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Collective decision making in Tibetan macaques: how followers affect the rules and speed of group movement

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Social organisms make collective decisions during group movement, thereby remaining cohesive and providing the ecological and evolutionary benefits of sociality. The ability for groups to make successful collective decisions is dependent on relationships between leaders and followers. We investigated how consistent followers (a fan structure) facilitated successful group movement in a group of Tibetan macaques, *Macaca thibetana*, at Mt. Huangshan in Anhui, China. We used structural equation modelling to determine the relative influences of sex, age, number of maternal familial connections within the group, dominance and social network centrality on the number of fans that an individual had and the number of other group members that an individual was a fan of (fandom). Our structural equation modelling revealed that dominant females had more fans, while younger, dominant individuals with more familial connections were fans of more individuals. Fans and fandom were most strongly influenced by dominance, displaying a strong network of females occupying top positions in the dominance hierarchy who consistently followed each other. In addition, we examined the relationship between fan structure and movement speed and success. Using regression, we found a positive relationship between fans and speed and a negative correlation between fans and number of unsuccessful movements, suggesting a link between the social connections maintained in a movement and the speed of the movement. Dominant females with more fans initiated slower movements, perhaps because the complex fan structure slowed the joining process. However, individuals with more fans led fewer unsuccessful movements, suggesting a relationship between fans and initiation success. Our findings show a network of social relationships within Tibetan macaque groups that are used during movement organization to maintain cohesion and mediate the benefits of sociality.

Sociality can be beneficial to members of a group through reduced predation risks (Cresswell & Quinn, 2004), facilitation of information transfer (Couzin & Krause, 2003) and improved decision making (Ward, Krause, & Sumpter, 2012). To reap such benefits, however, successful decision making by consensus must occur to promote cohesion of the group. This is particularly important in collective movement when group members coordinate their activities.

Consensus in collective decision making can emerge from simple interaction rules (e.g. Ame, Halloy, Rivault, Detrain, & Deneubourg, 2006). This is demonstrated in a variety of organisms, including insects (e.g. Cronin, 2013; Passino & Seeley, 2006), birds (e.g. Farine, Aplin, Garroway, Mann, & Sheldon, 2014), fish (e.g. Sumpter, Krause, James, Couzin, & Ward, 2008), nonhuman primates (e.g. Fernandez, Kowalewski, & Zunino, 2013; Jacobs, Watanabe, & Petit, 2011; Sueur, Deneubourg, & Petit, 2010; Sueur, Petit, & Deneubourg, 2009) and humans (e.g. Pratt & Sumpter, 2006; Sumpter & Pratt, 2009). Although the processes of collective decision making, such as when animals decide on the best resource to exploit (e.g. Beckers, Deneubourg, Goss, & Pasteels, 1990; Deneubourg & Goss, 1989; Mallon, Pratt, & Franks, 2001),

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have been examined, the underlying rules and principles governing the leader–follower dynamics responsible for driving collective decisions remain obscure.

Two hypotheses, quorum and mimetism, have been proposed for how collective decisions are made, with some organisms using a combination of these processes. The quorum hypothesis states that once a certain number of individuals join a movement, a quorum is reached and entire group movement will occur. This mechanism can help promote accuracy and cohesion during group decision making (Passino & Seeley, 2006; Pratt, Mallon, Sumpter, & Franks, 2002; Sumpter & Pratt, 2009) and has evolved separately in many organisms such as bees (Passino & Seeley, 2006), ants (Cronin, 2013) and monkeys (Wang et al., 2015). Alternatively, the mimetism hypothesis proposes an individual's probability of joining a movement increases with the number of individuals who have already joined the movement (Wang et al., 2015). This mechanism is observed during collective movement in such macaque species as Tibetan macaques, *Macaca thibetana* (Wang et al., 2015), Japanese macaques, *Macaca fuscata* (Jacobs et al., 2011) and Tonkean macaques, *Macaca tonkeana* (Sueur et al., 2009). Additionally, in many study systems, such as Tibetan macaques, collective decision making can be driven by a combination of quorum and mimetic factors, and mimetism may aid in achievement of a quorum threshold (Wang et al., 2015).

Tibetan macaques have social relationships that may influence collective decision making during group movements. These primates live in groups with linear dominance hierarchies (Berman, Ionica, & Li, 2004). Groups are female philopatric with males dispersing at maturity, leading to a female-bonded group (Berman et al., 2004; Li, Wang, & Han, 1996). Researchers have found that Tibetan macaques, particularly the YA1 group at Mt. Huangshan, China, have distributed leadership during collective movements and use a combination of quorum thresholds and mimetism. Once a threshold of seven out of 12 members is reached, entire group movement occurs (Wang et al., 2015, 2016). However, initiation success is positively correlated with the degree of social affiliation, which indicates that rules used during affiliative interactions may aid in selective mimetism to achieve successful group movement (Wang et al., 2016).

To further investigate these findings and address the gap in knowledge regarding how followers influence the decision-making process in Tibetan macaques, we dissected the mimetic principles that have been shown to aid in quorum achievement through evaluation of a fan structure consisting of fans and fandom. A fan is an individual who consistently follows a specific individual during movement. Fandom is the number of other group members that an individual is a fan of.

To investigate what parameters make an individual have more fans and what makes one a fan of more individuals, we used structural equation modelling (SEM) to test predicted associations of an a priori model (Fig. 1, see below) against collected data. Discrimination in sex, number of maternal familial connections within the group, dominance and age, along with the association of these parameters with social network centrality, is known to play an important role in the formation of strong bonds in primate groups. As such, we hypothesized that these parameters would influence the degree of fans and fandom for each individual of the group through a network of complex interactions uncovered through SEM (Hypothesis 1). In association with Hypothesis 1, we incorporated the following predictions into creation of an a priori model to be tested using SEM (see Table 3).

Tibetan macaques' female philopatric groups lead to stronger female–female bonds and weaker male–male and male–female bonds (Xia et al., 2012). Male relationships are formed based on reciprocity and creation of alliances for support in the acquisition and maintenance of dominance positions, which influence access to females. Dominance in male primates is influenced by age through the acquisition of top dominance positions by younger males determined through agonistic encounters (Cheney, Seyfarth, & Smuts, 1986). The formation of a strong female-bonded group with the inclusion of weak male–male relationships based on reciprocity and weak male–female relationships based on copulation led to our prediction that a strong association between sex and fans/fandom would exist, with female Tibetan macaques having more kin in the group, thus displaying higher degrees of fans and fandom (Prediction 1).

