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SPECIAL FEATURE: ORIGINAL ARTICLE

Social networks analysis in primates, a multilevel perspective

Grooming networks reveal intra- and intersexual social relationships in *Macaca thibetana*

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Abstract

The analysis of grooming networks is a powerful tool to examine individual social and sexual relationships and how these relationships change over time. In this study, we investigated the seasonal dynamics of intra- and intersexual social relationships in Tibetan macaques (*Macaca thibetana*) based on grooming interactions. Similar to other female philopatric and male dispersal primates, female Tibetan macaques form the core of the social group with higher values of centralities, compared to the males who tend to be distributed on the periphery of the grooming network. The results of this study indicate that females formed stable clusters with maternal kin-related female partners both during the mating and non-mating season. Males were not included in the females' clusters during the mating season, however, during the non-mating season high-ranking males joined females to form loosely connected clusters. Male–female clustering was associated with the frequency of grooming (bouts per hour) rather than grooming duration (bout length). Our results illustrate that Tibetan macaque social networks fluctuate in response to reproductive seasonality and appear to play a role in mating choice and male reproductive success. Moreover, our results indicate that the frequency of grooming interactions might be more effective than the duration of grooming interactions in establishing cluster pattern on group level. It appears that changes in male mating strategies may drive these shifting social relationships and networks. Future studies on Tibetan macaques will need to investigate the degree to which changes in male grooming strategies directly correlate with male reproductive success.

Keywords *Macaca thibetana* · Social network · Grooming · Intra- and intersexual relationships

Introduction

Given that individual fitness in group living species may be enhanced through the collective benefits of residing in a well-functioning social unit (Sussman and Garber 2011), individuals may exhibit strong partner preferences and form long-term social bonds with several group members (Dunbar 2010; Massen et al. 2010). Females, for example, may use affiliative interactions or mate fidelity as an incentive for group members to remain in the group (e.g., *Papio cynocephalus*, Silk et al. 2003). There also is evidence that in some primate species, males who formed agonistic coalitions against extra-group males or particular resident males sired more offspring than males who were the recipients of these attacks (e.g., *Macaca assamensis*, Schülke et al. 2010; *Alouatta pigra*, Van Belle et al. 2014; *Rhinopithecus roxellana*, Xiang et al. 2014). Additionally, males who formed stronger intersexual bonds with resident females experienced increased mating access and paternal certainty compared to

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males who did not form such bonds (e.g., *Macaca mulatta*, Massen et al. 2012).

Primates live in complex social groups that vary in size, composition, organization, and the frequency and nature of affiliative and competitive social interactions (Sussman and Garber 2011). Moreover, what is often described as the social group may better be understood as a collection of component parts that include the set of individuals who feed, forage, rest and travel together, the set of individuals who assist in infant caregiving, the set of individuals who defend the group's territory, the set of individuals who copulate, and the set of individuals who contribute genes to the next generation (Garber et al. 2016). Individual group members may participate in some or all of these aspects of group living, however, their roles are likely to vary as their social relationships change with other group members (Clutton-Brock and Sheldon 2010). Social network analysis, a method based on mathematical graph theory developed to examine human interactions (Scott 2000), provides an effective tool to quantify patterns of complex interactions in social animals (Croft et al. 2008; Whitehead 2008; Flack et al. 2006; Sueur et al. 2011a; Kanngiesser et al. 2011; Barrett et al. 2012). The extent to which individuals interact in clusters can influence both the persistence of cooperation and competitive interactions (see Brent et al. 2013). Social network analysis has been used to study the dynamic changes in social interactions (e.g., *Rhinopithecus roxellana*, Zhang et al. 2012; Qi et al. 2017; *Mandrillus sphinx*, Bret et al. 2013; *Chlorocebus pygerythrus*, Borgeaud et al. 2016; *Macaca sylvanus*, Sosa et al. 2017), including individual's social role (*Macaca nemestrina*, Flack et al. 2006; *Pan troglodytes*, Kanngiesser et al. 2011), and dominance style in several primate species (Sueur et al. 2011b; Balasubramaniam et al. 2018). Social network analysis also provides a more detailed method to quantify the role of social structure in shaping the emergent characteristics of a social group (Flack et al. 2006; Sueur et al. 2011a; Kanngiesser et al. 2011; Barrett et al. 2012). For example, in a study of chacma baboons (*Papio hamadryas ursinus*), Henzi et al. (2009) demonstrated that female–female social relationships varied with changes in food availability. In rhesus macaques (*Macaca mulatta*), Brent and colleagues (2013) proposed that in response to reproductive seasonality, female clustering patterns were stronger in the mating season than in the birth season. Similar seasonal or temporal changes in social relationships are reported among male primates, for example in Barbary macaques (*Macaca sylvanus*, Henkel et al. 2010).

