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# Social connectivity among female Tibetan macaques (*Macaca thibetana*) increases the speed of collective movements

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## Abstract

Social network analysis provides insights into patterns of group movements in primates, but fewer studies to date have focused on the dynamics of how such movements occur. In this study, we proposed and tested two hypotheses about the influence of sex on social connectivity and group movement in Tibetan macaques (*Macaca thibetana*): (1) adult females are socially more connected than are adult males and (2) social connectivity facilitates the speed of collective decision-making. We collected data from 128 successful collective movements ($\geq 2$ individuals followed an initiator within 5 min) over a 2-month period in a group of adult Tibetan macaques at Mt. Huangshan, China. Although high-ranking individuals of both sexes in our dataset were more central in their social network than were low-ranking individuals, our results show that affiliations between females were stronger, with more preferred associations than those between males. Groups with more females reached collective decisions faster than groups with fewer females. We conclude that female Tibetan macaques use their social networks to enhance the speed of collective decision-making, which may have associated fitness benefits.

## Introduction

Social network analysis enables exploration of complex collective movements in primates (Jacobs and Petit 2011), with considerable research to date focused on female-bonded Old World monkey taxa such as macaques (*Macaca*) (Sueur and Petit 2008; Jacobs et al. 2011). However, detailed information on the dynamics of social movements, such as which individual(s) initiates movements (*Macaca*, Sueur et al. 2011a; *M. fuscata*, Jacobs et al. 2011), the identities and progression of those following (*M. thibetana* Wang et al. 2015), and the speed of movement progression (*Macaca*, Sueur et al. 2011a) are just beginning to be described. The dynamics of how collective movements occur provide the evidence needed to further explore the fitness consequences of group movements, particularly because fitness impacts likely vary among individuals involved in the movement.

Tibetan macaques are a female-philopatric species (Li et al. 2007) with female social bonds maintained through grooming directed toward individuals of higher rank and toward close female kin (Xia et al. 2012). Wang et al. (2016) found that while all adult Tibetan macaques can initiate group movements, adult males and adult females with stronger social centrality are more likely to do so, and their movement initiations are more likely to be successfully completed, leading these authors to characterize this population as having a distributed leadership style. With respect to those joining movements, Wang et al. (2015) found that Tibetan macaques use selective mimetism (rank and affiliation

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determine who follows an initiation) when the number of movement joiners ranges from three to six individuals (of 32 total), but that a quorum pattern (simple majority) occurs when the number of joiners reaches seven or more. They also found that the earlier an individual joined a movement, the more central her or his role is in the joining network (Wang et al. 2015). Focusing on the same Tibetan macaque population, we set out to further explore whether differences in adult male and female Tibetan macaque social connectivity influence their respective roles in group movements. We tested two hypotheses to provide additional details on how collective movements occur in this population: (1) adult females are socially more connected than are adult males, and (2) social connectivity facilitates the speed of collective decision-making.

## Methods

We collected data from July to September 2014 on a free-ranging group of Tibetan macaques at Mt. Huangshan National Reserve in Anhui province, China (118.3E, 30.2N, elevation 1814 m). The Yulingkeng A1 (YA1) group, the focus of this study, consisted of 45 individuals during July 2014. The troop has been monitored since the 1980s (Berman et al. 2007) and in 2014 was provisioned by park staff with corn three or four times daily (times varied based on tourist presence), during which time the monkeys came to the provisioning site to feed followed by time spent resting in forested areas adjacent to the provisioning site. Collective movements often occurred during the monkeys' switch between feeding and resting periods. We collected collective movement data ($n = 128$) when the troop was leaving the provisioning area because this gave the best visibility

of group members, direction of movement, and movement progression.

Juveniles and infants do not lead group movements in this population (Wang et al. 2016), so we collected data on movements initiated by adults (nine males and 11 females; see Table 1). We identified each adult based on unique physical features such as scars, injuries, and hair color patterns. GF and LKS established inter-observer reliability ≥ 90% agreement for adult monkey identification prior to data collection.