While maternal kinship, rank, sex and age in primate groups have all demonstrated an influence on rate, direction and degree of

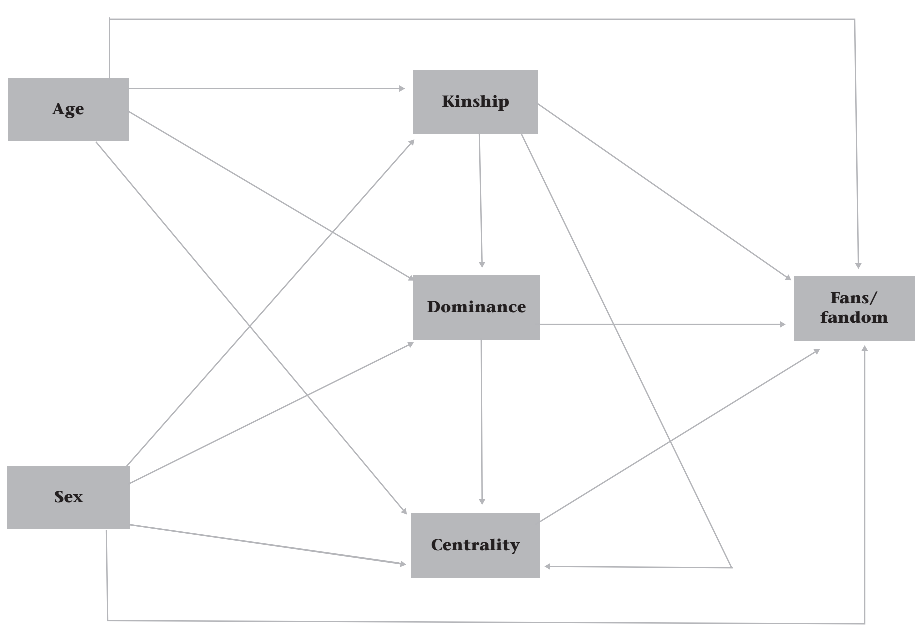

Figure 1. A priori model prediction of the relationship among the number of fans/fandom and age, sex, dominance, centrality and maternal kinship. Boxes represent measured variables and arrows represent hypothesized causal relationships. Based on previous research, strong relationships exist between age, sex, maternal kinship, dominance and centrality that are hypothesized to strongly influence fans and fandom (see Introduction).

reciprocity of interactions, maternal kinship often plays the strongest role in a social network (Silk, Samuels, & Rodman, 1981). The 'kin-biased attractiveness hypothesis' posits that the degree of maternal relatedness influences affiliative relationships (Sade, 1965; Yamada, 1963), and it has support as an important organizing principle of alliance formation and affiliative interactions in female philopatric groups (Bernstein & Ehardt, 1985; Kapsalis & Berman, 1996; Silk, 1982; Widdig, Nurnberg, Krawczak, Streich, & Bercovitch, 2001; Yamada, 1963).

Maternal kinship can lead to more affiliative interactions such as grooming and support during agonistic encounters (Widdig et al., 2001). The formation of strong matrilines influences the acquisition and maintenance of female dominance rank (Berman, 1983; Kawai, 1965; Kawamura, 1965). In female philopatric primate groups, females form dominance hierarchies based on maternal kinship (Berman, Yin, Ogawa, Li, & Ionica, 2008), where entire matrilines rank above or below other matrilines (Kawai, 1958; Missakian, 1972; Sade, 1967). In these groups, where daughters typically are ranked below their mothers and adult sisters are ranked based on age (Kawamura, 1965), female linear dominance hierarchies often remain stable due to the support of these strong matrilineal kin relationships. As such, we predicted that a positive relationship would exist between the number of maternal familial connections within the group and fans/fandom (Prediction 2).

Dominance rank also influences social relationships through an attraction to higher rank (Seyfarth, 1976, 1977), where unrelated female cercopithecids benefit from associating with high-ranking females through reciprocity. Low-ranking individuals attempt to associate with high-ranking individuals (Kapsalis & Berman, 1996; Seyfarth, 1977; Silk, 1982), and rank distance negatively correlates with affiliative behaviours among female macaques (Estrada, Estrada, & Ervin, 1977; Thierry, Gauthier, & Peignot, 1990). In female philopatric primate groups, a distinct relationship exists between maternal kinship and dominance, both of which influence social interactions. Based on these relationships, we predicted that there would be a positive relationship between dominance and fans and a negative relationship between dominance and fandom (Prediction 3).

Strong support also exists in primate groups for the similarity principle, by which individuals most often affiliate with those of similar maternal and paternal kin, age and rank (de Waal, 1991; de Waal & Luttrell, 1986; Silk, Alberts, & Altmann, 2006). Individual macaques who affiliate tend to be closely matrilineally related and close in rank and age (Kapsalis & Berman, 1996). Based on these findings, we predicted that individuals at the core of the social network (highly connected to individuals of varying traits) would be fans of more individuals (Prediction 4).

Additionally, we hypothesized that the revealed interactions among the above parameters would influence collective movement speed and success (Hypothesis 2). In association with Hypothesis 2, we predicted that monkeys with more fans would lead faster movements (time it takes each individual to join) because more individuals would follow the initiator more quickly (Prediction 5) and that monkeys with more fans would lead more successful movements (Prediction 6) (see Table 3). We tested these hypotheses and predictions through observation and subsequent analyses of the YA1 group of Tibetan macaques.

METHODS

Study Subjects and Site

We conducted this study at the Valley of the Wild Monkeys, Mt. Huangshan National Reserve in Anhui, China (30°04′25.1″N, 118°08′59.3″E). This location is a UNESCO World Heritage site, classified as such for biodiversity and cultural reasons, and a popular tourist destination. The terrain is made up of a mountainous ecosystem ranging from scarce vegetation to dense deciduous and evergreen forests. There are several groups of protected Tibetan macaques at this site. At present, no known predators threaten these groups (Berman, Ionica, Dorner, & Li, 2006).