In the present study, we examine the context and function of temporal changes in social relationships among male and female Tibetan macaques based on grooming relationships. Social grooming is an important bonding mechanism in all primates (Lehmann et al. 2007; Dunbar 2010), and changing patterns of intersexual grooming offer an important behavioral index from which to evaluate conditional behavioral responses to different mating strategies and mating opportunities (Sonnweber et al. 2015). We explored the variation of grooming networks in relation to reproductive seasonality in free-ranging and provisioned group of Tibetan macaques (*Macaca thibetana*).

Prediction 1

Tibetan macaques live in multi-male, multi-female social groups, with female philopatry and male dispersal (Li 1999). Females remain in their natal group throughout their lives (except during periods of group fission), whereas males disperse from their natal group at 6–7 years of age when they become sexually mature (Li 1999). Consistent with other macaque species characterized by female philopatry (e.g., *Macaca mulatta*, Brent et al. 2013), we predict that related female Tibetan macaques will have higher values of centrality and form same sex clusters within a grooming network, whereas males will be distributed on the periphery of grooming networks with lower centralities during both the mating and non-mating seasons.

Prediction 2

Tibetan macaques have been described as seasonal breeders and form a linear dominance hierarchy (Li et al. 2005; Berman et al. 2004). The mating season typically lasts from July to January (Li et al. 2005; Xia et al. 2010). High-ranking males have mating priority and have been observed to form consortships designed to mate-guard a presumably ovulating female for periods of several hours to several days (Li 1999). Nevertheless, a single male cannot monopolize all matings, and thus multiple males compete for mating opportunities with multiple females (Li et al. 2005; Xia et al. 2010). As such, males may be expected to opportunistically mate with most/all females, even if they are guarded by a rival male. For example, a male who is guarding a female may still have an opportunity to mate with other females (although at the cost of reducing paternal certainty), and a female who is guarded by high-ranking male may attempt to mate with other males during periods when the guarding male is less vigilant. Accordingly, we predicted that male Tibetan macaques will not be part of female grooming networks during the mating season.

Prediction 3

However, during the non-mating season (February through June, Li et al. 2005), individuals do not compete for access to mating partners. Females give birth during this period (Li 1999; Li et al. 2005) and are principally engaged in caring for and protecting their infants. Given that extragroup males attempt to enter a group during the birth season, and social bonds formed between mothers with newly born infants and resident males may continue into the next mating season, we expect mothers to engage in affiliative interactions with both resident females and resident males at the same rate during birth season as they do during the breeding season. As such, we predict that males will fall bisexual grooming clusters with mothers with young infants within the social network during the non-mating (birth) season.

Methods

Study site and subjects

This study was conducted at the Valley of Wild Monkeys at Mt. Huangshan located in Anhui Province, China. This site is home to a population of Tibetan macaques (*Macaca thibetana*) that have been studied for the past 35 years (for more detail about the study site and population, see Xia et al. 2008, 2010 and 2012). Beginning in 1986, we initiated observations of a single macaque group known as YA1. Matrilineal kin relationships are well known for all female members of YA1 as demographic data have been collected since 1986. In 1996, YA1 underwent a group fissioning event, which resulted in the formation of a second group known as YA2 (Li et al. 1996). YA2 was the subject group of this study (see Table 1 for a summary of the group composition). In this group, matrilineal kin relationships of female members are also well known based on the history of demographic data.

This study was conducted during three observation periods between 2009 and 2010. Period one was 3 months in length (May to July 2009) when YT was the highest ranked adult male. Period two was 5 months in length (August to December 2009) and period three was 5 months (April to August 2010) when LY was the highest ranking male. Maternal kin relationships within the study group included seven mother-daughter pairs (ZMZ-ZY, HON-HPG, HON-HY, BAI-BLG, BAI-BLN, LAN-LMN and HEI-HMG) and two sister-sister pairs (HPG-HY and BLG-BLN, Xia et al. 2012).

Behavioral data collection

All behavioral data were collected during an intensive study period totaling 311 days across the three observation periods (mean ± SE = 23.9 ± 1.26 days/month, range = 16–28). We followed the subject group from dawn to dusk, beginning at approximately 0700–0800 and ending at 1700–1800 each day (depending on the time of year). Behavioral data were collected on all 24 adults by a single observer (DPX) using a digital voice recorder (model News my RV50) (Xia et al. 2012, 2013). Animals were observed from a distance of 5–10 m and data were recorded using the continuous focal animal sampling method (Altmann 1974). Focal samples were 20 min in length. During each 20-min period, the following behavioral data were recorded: grooming initiated and received. To avoid the potential influence of the presence of human observers on the monkeys' behavior, we collected all focal sampling in the forest, away from tourists and viewing platforms. Only data from completed 20-min focal sampling periods were used for analysis. If the focal male was lost from view during the sampling, then another subject was randomly selected (Li et al. 2007; Shutt et al. 2007).