GF collected group movement data using an all-occurrences method (Altmann 1974). Following Sueuer and Petit (2008) and Wang et al. (2015, 2016), GF noted a movement initiation when one individual moved > 10 m away from a stationary group in less than 40 s followed subsequently by an individual who moved > 5 m within a 45° angle of the initiator's movement direction and within 5 min (GF designated this a "follower"). GF applied the same set of rules to each subsequent follower. A successful movement occurred when ≥ 2 individuals followed an initiator within 5 min; otherwise, GF scored the movement as unsuccessful. GF scored the progression stage of a collective movement as finished when no others joined within this 5-min period (following Jacobs et al. 2011).

LKS collected behavioral data used to assess social connectivity and rank. Using a focal animal sampling method (Altmann 1974) with samples of 5-min duration on a randomized schedule for all adults, LKS recorded proximity (individuals within arm's reach of one another) and grooming (as defined in Berman et al. 2004). When no group movements were occurring, GF used a scan sampling method (Altmann 1974) with a 6-min sample point as another means of gathering proximity data. During focal samples and ad libitum, LKS and GF recorded occurrences of and participants in aggressive interactions (as defined in

**Table 1** Sociodemographic characteristics of YA1 adult members in 2014

| ID | Sex | Rank | YOB[a] | Focal duration (s) | ID | Sex | Rank | YOB[a] | Focal duration (s) |
|---|---|---|---|---|---|---|---|---|---|
| ZB | Male | 1 | 2000[b] | 6250 | TRY | Female | 11 | 2009 | 6860 |
| TG | Male | 2 | 2003 | 5073 | HH | Female | 12 | 2003 | 5327 |
| YH | Female | 3 | 2003 | 5943 | TH | Female | 13 | 2003 | 6686 |
| GS | Male | 4 | 1984 | 6328 | TXX | Female | 14 | 2008 | 6387 |
| ZL | Male | 5 | 1997[b] | 6596 | TR | Female | 15 | 2004 | 5710 |
| YRB | Male | 6 | 2008 | 2887 | DS | Male | 16 | 2000[b] | 6847 |
| YM | Female | 7 | 1990 | 6769 | HT | Male | 17 | 1992[b] | 7481 |
| BT | Male | 8 | 1988[b] | 6035 | TRB | Male | 18 | 2008 | 6612 |
| YCY | Female | 9 | 2009 | 6977 | TT | Female | 19 | 1991 | 7139 |
| THY | Female | 10 | 2009 | 4758 | YZ | Female | 20 | 1992 | 7410 |

[a]YOB represents the year each individual was born

[b]These individuals immigrated into the group, so their birth years are estimated based on physical features

Berman et al. 2004). We used aggregation data to calculate rank by applying the Clutton-Brock fighting index (Clutton-Brock et al. 1979). We excluded subadult male YeRongBing (YRB) from social network analysis due to a focal duration period that was lower for him than for the other adults (see Table 1).

We conducted two social network analyses for affiliations during daily activities and during collective movement, respectively, with SOCPROG 2.4. We used NETDRAW for visual representations of the networks. To measure the strength of association between two individuals during their daily activities, we used the dyadic association index (DAI) (Altmann 1974) based on the rates of affiliative behavior (Croft et al. 2008; Pyritz et al. 2011; Sueur et al. 2011a, 2011b) documented by Wang et al. (2016). We then used the half-weight index (HWI) to measure associations during collective movement (Cairns and Schwager 1987; Croft et al. 2008; Whitehead 2008). For each individual and her/his direct connections, we calculated eigenvector centrality as the strength of connectivity (Sueur and Petit 2008; Whitehead 2008; Kasper and Voelkl 2009; Sueur et al. 2011b; Zhang et al. 2012) and clustering coefficient to show how nodes clustered in space (Bejder et al. 1998; Hanneman and Riddle 2005; Croft et al. 2008; Whitehead 2008; Henzi et al. 2009; Zhang et al. 2012). We used Spearman rank tests to examine correlations between these social network properties (Zhang et al. 2012).

To test the hypothesis of strong female social bonds, we conducted permutation tests for preferred/avoided associations with the affiliative data (Whitehead 2008). If individuals preferentially associate with specific group members, then the standard deviation (SD) and coefficient of variation (CV) of association indices should be greater in the real dataset than in the random dataset based on permutations. Also, a significantly low mean of the real association index is indicative of preferred associations (Whitehead 2008). Conversely, if individuals tend to avoid specific group members, the proportion of non-zero association indices should be less in the real dataset than in the random datasets. To decide how many permutations to run, we increased the number of permutations until the given $P$ value stabilized (Bejder et al. 1998). With this criterion met, we conducted 1000 permutations with 1000 trials per permutation for each randomization, which has proven to be optimal in most scenarios (Whitehead 2008). To examine the difference between female and male affiliation, we performed separately permutation tests on female–female associations and male–male associations.