Researchers from Anhui University have monitored the Tibetan macaques at Mt. Huangshan since 1986. In February 1992, wildlife wardens supervised by the local government drove the macaques 1 km from their natural range to an unoccupied area, for tourist viewing (Berman et al., 2006). Since 1986, wardens provisioned the group four times daily and restricted its movement, causing a reduction in range from 7.75 km^2 to <3 km^2 (Li et al., 1996). This range restriction and provisioning led to strong intragroup competition for food, subsequently leading to group fission 1 year after relocation (Berman & Li, 2002). This fission consisted of 10 individuals forming a group (YB) that succeeded in returning to their original range (Li et al., 1996). A second fission occurred in 1996 when nine members of the original group (YA1) also broke off and returned to their original range (YA2) (Berman & Li, 2002).

For this study we observed the Yulinkeng 1 (YA1) group of wild, but habituated, Tibetan macaques. Members of the YA1 group engage in social activity in the forest during the day with no reduced range restriction, but the group is provisioned with 3–4 kg of corn daily at a viewing platform (Berman et al., 2008; Berman & Li, 2002; Xia et al., 2012). Movement from the platform to the forest occurs several times a day, giving us the opportunity to observe collective decision making during group movements. The observation of these macaques since 1986 has allowed for data acquisition regarding individual identities and life histories (Berman & Li, 2002). Information regarding identities, number of maternal familial connections within the group, dominance, age and sex are known and kept by Anhui University researchers. During the study period, the YA1 group consisted of 47 individuals, composed of eight adult males, 13 adult females, four subadult males, six juvenile males, 10 juvenile females and six infants (Table 1).

Ethical Note

Our data collection entailed noninvasive behavioural observation of 47 wild, but provisioned, Tibetan macaques. The Tibetan macaques at Mt. Huangshan were habituated for scientific research beginning in 1986 and provisioned by park staff for tourism beginning in 1992 (Berman et al., 2007). The study group was fed by park staff with 3–4 kg of corn daily during our study period. The research protocols we report in this manuscript were reviewed and approved by Central Washington University's Institutional Animal Care and Use Committee (Protocol No. A121501) and our data were collected through permission of the Huangshan Garden Bureau in accordance with Chinese wildlife laws (in particular Article 6, which prohibits the illegal hunting or catching of wildlife; https://eia-international.org/wp-content/uploads/WPL-Final-Law_translation_July-5-2016.pdf). We collected observational data from a distance of several metres away from the monkeys. We avoided directly looking at subjects and stopped observations if monkeys directed threats towards us. When a focal monkey moved, we observed him or her through binoculars and only followed from a distance of several metres. We did not touch our study subjects and attempted to evade any efforts they made to touch us by maintaining a distance of 1–3 m away from them at all times. In our observational protocols, we followed the rules and regulations published in *Animal Behaviour*.

Table 1
Yulinkeng 1 (YA1) focal animals (adults and subadults)

Individual	Full name	Sex	Age (years)[a]	Rank	Kinship
YRB	YeRongBing	M	7–10	1	2
TG	TouGui	M	11–15	2	5
YH	YeHong	F	11–15	3	4
GS	GaoShan	M	21+	4	0
YXX	YeXiaXue	F	1–6	5	4
BT	BaiTou	M	16–20	6	0
YCY	YeChenYu	F	7–10	7	4
YM	YeMai	F	21+	8	4
TXH	TouXiaHua	F	7–10	9	2
HH	HuaHong	F	11–15	10	1
ZB	ZouBa	M	11–15	11	0
TH	TouHong	F	11–15	12	2
HT	HeiTou	M	16–20	13	0
DS	DuanShou	M	11–15	14	0
YCL	YeChunLong	M	1–6	15	4
TXX	TouXiaXue	F	7–10	16	2
TT	TouTai	F	21+	17	5
HM	HuangMa	M	16–20	18	0
TR	TouRui	F	11–15	19	3
HXM	HuaXiaMing	M	1–6	20	1
TRG	TouRouGong	M	1–6	21	4
YRQ	YeRongQiang	M	1–6	22	2
TRY	TouRongYu	F	7–10	23	4
THY	TouHuaYu	F	7–10	24	5
YZ	YeZhen	F	21+	25	2

[a] Age was either known or estimated by long-term researchers. Individuals were broken into age groups due to questionable exact ages in some group members. Dominance was calculated using the Brown (1975) index. Maternal kinship was calculated through the number of familial connections within a group.

Procedures

We collected data during 26 June–27 August 2016, 6–8 h per day, 6–7 days per week. We conducted all observations from the feeding platforms. We collected data regarding group movement using an all-occurrence sampling method (Altmann, 1974). Focal animals were all adults and subadults of the group, totaling 25 individuals (Table 1). We considered an individual an initiator of a movement when s/he moved >10 m away from the stationary group in less than 40 s (Lusseau & Conradt, 2009; Petit, Gautrais, Leca, Theraulaz, & Deneubourg, 2009; Pyritz, King, Sueur, & Fichtel, 2011; Sueur et al., 2011; Sueur & Petit, 2008). We considered an individual a follower when s/he moved >5 m within a 45° angle of the initiator's movement direction, within 5 min of the initiator (Jacobs et al., 2011; Sueur et al., 2011). We treated each individual who met this rule in relation to the previous follower(s) as a follower. We identified a movement as successful when more than two individuals followed an initiator, unsuccessful when two or fewer individuals followed an initiator within 5 min (Jacobs et al., 2011; Pyritz et al., 2011), and finished when no individual joined the movement within 5 min (Jacobs et al., 2011; Sueur et al., 2011).

During group movement, we recorded the identity of the initiator along with the time of initiation. We recorded the sequence of subsequent followers, and each follower was given a time stamp for when her/his movement began and when movement was completed. We recorded movement data throughout the day when monkeys were approaching or leaving the provisioning area. When group movement was not occurring, we used focal animal sampling (Altmann, 1974) to record affiliative and agonistic interactions to build a social network model and calculate centrality indexes for individuals involved. Our focal samples were 5 min long and were completed per a previously established, randomized sampling schedule.

We assigned focal animals a number (1–25) and scheduled them using a random number generator. We followed the sampling schedule when the individual scheduled was found within 5 min of searching. If the scheduled individual was not found, we moved to the next individual scheduled and returned to the previous individual later. Sampling was completed so that all individuals were sampled an equal number of times throughout the field season.