Table 1 Composition of the YA2 group during the study period

Age/sex class	Adult males	Adult females	Sub-adults/juveniles	Infants	
	LY (7,1,1)	ZMZ*			
	BL (2,2,2)	HON*			
	HL (3,3,3)	BAI*			
	JT (4,4,4)	LAN			
	CBG (6,5,5)	HPG			
	YG (8,8,8)	BLG*			
	SX (5,6,6)	BLN*			
	BY (9,9,9)	HY*			
	DC (10,10,10)	LMN*			
	YT (1,7,7)	ZY*			
	HG (–,11,11)	HMG			
	YZ (–,12,12)	HT			
Total numbers	12	12	40	8	72

The numbers in the brackets represent social ranks by study periods. The smaller number, the higher social rank (i.e., 1 equals α-male, 2 equals β-male, and so on). More detail on social ranks about female members can be found in Xia et al. (2012) and male members in Xia et al. (2013). "–" indicates that the individuals were not in the group during that study period (HG and YZ immigrated on August 19 and September 20, 2009, respectively). "*" indicates that females who have newborn infants during the study periods

We defined grooming as any act in which a groomer used its hand or mouth to touch, clean, or manipulate the fur of another individual (groomee) for a continuous period lasting at least 5 s (Xia et al. 2012, 2013). A grooming bout began when one of the two partners initiated the first grooming, and ended when the individuals separated from each other (Xia et al. 2013). A new bout of grooming was counted if there was a pause of > 30 s during a grooming bout or if the direction of grooming changed.

We collected a total of 759.66 h of behavioral data, and data were approximately equally distributed among the adults (mean ± SE = 31.65 ± 1.19 h, $n = 24$, range, 13–35.33 total h per monkey).

Data analysis

Grooming was calculated as the number of bouts per hour (i.e., frequency) or minutes per hour (i.e., duration) that a focal subject initiated or received grooming from another individual (Xia et al. 2012, 2013). Grooming data were summarized via a sociomatrix for subsequent social network analysis.

We used weighted data as they provide a greater resolution to social interactions than only do binary data (presence/absence of interactions) and are less prone to sampling errors or biases (see Brent et al. 2013). We constructed weighted networks to quantify not only who interacts with whom (with direction), but also how often or how long. The "weighted" data with connections (edges) representing the amount of time a pair engaged in grooming, including both the presence or absence of interactions and their frequency or duration.

We measured group density, which indicates the cohesiveness of the social group. Density represents the level of dyadic connection in a population and is calculated by dividing the total sum of all tie weights by the number of possible ties, where ties represent the frequency at which social association occurs (Hanneman and Riddle 2005). We measured network centrality, which indicates the extent to which the existing preferences were centralized around one particular individual within the grooming network, including an individual grooming others and being groomed by others. That is, it provides a measure for how evenly preferences were distributed among individuals. We used *eigenvector centrality*, an index that represents the number and strength of connections an individual exhibits, as well as the number and strength of the individuals is connected to. Individuals will score highly on eigenvector centrality if they themselves are highly connected, or if they are connected to other highly connected individuals (Zhang et al. 2012).

We used hierarchical cluster analysis to assess the number of clusters that existed in the subject group's network, according to Zhang et al. (2012). We reported the cophenetic correlation coefficient to indicate how well the dendrogram matches the matrix of grooming indices. Cophenetic correlation coefficients greater than 0.80 are taken to indicate an effective division (i.e., cluster) of the social group (Zhang et al. 2012; Levé et al. 2016).

To obtain a graphical representation of the grooming network, we constructed a weighted grooming network using Netdraw in Ucinet 6.0 (Borgatti et al. 2002). We also calculated the densities and eigenvector centralities using SOCPROG 2.5 network software (Whitehead 2009).

We calculated eigenvector centralities as means (± SE). We used a one sample Kolmogorov–Smirnov test to examine whether the data did not deviate from a normal distribution ($P > 0.05$). We used paired-sample t tests to analyze the difference of eigenvector centrality between males and females, and the difference of female/male individual index between the mating season and non-mating season.