To test whether females could facilitate decision-making, we first analyzed the relationship between time needed at the progression stage and the number of individuals (regardless if they were male or female, i.e., unweighted) involved in a successful movement. We then examined the same relationship weighted by the proportion of females involved. Because the number of individuals involved in each group movement differed (from three to ten individuals), we factored out the effect of group size by calculating progression time per the number of individuals involved in a successful movement. We then compared the slopes of both unweighted and weighted movements using a $t$ test to examine how females affected the speed of the decision process.

## Results

To test the hypothesis that social connections in females were stronger than those in males, we conducted a social network analysis on grooming and proximity data and on movement behavior. The weighted affiliative social network of the adults is shown in Fig. 1, which reveals two major clusters of adults within the troop (one cluster consisted of the females TRY, TH, YH, YM, YCY, TXX, and HH and the males TG, ZL, ZB, BT, and GS, and one cluster consisted of the males THY, TR, TT, and YZ and the males DS, TRB, and HT). We found a significant correlation between affiliative strength and eigenvector centrality coefficients (Spearman rank correlation $r_s = 0.989$, $n = 20$, $P < 0.001$), eigenvector centrality coefficients and clustering coefficients ($r_s = 0.781$, $n = 20$, $P < 0.001$), and strength and clustering coefficients ($r_s = 0.696$, $n = 20$, $P < 0.001$).

The social network in weighted collective movement revealed four clusters based on individual clustering
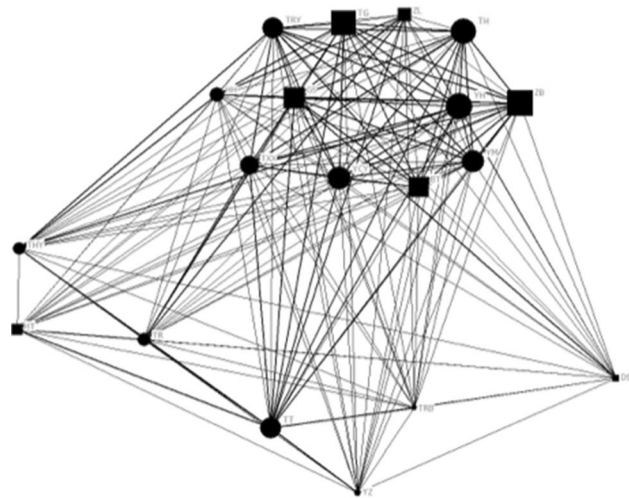


**Fig. 1** Weighted social network of affiliation (*circles* for females and *squares* for males). *Nodes* represent individuals with their name abbreviations above each. Distances between individuals represent their relationships in terms of proximity and grooming. The size of a node is directly related to the individual eigenvector centrality coefficient. Individuals are clustered in space based on clustering coefficients

coefficients. Some individuals did not belong to any of the four clusters. We found a correlation between collective movement HWI and eigenvector centrality coefficients (Spearman rank correlation $r_s = 0.988$, $n = 20$, $P < 0.001$). The relationships between eigenvector centrality coefficients and clustering coefficients and between HWI and clustering coefficients were not significant. The affiliative and collective movement networks were positively correlated with each other in regard to strength ($r_s = 0.946$, $n = 20$, $P < 0.001$), eigenvector centrality coefficients ($r_s = 0.923$, $n = 20$, $P < 0.001$), and clustering coefficients ($r_s = 0.491$, $n = 20$, $P < 0.05$).

Permutation tests of female–female affiliative behavior revealed 21 preferred associations that significantly differed with nine significant individuals (see Table 2). The real association indices differed from the random dataset (Real: M = 0.40, Random: M = 0.48, $P < 0.001$). Both the standard deviation and the coefficient of variation were greater in the real dataset than in the random dataset (Real: SD = 0.19, Random: SD = 0.16, $P < 0.05$; Real: CV = 0.47, Random: CV = 0.34, $P < 0.001$). The permutation tests of male–male affiliative behavior revealed nine preferred associations that significantly differed but with no significant individuals. The real association indices differed from the random dataset (Real: M = 0.25, Random: M = 0.30, $P < 0.05$). The coefficient of variation was greater in the real dataset than in the random dataset (Real: CV = 0.76, Random: CV = 0.69, $P < 0.05$), but the standard deviations did not differ (Real: SD = 0.19, Random: SD = 0.21, $P > 0.05$).