During samples, we recorded affiliative behaviours (Table 2). The ethogram of behaviours was adapted from previous work on Tibetan macaques (Berman et al., 2004; Ogawa, 1995). Between focal animal samples, we used scan sampling (Altmann, 1974) to record proximity (<1 m) of all visible individuals in relation to one another. Any time when group movement occurred, we switched our sampling back to an all-occurrence method.

During the study period, we completed 972 focal samples, totaling 81 h of focal animal sampling; we completed 953 proximity scans to aid in the construction of a social network; we observed and recorded 1102 group movements, including 410 successful movements and 692 unsuccessful movements.

Analysis: Construction of Fan/Fandom Definitions

We analysed 1102 movements at the dyad scale, breaking down movements into leader–follower dyads, to derive a definition of fans and fandom. Within these movement dyads, we recorded the number of times one individual followed another within 180 s. For example, if individual A initiated a movement, and both individuals B and C followed individual A within 180 s, then we designated A the leader to B and C, B the follower of A and the leader of C, and C the follower of A and B.

We selected 180 s because the majority of the movement data fell within this period. We grouped the totals from this analysis into percentage groups (the percentage of movements that individual A was involved as either an initiator or follower where individual B followed individual A) to determine a threshold of fans and fandom (Fig. 2). These data deviated from a normal distribution above 10%. Values below 10% fit a normal distribution (Anderson–Darling test: $A^2 = 1.0574$, $P = 0.4955$), values over 10% were not consistent with a normal distribution ($A^2 = 0.895$, $P = 0.013$), and the overall data were not consistent with a normal distribution ($A^2 = 1.0574$, $P < 0.01$).

These results suggested a threshold in the data, where below 10% there was a high degree of following throughout the group, while above 10% there was a decline in following and this following was confined to specific individuals. We interpreted this as a threshold representing when consistent following became clear.

Therefore, we defined an individual as a fan when that individual (individual B) followed another individual (individual A) within the first 180 s of movement during at least 10% of movements in which individual A was involved. We defined fandom as the opposite: the number of other group members that individual B followed within 180 s of movement during at least 10% of movements that those individuals were involved in.

These data showed the occurrence of “super fans”, where individual B followed individual A within 180 s during greater than 20% of the movements in which individual A was involved. Due to the occurrence of these “super fans”, we weighted the fan and fandom rate of each individual so as to not mask this important phenomenon in our analysis. We calculated fan indexes through the addition of percentages of time above 10% in which all focal individuals followed individual A, while we calculated fandom indexes through addition of percentages of time above 10% in which individual A followed all focal individuals.

Analysis: Testing a Priori Predictions for Fans/Fandom (Hypothesis 1, Predictions 1–4)

Sociality leads to the development of bonds that can be hierarchical or affiliative. Social network analysis can be used to examine

Table 2
Ethogram of affiliative behaviours recorded during focal animal samples (following Berman et al., 2004; Ogawa, 1995)

Affiliative behaviour	Definition
Agonistic support	An individual joins an ongoing aggressive interaction on the side of one of the opponents. The receiver of support may be either the original attacker or target of the attack. We excluded cases in which the target was human
Co-feeding	A bout in which a focal subject and another individual begin to eat within 1 m of each other
Grooming	One individual orally or manually manipulates the fur of another
Proximity	An individual is within 1 m of another individual
Bridge	A pair of individuals holds an infant between them and simultaneously lick the infant's genital or body while teeth chattering vigorously
Present	One individual displays his or her rump to another
Copulate	One individual approaches from behind and mounts. Thrusting and intromission occur
Social mount	One individual approaches from behind and mounts. A full ankle clasp may be used but there is no thrusting or evidence of intromission
Embrace	One individual approaches another and one or both individuals hold each other and may lightly bite each other

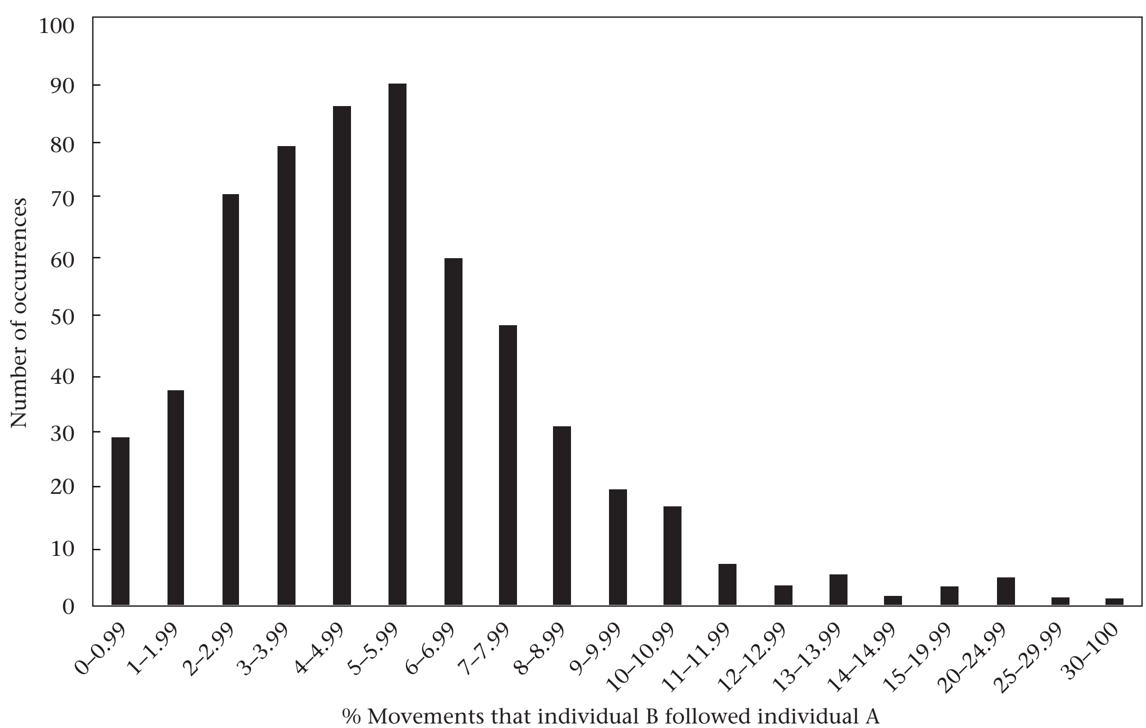

Figure 2. Distribution of occurrences of individual B following individual A within 180 s during a percentage of movements where individual A was involved.

social groups and determine whether differences exist in terms of associations and whether certain individuals are more central to the group (Sueur & Petit, 2008). We collected affiliative, agonistic and movement data to build a social network for the YA1 group. We completed social network analysis using SOCPROG 2.7 (Whitehead, 2009).