All analyses, unless specified, were two-tailed and were carried out using the SPSS 13.0 software (SPSS Inc., Chicago, IL, USA) (Norusis 2005), with the significance level set a priori at 0.05.

Results

Grooming network

Social structure topologies based on grooming interactions were fully connected during both the mating and non-mating seasons. Group density measures during the mating season were 0.62 for grooming frequency and 0.49 for grooming duration (Fig. 1a, c provide sociograms of these respective grooming networks). Group density measures during the non-mating season were 0.89 for grooming frequency and 0.77 for grooming duration (Fig. 1b, d provide sociograms of these respective grooming networks).

Variation of eigenvector centralities

Based on grooming frequency within a grooming network, the eigenvector centralities of females were higher than those of males, during both the mating season (females: 0.253 ± 0.009, males: 0.123 ± 0.017, disparity $= 0.130 \pm 0.013$, $t = 9.641$, $df = 11$, $P < 0.001$) and non-mating season (females: 0.250 ± 0.011, males: 0.126 ± 0.018, disparity $= 0.125 \pm 0.013$, $t = 9.329$, $df = 11$, $P < 0.001$). However, there were no difference in the eigenvector centralities between the mating and non-mating season, for either females (disparity $= 0.003 \pm 0.004$, $t = 0.609$, $df = 11$, $P = 0.555$) or males (disparity $= 0.003 \pm 0.003$, $t = 0.897$, $df = 11$, $P = 0.389$) (see Fig. 2a).

Based on grooming duration within a grooming network, the eigenvector centralities of females were higher than those of males during both the mating season (females: 0.236 ± 0.008, males: 0.156 ± 0.016, disparity $= 0.080 \pm 0.019$, $t = -4.046$, $df = 11$, $P = 0.002$) and non-mating season (females: 0.243 ± 0.009, males: 0.139 ± 0.017, disparity $= 0.104 \pm 0.017$, $t = -5.875$, $df = 11$, $P < 0.001$). Moreover, although the eigenvector centralities of females during the mating and non-mating season were not different (disparity $= 0.008 \pm 0.004$, $t = -1.750$, $df = 11$, $P = 0.108$), the eigenvector centralities of males during the mating season were higher than the values during the non-mating season (disparity $= 0.012 \pm 0.003$, $t = 4.690$, $df = 11$, $P = 0.001$) (see Fig. 2b).