We recorded 128 successful collective movements. In testing the hypothesis that females could facilitate collective decision-making, we found that movement progression occurred at a faster pace when there were fewer individuals participating for both weighted and unweighted data.

**Table 2** Permutation test results of preferred affiliative associations

| Female[a] | Preferred association[b] | Index[c] | Male[a] | Preferred association[b] | Index[c] |
|---|---|---|---|---|---|
| YH ($P < 0.05$) | TRY ($P < 0.05$) | 0.82 | ZB ($P > 0.05$) | NA | NA |
| | HH ($P < 0.05$) | 0.37 | | | |
| | TXX ($P < 0.05$) | 0.47 | | | |
| | TR ($P = 0.001$) | 0.21 | | | |
| | TT ($P < 0.05$) | 0.41 | | | |
| | YZ ($P < 0.001$) | 0.18 | | | |
| YM ($P < 0.001$) | HH ($P < 0.05$) | 0.26 | TG ($P > 0.05$) | DS ($P = 0.001$) | 0.12 |
| | TXX ($P < 0.05$) | 0.24 | | | |
| | TR ($P < 0.05$) | 0.24 | | | |
| | TT ($P = 0.001$) | 0.39 | | | |
| | YZ ($P < 0.001$) | 0.06 | | | |
| YCY ($P < 0.05$) | THY ($P < 0.05$) | 0.30 | GS ($P > 0.05$) | TG ($P < 0.05$) | 0.41 |
| | TRY ($P < 0.05$) | 0.44 | | | |
| | HH ($P < 0.05$) | 0.34 | | | |
| | TT ($P < 0.05$) | 0.41 | | | |
| | YZ ($P < 0.05$) | 0.12 | | | |
| THY ($P < 0.05$) | NA | NA | ZL ($P > 0.05$) | ZB ($P < 0.05$) | 0.40 |
| | | | | TG ($P < 0.05$) | 0.26 |
| TRY ($P < 0.05$) | NA | NA | YRB ($P > 0.05$) | NA | NA |
| HH ($P < 0.05$) | NA | NA | BT ($P > 0.05$) | HT ($P < 0.05$) | 0.21 |
| TH ($P < 0.05$) | HH ($P < 0.05$) | 0.29 | DS ($P > 0.05$) | ZB ($P = 0.001$) | 0.14 |
| TXX ($P > 0.05$) | NA | NA | HT ($P > 0.05$) | ZB ($P < 0.05$) | 0.20 |
| TR ($P < 0.05$) | TH ($P < 0.05$) | 0.24 | TRB ($P > 0.05$) | ZB ($P < 0.05$) | 0.23 |
| | | | | HT ($P < 0.05$) | 0.34 |
| TT ($P > 0.05$) | TRY ($P < 0.05$) | 0.33 | | | |
| YZ ($P < 0.05$) | TH ($P < 0.05$) | 0.09 | | | |
| | TT ($P < 0.05$) | 0.58 | | | |

[a]Individuals are listed in descending hierarchy with $P$ values indicative of their significance among others of the same sex

[b]Preferred association indicates which other individual of the same sex the individual of interest prefers to associate with, as well as a $P$ value indicative of the strength of association between the two

[c]Index refers to the association between two individuals based on the simple association index (Whitehead 2008)

However, the slope for the weighted data was significantly shallower than that for the unweighted data ($t = 3.87$, $df = 253$, $P < 0.001$, see Fig. 2), indicating that the more females involved, the less time was needed in collective decision-making even after group size was factored out.

## Discussion

Using social network analysis, we found that the social network for proximity and grooming interactions during Tibetan macaques' daily activities was significantly correlated with collective movement in three social network metrics, indicating that the social ties remained stable in the contexts of social movements and other daily activities.