Through SOCPROG 2.7, we used group movement data and affiliative data to calculate the half-weight index (HWI). We used HWI matrices to calculate an eigenvector centrality coefficient (ECC) for each individual. A high ECC represents an individual who is connected to many individuals or is connected to others that are highly central (Whitehead, 2008).

Univariate analyses of data are weak in describing systems composed of complex networks of interactions, as in our study group (Grace, 2006; Grace & Keeley, 2006). The evaluation of these complex networks is best completed using multivariate techniques such as structural equation modelling (SEM). SEM is a form of path analysis that models multivariate relationships, allowing researchers to test their data against hypothesized causal inferences based on previous research (Bollen, 1989). Where traditional statistics emphasize the importance of a null hypothesis, SEM places the priority on the a priori model consisting of a network of causal relationships hypothesized by researchers, usually based on previous literature (Grace, 2006). SEM allows for the investigation of both direct and indirect effects of a system on a response variable through the comparison of the covariances of observed variables in a data set to hypothesized covariances (Bowker, Belnap, Davidson, & Phillips, 2005; Grace & Jutila, 1999; Grace & Keeley, 2006).

While traditionally SEM is commonly used in social sciences such as psychology (Breckler, 1990; MacCallum & Austin, 2000) and sociology (Golob, 2003; Regoeczi, 2002), recently it has been used in fields like ecology (Bokoney et al., 2012; Bowker et al., 2005; Grace & Keeley, 2006) and animal behaviour (Yang & Wilczynski, 2002). Using SEM in the field of primatology is a novel approach. To determine the relationship between the fan or fandom assignments and age, sex, dominance, number of maternal familial connections within the group and centrality, we constructed structural equation models (SEM) using SPSS Amos (Arbuckle, 2006).

We used SEM to investigate the network of interactions influencing fans and fandom in the YA1 group. This method of analysis allowed us to determine how measured parameters work collectively to influence fans and fandom within the YA1 group rather than individually investigating each parameter. We created an a priori model of hypothesized pathways based on available literature (Fig. 1, see Introduction). We calculated the Brown (1975) dominance index for each individual through SOCPROG 2.7 using existing agonistic data collected during 13 August 2015–24 May 2016. This metric showed the best fit in the model through preliminary analysis, and it tends to minimize interactions where the actor is the lower-ranking individual (Whitehead, 2008). We either knew age or could precisely estimate it for each monkey (with an error within 1–2 years at most based on our long-term observation of the group). We assigned individuals age groups of 1–6, 7–10, 11–15, 16–20 and 21+ years. We represented maternal kinship as the number of known familial connections within the YA1 group. We selected variables for the structural equation model through the completion of Spearman rank correlation tests, where the variables with the strongest regressions were included in the model.

We placed data in the model to create path coefficients based on correlation values that estimate effect sizes and the direction between variables. The variation explained by the model of each endogenous variable was estimated by R^2 values, the coefficient of variance. We ran all models using a Bollen–Stine bootstrap method with 1000 repetitions. Once the models were complete, we used chi-square goodness-of-fit tests and Akaike's information criterion (AIC) values to determine the best-fitting models. We tested structural equation models using ECC calculated using both affiliative and movement data.

Analysis: Testing Association between Fans/Fandom and Movement Speed/Success (Hypothesis 2, Predictions 5–6)

To determine the relationship between fan structure and speed and success of movement, we performed Spearman rank correlations and regression analyses of fans and fandom against movement speed and rate of success using R statistical programming (R Core Team, 2015).

RESULTS

SEM Parameters

The weighted fan index varied between 0 and 124. The weighted fandom index varied between 0 and 119. Eigenvector centrality coefficient values based on affiliative behaviours ranged from 0 to 0.4 (Fig. 3). Eigenvector centrality coefficient values based on movement data ranged from 0 to 0.23.

The Brown dominance index was selected based on the largest number of strong relationships with fans and fandom. There was a significant negative correlation between fandom and dominance (Spearman rank correlation: $r_S = -0.595$, $N = 25$, $P = 0.002$), meaning that individuals lower in the hierarchy were fans of more group members. There were also strong, but nonsignificant, correlations between total fans and dominance ($r_S = -0.325$, $N = 25$, $P = 0.113$). We dropped all other dominance indexes from the model.

Testing a Priori Predictions for Fans (Hypothesis 1, Predictions 1–4)

The causal scenario of the a priori model was consistent with the data in variation of fans. There were no significant differences in model fit using movement data or affiliative data in calculation of ECC (SEM: $\chi^2{}_3 = 61$, $P = 0.892$, AIC = 36.619). We dropped the movement model to incorporate a broader range of data, accounting for both affiliative (through ECC) and movement (through fans) interactions in the model. The model explained nearly 60% of the variation in fans ($R^2 = 0.598$; Fig. 4). Furthermore, we observed significant positive direct effects of sex on maternal kinship ($R = 0.511$, $P = 0.002$) and fans ($R = 0.794$, $P < 0.001$) and significant positive direct effects of dominance on fans ($R = 0.498$, $P < 0.001$). Total effects, including direct and indirect effects, revealed strong positive effects of sex and dominance on fans ($R = 0.558$ and $R = 0.507$, respectively) and weaker effects of maternal kinship, age and centrality on fans ($R = -0.16$, R = 0.12, $R = -0.02$; Fig. 5).