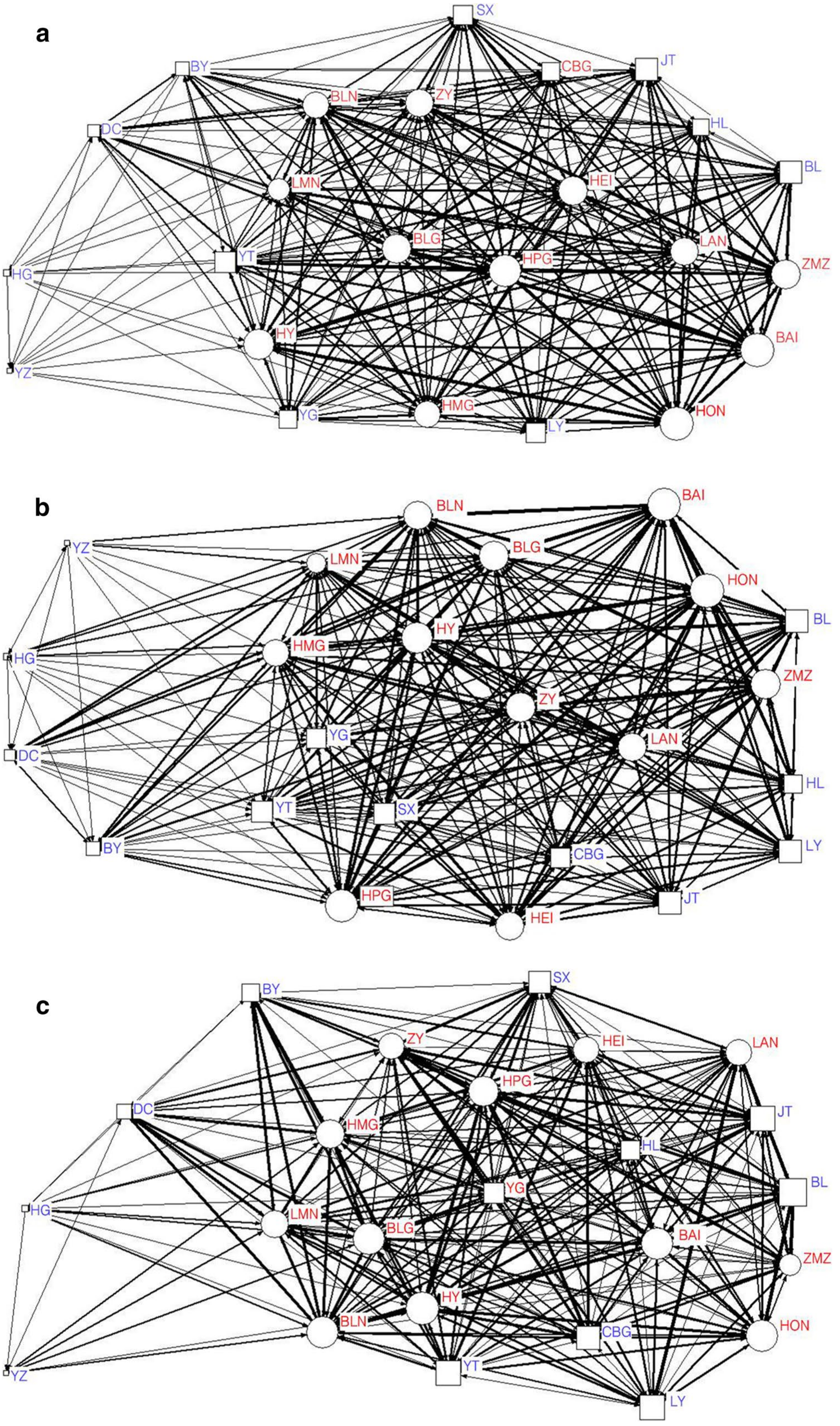
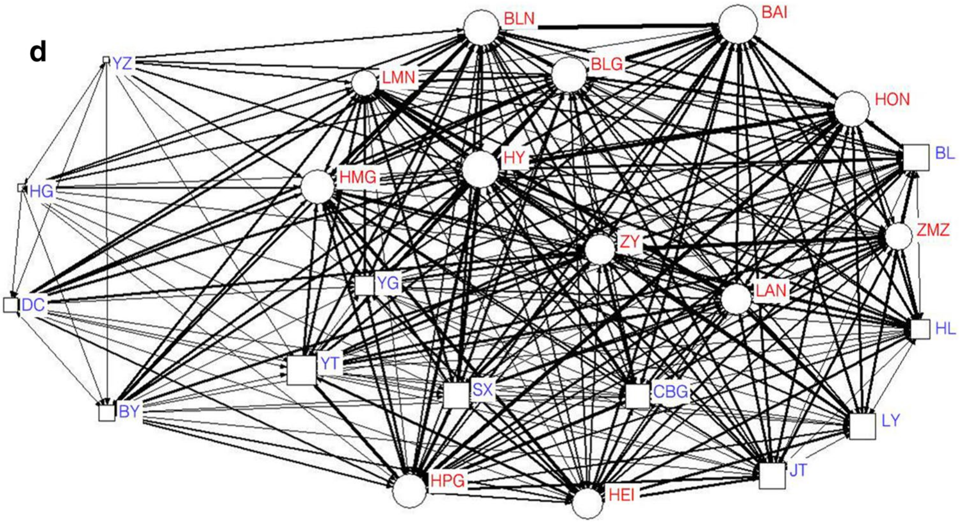


Fig. 1 A sociogram created with Netdraw in Ucinet 6.0 illustrating the grooming network based on grooming frequency (**a** the mating season; **b** the non-mating season) and duration (**c** the mating season; **d** the non-mating season) of all adult males (*open square*) and adult females (*open circles*) in a group of Tibetan macaques. *Line thickness* represents the amount of time pairs of individuals spent grooming each another, with *thicker lines* representing more frequent grooming. *Nodes* represent individuals and the size of a node represents the individual's eigenvector centrality

Fig. 1 (continued)