The affiliative social network (see Fig. 1) revealed two clusters, demonstrating that high-ranking individuals were more central than low-ranking individuals in the networks. This result is consistent with findings by Flack et al. (2006) and Barrett et al. (2012), both showing that social structures change with the removal of high-ranking individuals. The pattern, however, may not be universal in primate societies. For example, the dominance style of Tonkean macaques (*M. tonkeana*) weakly influences movement behavior and, as a result, individuals tend to be equally likely to join a collective movement (Lusseau and Conradt 2009). In baboons, the removal of high-ranking males may not cause significant changes in grooming and association networks measured by clustering coefficients, suggesting that clusters are not indicative of the strength of social ties (Franz et al. 2015). This may also be the case in our study because the clustering coefficients of the collective movement social network did not correlate with HWI and eigenvector centrality.

Our first hypothesis that females are more socially connected than their male counterparts is supported from three lines of evidence in our study. First, permutation tests revealed a higher level of social connectivity in females than in males, despite the fact that analysis of the



**Fig. 2** Duration of successful movements per proportion of females

affiliative social network alone failed to show differences between the two sexes. Also, the female–female affiliative network showcased significant individuals and social ties, whereas the male–male affiliative network failed to show significant individuals. Finally, the indices of male–male association were not significant, which may indicate that males do not preferentially associate with specific group members. Because Tibetan macaques are matrilineally organized (Xia et al. 2012) and most adult females in our study were first-degree relatives (Li, unpublished data), kinship should be an important factor for the tighter connectivity among females than among males (typically without genetic relationship) in our study group. It is important to note that, while we recorded and analyzed grooming data, the majority of our affiliative data come from proximity measures, which may not fully reflect affiliative interactions (Sueur et al. 2011a). We are testing our results further in this population with additional grooming data (Xia et al. under revision) and data from other affiliative behaviors such as bridging.

What is the evolutionary driver of increase female sociality in Tibetan macaques? Female sociality in this and other species may serve as a counterstrategy against infant-directed aggression (Treves and Chapman 1996; Soltis et al. 2000; Silk et al. 2003, 2009; Silk 2007; Henzi and Barrett 2007; Ogawa 2006; Berman et al. 2007; Self et al. 2013). Berman et al. (2007) found that adult members of our study group redirected their aggression to infants, leading to increased occurrences of serious bite wounds and infant mortality. Self et al. (2013) found that alpha and beta males at our site engaged in more infant-directed aggression than expected by chance. The potential of infant wounding could explain why females tend to band together. For instance, female blue monkeys (*Cercopithecus mitis*) seek protection with other adult females when their infants face danger from adult males (Cords 2002). Female baboons also create strong, persistent bonds with other females in their group, especially with related peers (Silk et al. 1999, 2003, 2006, 2009) to increase their reproductive success (Silk et al. 2003, 2006, 2009). In our dataset, prevention of aggression from high-ranking males redirected toward infants may explain why the two females TH and YH with infants preferred to move together and with lower-ranking male BT, as is shown in the collective movement network.

We found that movements with fewer individuals progressed faster than movements with more individuals (see also Jacobs et al. 2011; Sueur et al. 2011a; Bode et al. 2012). Even so, compared with data unweighted by the number of females, the time needed for the progression of a successful collective movement increased at a slower rate when more females were involved. This result, therefore, supports our second hypothesis that a higher proportion of females facilitated collective decision-making.
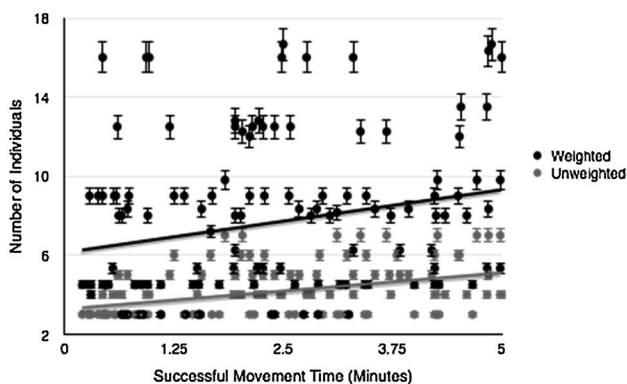
Tradeoffs between speed and accuracy of decisions made are vital to the success of collective movements. Wang et al. (2016) found that Tibetan macaques at our study site participate in a combination of selective mimetism and quorum response depending on the number of individuals involved in the movement. In future studies, we plan to investigate how the participation of Tibetan macaque females, via their social connectivity, can reduce the time required in using mimetism and/or quorum rules for collective decision-making.

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