Testing a Priori Predictions for Fandom (Hypothesis 1, Predictions 1–4)

When investigating variation of fandom within the system, criteria were satisfactorily fitted when using affiliative or movement

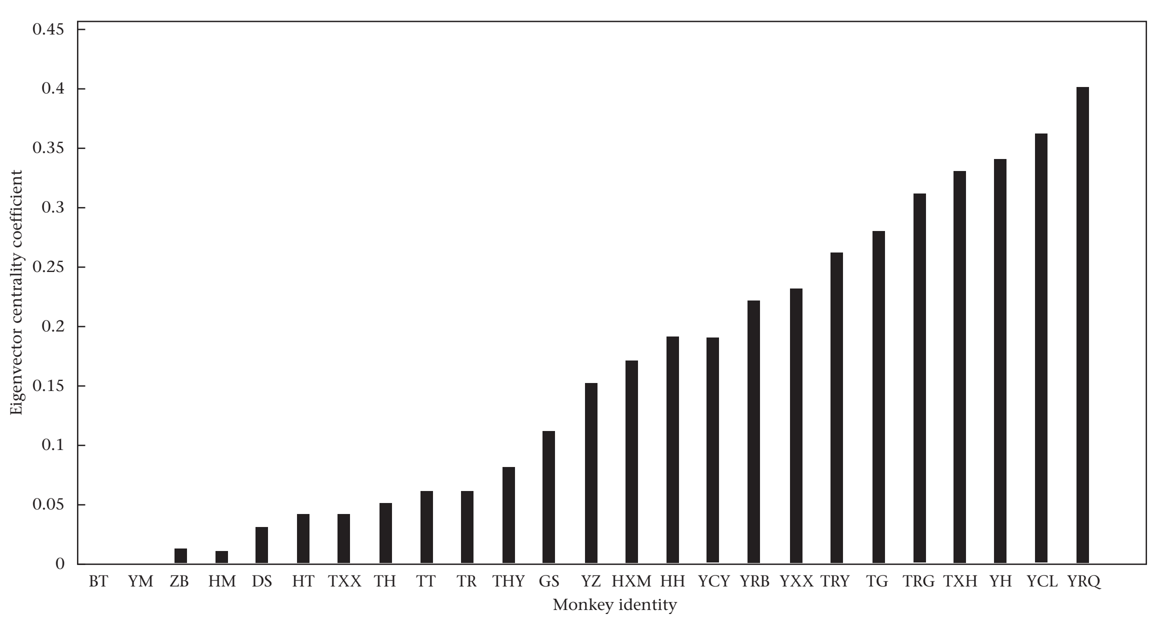

Figure 3. Eigenvector centrality coefficient calculated using affiliative behaviours for each adult or subadult of the YA1 group of Tibetan macaques.

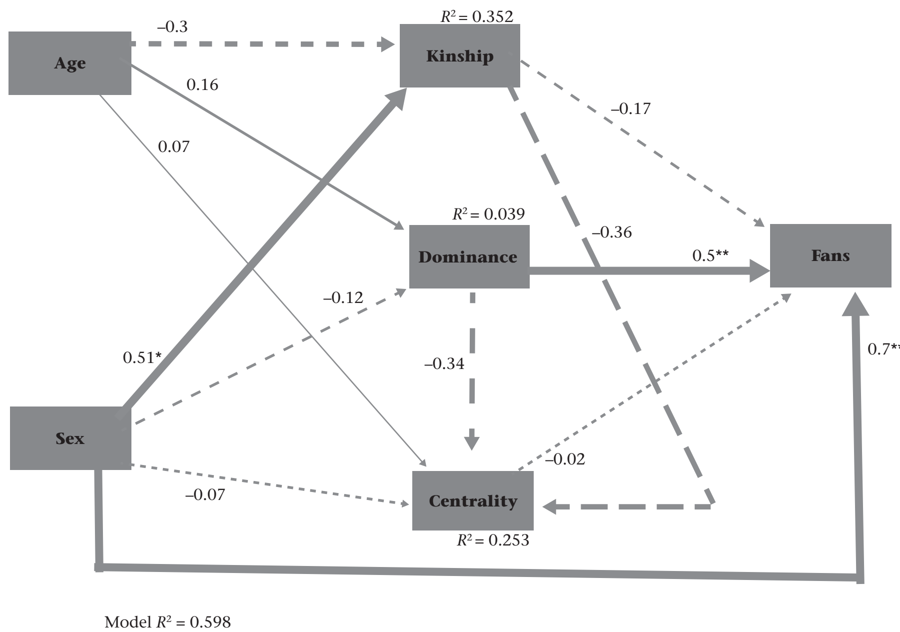

Figure 4. Structural equation model of demographic factors and sociality variable effects on fans built using affiliative data ($\chi^2_3 = 0.619$, $P = 0.892$). Boxes represent measured variables, arrows show regressions within the model and are scaled to effect size (dashed = negative, solid = positive). For the sex parameter, the solid line is female, the dotted line is male. Standardized correlative path coefficients show estimated effect sizes. Percentage variance (R^2) is displayed above each measured variable. Starred pathways were significant (*$P < 0.05$; **$P < 0.01$).

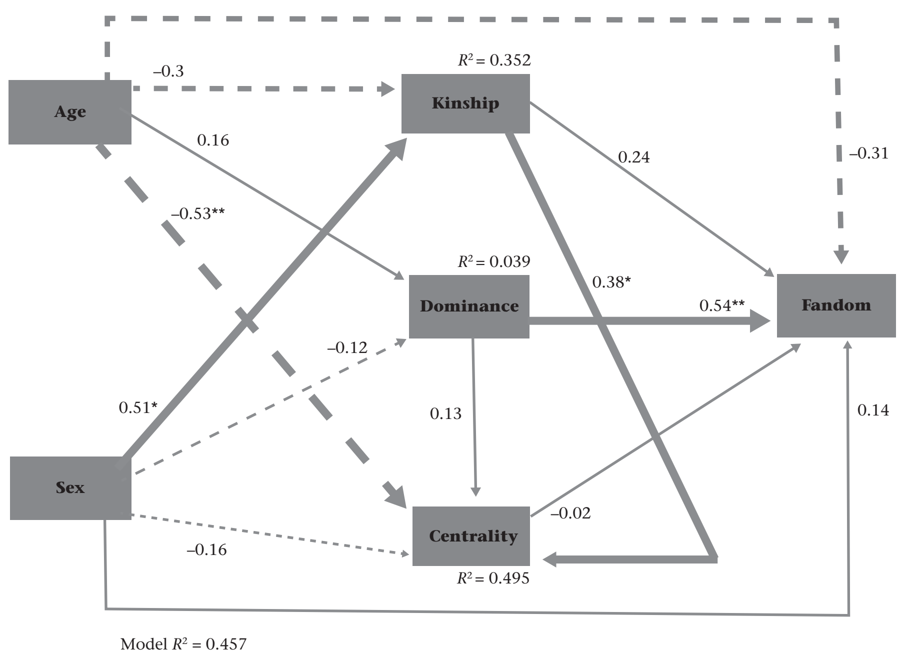

Figure 5. Structural equation model of demographic factors and sociality variable effects on fandoms built using affiliative data ($\chi^2_2 = 0.271$, $P = 0.873$). Boxes represent measured variables, arrows show correlations within the model and are scaled to effect size (dashed = negative, solid = positive). For the sex parameter, the solid line is female, the dotted line is male. Correlative path coefficients show estimated effect sizes. Percentage variance (R^2) is displayed above each measured variable. Starred pathways were significant (*$P < 0.05$; **$P < 0.01$).