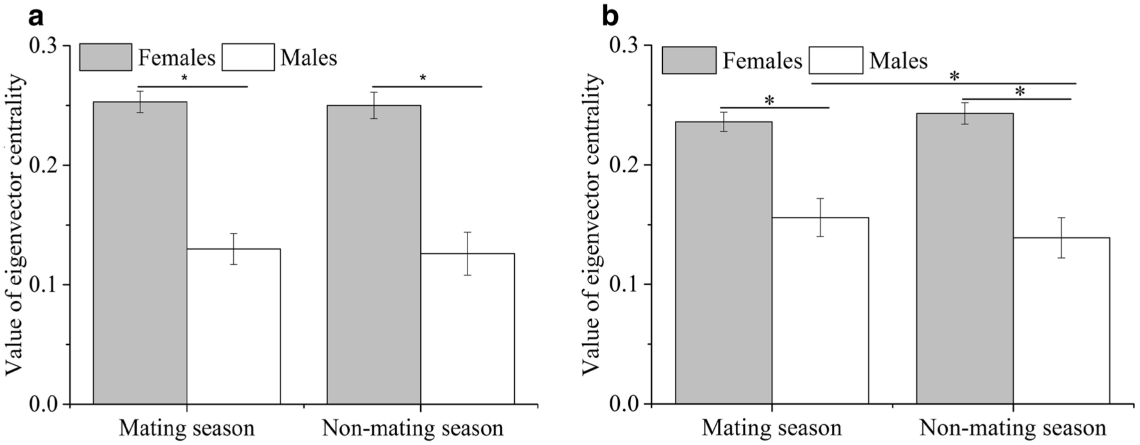


Fig. 2 Variation of eigenvector centralities between males and females based on grooming frequency and duration (*Left*: grooming frequency between males and females in the mating and non-mating season; *Right*: grooming duration between males and females in the mating and non-mating season)

Clusters

During the mating season, a hierarchical cluster analysis of grooming frequency in the network showed five clusters consisting of the following: two females (HEI and HMG), two females (LAN and LMN), three females (BAI, BLG and BLN), three females (HON, HY and HPG), and two females and one male (ZMZ, ZY and BL). None of the remaining 11 males (JT, YT, LY, SX, YG, CBG, HL, BY, DC, HG and YZ) belonged to any cluster (see Fig. 3a). The cophenetic correlation coefficient was 0.817, indicating that the social group was divided into effective clusters based on grooming interactions. The clustering distinguished points at 1.1487 on the horizontal ordinate. All of the clusters, except one consisting of ZMZ, ZY and BL, the adult male, were composed of females and their daughter(s).

During the non-mating season, we identified only one cluster based on grooming frequency with a cophenetic correlation coefficient of 0.814. The clustering distinguished points at 0.7427 on the horizontal ordinate. As indicated in of Fig. 3b, this cluster consisted of all of the 12 females (ZMZ, ZY, HON, HPG, HY, BAI, BLG, BLN, HEI, HMG, LAN, and LMN) and seven males (YG, CBG, SX, YT, LY, BL, and JT). Five adult males (HL, BY, DC, HG, and YZ) did not belong to this cluster. This suggests that female Tibetan macaques formed cluster patterns with female maternal kin partners during both the mating and non-mating season. Males were not part of females' clusters during the mating season, however, during the non-mating season several high-ranking males joined the female cluster, although they were loosely connected.

