The comfort and hygiene of the genitals may influence the likelihood of copulation, and poor reproductive health can cause disease, affect pregnancy, or reduce the health of the next generation. In this study, we found that monkeys spent more time grooming this area before the mating season. We suggest several reasons for the extra attention. Before mating, female snub-nosed monkeys engage in solicitation behavior. This generally involves the female monkey lying on the ground and turning its rear towards the male monkey (Qi, 1988; Shi, 1982). We observed that the anogenital area was groomed more frequently in both female-female and female-male grooming dyads in the time leading up to the mating season than at any other time. The frequency of grooming the anogenital area may give information about sexual readiness or be a cue for sex. Alternatively, this could be viewed as another solicitation behaviour or preparation for future mating. As a polygynous species, female Yunnan snub-nosed monkeys should compete for resources, especially mating access. Normally, only the dominant females in the OMU can mate with the resident

male, and the subordinates do not, or barely, copulate. However, in our experimental group, all females gave birth to infants. One hypothesis for this finding is that the male may give preference to low-ranking females based on reciprocal grooming of the anogenital region. Further research is needed to determine whether a relationship exists between mating, fertility, and the frequency of grooming the anogenital area.

We found that females direct more grooming toward their OMU's resident male during the mating season than the birth season. According to biological market theory, grooming, as a tradable commodity, can be exchanged for other valuable resources. During mating season, females might initiate grooming bouts with males to get a greater share of the limited opportunities for copulation. Similar patterns of increased female grooming of males when there is a chance to breed have been found in golden snub-nosed monkeys (*Rhinopithecus roxellana*) (Yu et al., 2013; Wei et al., 2012; Li and Zhao, 2007), chacma baboons (*Papio hamadryas ursinus*) (Barrett et al., 2002) and sooty mangabeys (*Cercocebus atys*) (Fruteau et al., 2010). In contrast, male macaques direct more grooming towards females to gain mating chances (Gumert, 2007). Generally speaking, individuals of many primate species were found to exchange grooming as a commodity. For adult female *R. bieti* in the mating season, access to the resident male in their OMU is the most desirable thing they can "purchase".

After the mating season, females divert their attention from males to babies, which is directly reflected by the change in the proportion of time spent grooming each. In this study we found a significant difference in the frequency of grooming of babies between the mating season and the birth season. The usual inter-birth interval in *R. bieti* is two years and can be longer. Once a female has an infant, it is more beneficial for her to take care of her offspring than compete for the attention of the male, which is why females without dependent offspring groomed the males more often than mothers of infants during the mating season. In the subsequent spring, most of these females gave birth, and our data showed that these new mothers paid more attention to babies in the birth season than in the mating season. The proportion of their time spent grooming infants as opposed to the resident male changed to match the females who were already mothers of dependent offspring, with no significant difference between them.

Although mothers of dependent offspring need not compete for mating access, grooming the resident male at a baseline level is still necessary to establish a good social relationship and ensure access to other resources. While the time that females spend grooming males and infants fluctuated over time, female-female grooming

didn't change. OMUs are organized around a core of adult female members, and there is a complex network of social relationships among them. Through grooming, individuals can form durable alliances (De *et al.*, 1989; Masataka and Nakamichi, 2018; Nakamichi *et al.*, 2020; Terry, 1970), which is helpful for maintaining dominance ranks (Chiarello, 1995; Dunbar, 1991).

Female monkeys in polygynous units, especially ones without dependent offspring, preferentially groom to males to establish strong ties to their resident male and secure enough opportunities to get pregnant. As there is a rigid dominance hierarchy among female snub-nosed monkeys (Yu *et al.*, 2009; Zhao *et al.*, 2011), high-ranking individuals can monopolize access to limited resources. The focal monkeys in this study live within a conservation area, and are provisioned sometimes. Thus, particularly in the mating season, the only limited resource for these groups is priority in copulation. Low-ranking females initiate more grooming bouts with their OMU's male to get improved access. In addition, the high-quality habitat and abundant food resources result in high tolerance among adult females. Without overt displays of aggression, unbalanced grooming relationships were the only available tool to socially rank females. In the mating season, the *R*-index can to some extent reveal the social status of females without dependent offspring based on their bids for access to the male. Mothers of infants do not need to compete for copulation, and in the case of DGZ's unit, all three females had already given birth that year. Consistent with biological market theory, they exchanged grooming for the sake of grooming and presumably to maintain social ties. The *R*-index values calculated for this group may simply reflect which individuals are better groomers.

In summary, the proportion of grooming females direct towards males and babies show large fluctuations by season, indicating that grooming can be exchanged as a commodity when a desirable resource is limited. Based on biological market theory, we calculated preliminarily ranks for adult females based on reciprocity. Grooming is essential to both the resource exchange and the maintenance of social network among the females Yunnan snub-nosed monkeys.

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IRB approval and ethics statement

Approval was obtained from the Ethics Committee of China West Normal University. This manuscript is only behavioral observation.

Field study permissions

This field experiments were approved by State Forestry Administration of China (the Second National Survey on Terrestrial Wildlife Resources in China).

Statement of conflict of interest

The authors have declared no conflict of interests.

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