data to calculate ECC. There was no significant difference in the fitted criteria or AIC values between the models (SEM: $\chi^2_2 = 0.271$, $P = 0.873$, AIC = 38.271; Fig. 5). As a result, we used the affiliative data in subsequent analysis to incorporate both affiliative (through ECC) and movement (through fans) interactions in the model. There were significant positive direct effects of sex on maternal kinship ($P = 0.002$, $R = 0.511$), of maternal kinship on centrality ($P = 0.034$, $R = 0.582$) and of dominance on fandom ($P < 0.001$, $R = 0.541$). In addition, there was a significant negative effect of age on centrality ($P < 0.001$, $R = -0.526$). Dominance ($R = 0.543$) and age ($R = -0.308$) had the strongest total effects on fandom. Maternal kinship ($R = 0.25$), sex ($R = 0.078$) and centrality ($R = 0.02$) had weaker total effects on fandom. Forty-six per cent of the variation in fandom was explained by the model ($R^2 = 0.457$; see Fig. 5).

Testing Association between Fans/Fandom and Movement Speed/Success (Hypothesis 2, Predictions 5–6)

There was a significant positive relationship between the number of fans that an initiator had and movement speed ($R^2 = 0.402$, $df = 1, 23$, $P < 0.001$), where the more fans an individual had, the slower the movement was. No significant relationship existed between fandom and movement speed ($R^2 = -0.041$, $df = 1, 23$, $P = 0.805$). There was no significant relationship between fandom and the number of successful initiation attempts (Spearman rank correlation: $r_S = 0.137$, $N = 25$, $P = 0.512$) or the number of unsuccessful initiation attempts ($r_S = 0.091$, $N = 25$, $P = 0.664$). Additionally, there was no significant relationship between the number of fans an initiator had and the number of successful initiation attempts ($r_S = 0.122$, $N = 25$, $P = 0.563$). However, we found a suggestive negative relationship between fans and the number of unsuccessful movements ($r_S = 0.367$, $N = 25$, $P = 0.072$).

DISCUSSION

We found a significant relationship between sex and the number of familial connections within the group in all structural equation models, with females having more familial connections within the group. This is consistent with the social characteristics of Tibetan macaque groups, where male dispersion and female philopatry lead to a female-bonded group that is essential to its stability (Berman et al., 2004; Li et al., 1996; Xia et al., 2012). Since females remain in their natal group their entire lives, they will have more kin in the group than do males. The relationship between sex and maternal kinship played an important role in the total effects of these variables on fans and fandom.

Fans (Hypothesis 1, Predictions 1–4)

In our study, we found that sex and dominance best described the variation in fans (Fig. 4). There were both direct and overall effects of sex on fans for females, which had more fans than did males (Table 3). This is consistent with a female philopatric group, where females who remain in the same group their whole lives tend to build strong, stable bonds with other females (Berman et al., 2004; Li et al., 1996; Xia et al., 2012). The significant direct and overall effects of dominance on fans indicates that more dominant individuals had more fans (Table 3). This was evident by dominant females within the YA1 group having the most fans. In addition, the complex fan structure may have facilitated achievement of higher dominance positions, suggesting that a network of social rules are used during social interactions within and outside of movements. This is consistent with recent findings showing that, within the YA1 group, a relationship exists between social affiliation and movement initiation success (Wang et al., 2016).

Female linear dominance hierarchies are matrilineal, and females use information regarding rank and maternal kinship during social interactions (Berman et al., 2008). Maintenance of these relationships is often completed through grooming, which takes up about 20% of females' total activity budget (Wang, Yin, Yu, & Wu, 2007). These behaviours are thought to promote cohesion and reduce conflict to maintain the social structure (Xia et al., 2012). The finding that dominant females had the most fans is consistent with this female-driven social structure, which is essential to the stability of Tibetan macaque groups and shows that this hierarchical, female-bonded group was maintained to aid in completion of faster, successful movements.

Fandom (Hypothesis 1, Predictions 1–4)

The variation we observed in fandom was best described by a direct positive relationship between dominance and fandom, and total effects of dominance, age and maternal kinship on fandom. Indirect effects of maternal kinship on centrality and of age on centrality, fandom and maternal kinship also existed (Fig. 5). There were both significantly positive direct and overall effects of dominance on fandom, suggesting that more dominant individuals were fans of more individuals (Table 3). Thus, the results suggest a highly connected group where not only do dominant individuals have more fans, but they are also fans of more individuals. In female philopatric primate groups, females form dominance hierarchies based on maternal kinship (Berman et al., 2008), where entire matrilines rank above or below other matrilines (Kawai, 1958; Missakian, 1972; Sade, 1967). The formation of strong matrilines influences the acquisition and maintenance of female dominance rank (Berman, 1983; Kawai,

Table 3
Summary of analysis outcomes

Hypothesis	Prediction	Statistical test	Supported by analysis?
(1) Sex, number of maternal familial connections within the group, dominance rank, age and social network centrality would influence the degree of fans and fandom for each individual of the group through a network of complex interactions uncovered through structural equation modelling	**(1)** A strong association between sex and fans/fandom will exist, with female Tibetan macaques having more kin in the group, thus displaying higher degrees of fans and fandom	Structural equation modelling	**Yes**: Females had more maternal kin in the group and displayed a higher degree of fans/fandom
	(2) A positive relationship would exist between the number of maternal familial connections within the group and fans/fandom	Structural equation modelling	**Partial**: Individuals with more maternal familial connections in the group had fewer fans but displayed a higher degree of fandom
	(3) There would be a positive relationship between dominance and fans, and a negative relationship between dominance and fandom	Structural equation modelling	**Partial**: Dominant individuals had more fans, but dominant individuals also displayed a high degree of fandom
	(4) Individuals at the core of the social network would be fans of more individuals	Structural equation modelling	**Partial**: While nonsignificant, individuals with higher centrality were fans of more individuals
(2) The revealed interactions among the above parameters would influence collective movement speed and success	**(5)** Monkeys with more fans would lead faster movements	Regression analysis	**Not supported**: Individuals with more fans led slower movements
	(6) Monkeys with more fans would lead more successful movements	Spearman rank correlation analysis	**Partial**: Individuals with more fans did not lead more successful movements, but they had fewer failed initiation attempts

1965; Kawamura, 1965). The result of dominance playing a strong role in both fan and fandom reflects highly connected, likely matrilineal social groups that occupy the top positions of the dominance hierarchy and travel consistently together. For example, during the collection period, the "Ye" matriline occupied the top positions of the hierarchy (Table 1), and Ye members were often seen travelling together.