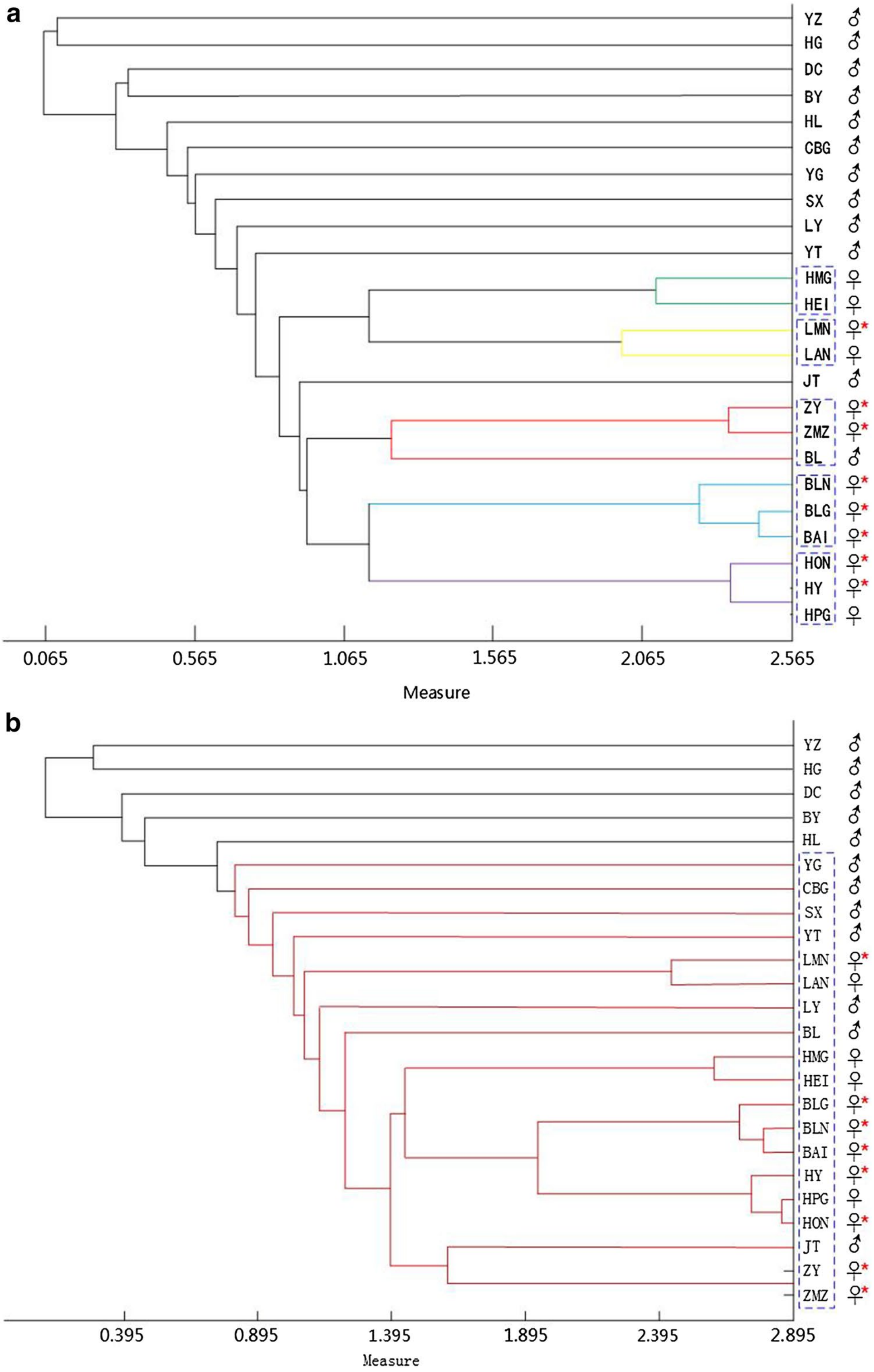


Fig. 3 Hierarchical cluster analysis of the subject Tibetan macaque social group based on grooming frequency during the mating (**a**) and non-mating season (**b**). The dendrogram was created in SCOPROG 2. Individuals are named on the right. "*" indicates that females who have newborn infants during the study periods. Individuals with same colors belong to the same cluster (individuals within the same cluster were included in the same *dotted box*), except for those denoted in *black*, which were solitary

With regard to grooming duration, no cluster pattern was observed during either the mating season (cophenetic correlation coefficient was 0.667, < 0.80) or non-mating season (cophenetic correlation coefficient was 0.757, < 0.80).

Discussion

Studying social networks and the preferred interactions among sets of individuals is important for understanding the general network properties and social roles of group members in animal societies (Flack et al. 2006). In our study, we found that the eigenvector centralities of female Tibetan macaques were higher than those of males during both the mating and non-mating seasons (see Fig. 2). The Prediction 1 that female Tibetan macaques will have higher values of centrality and male will have lower values within a grooming network was supported.

The topological features of social network, such as the extent to which individuals interact in clusters, also allowed us to gain new insights into the dynamics influenced by food resources or mating opportunity (Henzi et al. 2009; Brent et al. 2013). We found that, during the mating season, female Tibetan macaques formed several clusters based on maternal kin relationships, whereas except for one high-ranking male, BL, male Tibetan macaques were not part of a grooming cluster. Thus, the Prediction 2 that male Tibetan macaques will not be part of female grooming networks during the mating season was supported. During the non-mating season, however, the results showed that several higher-ranking males (i.e., LY, BL, YT, JT, CBG, SX, and YG) were part of a grooming cluster with particular females. This was not the case for lower-ranking males (i.e., HL, BY, DC, HG, and YZ). Therefore, the Prediction 3 that males will fall bisexual grooming clusters with mothers with young infants within the social network during the non-mating (birth) season was partially supported.

Similar to most macaque species with female philopatry and male dispersal (Thierry 2007), female kin-related social relationships were critical in the establishment of dyadic social bonds (e.g., *Macaca mulatta brevicaudus*, Wu et al. 2018; *Macaca thibetana*, Xia et al. 2012), and for cluster patterns (e.g., *Macaca mulatta*, Brent et al. 2013). Our results that female Tibetan macaques will have higher values of centrality provided supportive evidence for understanding female's social roles in those species. In most macaque species, males typically disperse singly from their natal group at the age of sexual maturity (Thierry 2007). These males establish weak social bonds with resident males and resident females in their new group (Koski et al. 2012). Similarly, our results indicate that male Tibetan macaques were distributed on the periphery of grooming networks. In addition, both males and females benefit by developing strong social relationships and alliances with opposite sex partners (Haunhorst et al. 2016; Arseneau-Robar et al. 2018). These bonds can act to increase opportunities for female mate choice (Koyama et al. 2012) and obtain access to a greater number of reproductive partners, especially during a female's fertile period (Massen et al. 2012). In some primate species, intersexual social bonds may be stable over an extended period of time (e.g., *Pan troglodytes*, Langergraber et al. 2013; *Macaca mulatta*, Massen and Sterck 2013; *Macaca assamensis*, Ostner et al. 2013; Haunhorst et al. 2016), lasting beyond a female's reproductive cycle (Smuts 1985). In the case of Tibetan macaques, however, we found that several males were included in a female grooming cluster during the non-mating season, but not during the mating season. This result provides more information to understand the dynamics of intra- and intersexual social relationships, beyond dyadic interaction (e.g., subgroup or group levels) in Tibetan macaques. We found that the social structure based on grooming relationships among sets of males and female fluctuated over time in response to seasonal mating.

In Tibetan macaques, females are fertile only during the mating season, however, they are characterized by concealed ovulation (Li et al. 2005). Males only produce sperm and form reproductive copulation when females are available to reproduce (Li et al., 2007; Xia et al. 2010). During our study, several females ovulated during the mating season. Given that the group contained 12 adult males, direct competition for mating opportunities is high during the mating season. Although higher-ranking males form consortships with females and mate guarding for varying lengths of time (e.g., several hours or days) (Li 1999), a single male cannot effectively monopolize all the ovulating females in his group. Thus, multiple males are able to compete for mating opportunities with multiple females. Previous studies by Li (1999) and Li et al. (2015) indicated that the most effective strategy for males to maximize reproductive success is to mate with as many females as possible. Female Tibetan macaques appear to exhibit a preference to mate with certain group males, however, this relationship is frequently disrupted by male aggression within intensive male–male competitions (Li 1999). In the present study, we found that male Tibetan macaques did not participate in female grooming clusters during the mating season. This suggests that for males, stable companionships with females declined or dissolved when within group competition for limited mating opportunities increased, and that stable grooming relationships present in the birth season were replaced by casual acquaintanceships in the mating season.

Intersexual social bonds also can be considered as an effective way to facilitate the survival of newborn infants. For example, in gorillas (*Gorilla gorilla beringei*), infants living in a group with a mature silverback male are rarely killed by extragroup males (Watts 1989). These silverback males serve an important role in infanticide avoidance (Watts 1989). Therefore, female who maintain strong social relationships with males (especially with high-ranking males) may experience increased protection for themselves and heir infants (Sonnweber et al. 2015). In some primate species, a males' future mating opportunity may be increased by forming a strong intersexual social bond with one or more resident females (Massen et al. 2012). In the case of Tibetan macaques (see Fig. 3b), several high-ranking males were part of a female cluster during the non-mating season. These shared associations bring females into frequent contact with female kin and high-ranking males. Taken together, these results suggest that selective pressure for increasing mating opportunities and/or mate choice act on both female and male Tibetan macaques and influence female–male relationships, female–female social relationships, and social network structure.

Surprisingly, we did not find any cluster patterns based on grooming duration both during the mating and non-mating season. This indicates that clustering was associated with frequency of grooming rather than grooming duration, and suggests that the frequency of grooming interactions might be more effective than the duration of grooming interactions in establishing cluster pattern on group level. In Tibetan macaques, however, the duration of post-copulation grooming appears to be longer than that of other daily grooming bouts (pers. obs., DPX). This would imply that grooming frequency and duration might serve as different behavioral strategies to adjust intersexual relationships in this multi-male primate society. Frequent grooming interactions may be a long-term strategy to establish strong intersexual relationships for future mating success (e.g., *Macaca mulatta*, Massen et al. 2012). The duration of grooming interactions, however, may reflect a short-term strategy to prevent a female from mating with another male (e.g., *Macaca sylvanus*, Sonnweber et al. 2015).

In conclusion, social structure topology is defined as the patterning of social interactions among individuals residing in the same group (Hinde 1976). The variation of networks can, in turn, feedback on individuals to differentially shape their intra- and intersexual relationships (e.g., reproductive seasonality). Our results suggest that in Tibetan macaques the frequency of social interactions might be more important for establishing and maintaining social clusters than the duration of grooming interactions. Moreover, long- or short-term mating strategies might be involved in the shifting social relationships and network affiliation. Therefore, the relationship between intersexual grooming and copulatory behaviors in different time scale, such as short-term (the mating and non-mating season) and long-term (the entire year), needs to be studied in greater detail in order to determine the extent to which mating strategies influences male–female, male–male, female–female relationships and social networks.

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