Individuals that occupied top positions in the hierarchy and that were seen associating and moving together were often individuals of similar age, specifically young females with similarly aged infants. This is consistent with the similarity principle, by which individuals most often affiliate with those of similar maternal and paternal kin, age and rank (de Waal, 1991; de Waal & Luttrell, 1986; Silk et al., 2006). Overall, individual macaques that affiliate tend to be close maternal kin and close in rank (Kapsalis & Berman, 1996), and a similarly strong connection between rank and fans/fandom was evident in our data set.

The strong negative overall effects of age on fandom suggests that younger individuals were fans of more individuals. Our finding that younger individuals consistently followed a variety of individuals and therefore had a higher fandom rate is consistent with both the attraction to higher rank hypothesis (Seyfarth, 1976, 1977) and the similarity principle (de Waal, 1991; de Waal & Luttrell, 1986; Silk et al., 2006). Young individuals of lower rank attempt to associate with higher-ranking individuals to benefit from reciprocity (Seyfarth, 1976, 1977), but they also consistently interact with individuals of their own age and rank (de Waal, 1991; de Waal & Luttrell, 1986; Silk et al., 2006). In our study, this behaviour was often seen in subadult males (Table 1), which consistently affiliated and travelled together, but were also seen interacting and travelling with higher-ranking individuals and kin. This interaction with a variety of individuals would lead them to have a higher fandom rate than older individuals. This might also lead them to be more central to the group, because they would be more connected to a variety of individuals.

The strong total effects of maternal kinship on fandom suggest that individuals with more familial connections were fans of more individuals (Table 3). Since individuals affiliate most with those of similar maternal and paternal kin (de Waal, 1991; de Waal & Luttrell, 1986; Silk et al., 2006), individuals with more kin in the group will have more individuals to consistently interact with and follow. Along with this, having more kin increased the connectivity to individuals of various rank and age, which would increase their centrality (Table 3). Therefore, individuals with a high number of familial connections would likely be older and more central and be fans of more individuals.

Fans/Fandom and Movement Speed/Success (Hypothesis 2, Predictions 5–6)

Our prediction that individuals with more fans would lead faster movements was not supported (Table 3). A significant relationship between fans and movement speed suggests that the more fans an individual had, the slower the movement in terms of how long it took for each individual to join the movement. The highly connected network of fans and fandom constructed through female-dominant matrilineal bonds hindered progress of the movement. A lag in joining occurred when individuals were waiting for their fans or waiting for individuals that they were fans of to join the movement, which influenced movement speed. If an individual had few or no fans, he or she left the group without caring who was following, while an individual with many fans needed to stop consistently to wait for their network of fans, slowing the movement. This finding is consistent with a previous unpublished study (Frattelone, 2015) at this site showing that it takes more time for movement to be completed when there are more individuals involved in a movement.

Wang et al. (2015) found that Tibetan macaques used a combination of mimetism and quorum thresholds in collective movements. In our study of the same population, the strong network of connections between fans may have complicated the process of selective mimetism at the beginning of a movement if top individuals wait for the entire network to move before they begin moving. However, although slow, the fan/fandom network suggests that selective mimetism is likely used when deciding when to join a movement. This selection process may allow for a quorum threshold to be reached so that movement by the entire group can occur.

While no other significant relationships existed between movement dynamics and fans/fandom, we found a negative relationship between the number of fans and the number of unsuccessful movements, suggesting that individuals with more fans initiated fewer unsuccessful movements (Table 3). Therefore, while having more fans may decrease speed, it may also decrease the number of failed movements that an individual initiates, displaying a strong link between fans and initiation success, which should be further investigated. Our findings show that individuals with more fans played a vital role in successful group movement and maintaining cohesion within the group.

Conclusions

Tibetan macaque groups are highly organized, and during our study, they displayed a network of parameters that influenced affiliative interactions and decisions about when and how to move. SEM showed that dominant females within the YA1 group had the most fans and therefore the most individuals who consistently followed them. However, dominant individuals were also fans of more individuals, reflecting a highly connected network of individuals occupying the top ranks of the dominance hierarchy. These individuals also tended to have more familial connections within the YA1 group, consistent with studies showing that matrilines that occupy the top ranks of the group most often affiliate and move together (Berman et al., 2008; Kawai, 1958; Missakian, 1972; Sade, 1967). In addition, young individuals tended to be fans of many individuals, due to their need to interact with kin and with individuals of higher rank and of similar rank (de Waal & Luttrell, 1986; Kapsalis & Berman, 1996; Seyfarth, 1977; Silk, 1982).

This highly connected group structure may have hindered overall movement speed, as all individuals of a fan/fandom network had to join before moving could commence, but it also may have influenced initiation success. This social network aided in decisions regarding selective mimetism and allowed the group to reach a quorum threshold stimulating entire group movement. The trade-off between movement speed and initiation success should be further investigated.

In conclusion, studying collective decision making during group movement through the lens of fans/fandom can help us to understand whether relationships observed in affiliative interactions are maintained in the structure of collective movements. Furthermore, our use of SEM in this study proves a powerful tool to study these complex primate social networks. Applying these methods to other primate and nonprimate groups may allow further insights into social relationships within groups and how these relationships facilitate group cohesion during movement. Additionally, these methods have the potential to disentangle the parameters most greatly influencing leader–follower dynamics and collective movement in previously studied systems (e.g. King, Douglas, Isaac, Huchard, & Cowlishaw, 2008; King, Sueur, Huchard, & Cowlishaw, 2011; King & Sueur, 2011).

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