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Coordination and consensus: the role of compromisers in Tibetan macaques

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Abstract

Coordination and consensus in collective behavior have attracted a lot of research interest. Although previous studies have investigated the role of compromisers in group consensus, they provide little insight into why compromisers would allow such social arrangements to persist. In this study, the potential relationship between group movements and conflict management in Tibetan macaques in Anhui province, China, was investigated using hierarchical cluster analyses. Some members with higher social centrality or social rank often formed a front-runner cluster during group movements. They had higher leadership success than individuals outside the front-runner cluster. Other members with lower social centrality or social rank often followed the group movements initiated by the front-runner cluster, and thus formed the compromiser cluster. Compromisers' proximity relations with front-runners increased with their following scores to front-runners. Compromisers had fewer events of being attacked when they followed group movements initiated by the front-runners. The compromising process made compromisers lose the choice of direction preference, but it could increase their individual safeties. This trade-off suggests that compromisers play a role of decision-maker in coordination and consensus scenarios among social animals.

Key words: collective decision-making, coordination, compromise, Tibetan macaque, trade-off.

In group-living animals, multiple members often have different nutritional demands, habitat selection, and the capacity to control resources (Hansen et al. 2015a, 2015b; Lihoreau et al. 2015; Muller et al. 2018); thus, their preferences on direction and timing of group movements also differ from each other (Kingma 2018). They must coordinate their actions to obtain benefits of group living, such as reducing predation threats and allowing for the exchange of social information (Chapman and Chapman 2000; Majolo et al. 2008). However, group living also has its disadvantages, including competition over foods (Miller et al. 2020) and mates (Thompson 2013). If some individuals favor their own choices above those of others in their society, it might cause a decrease in the group cohesion, by increasing antagonism and reducing affiliation, and eventually, make all group members lose the benefits of group living (Paukner and Suomi 2012; Dorning and Stephen 2017; Markham and Gesquiere 2017).

In group movements, a consensus process is often known as when "members of a group choose between 2 or more mutually exclusive actions with the specific aim of reaching a consensus" (Conradt and Roper 2005, p. 449). All group members usually have opportunities to affect the decision-making process in large collectives, but they play disproportionate roles (Solum et al. 2014; Ward et al. 2018). For example, bold homing pigeons *Columba livia* show a high propensity to lead a group movement, and they can arrive at

safe locations more quickly than less exploratory individuals (Sasaki et al. 2018). When individual choice deviates from optimality criteria for movement destination, conflicts of interest occur (Alexander 1974; Smith et al. 2015). Coordination in groups (leadership, overtaking, followership, and choice of distances: Pyritz et al. 2011) often imposes consensus costs on some group members (Conradt and Roper 2009). Consensus costs are defined as "members incurring reduced fitness by forgoing their own optimal action to comply with the decision outcome" (Conradt and Roper 2005). These costs can range from mild discomfort to danger to survivorship. For example, in spotted hyenas *Crocuta crocuta*, followers often spend extra time to provide services to dominating leaders, by helping in hunting and cooperative defense of resources (Boydston et al. 2001; Smith et al. 2015). Further, subordinate chacma baboons *Papio ursinus* usually accept despotic decisions, even where this forgoes their optimal activity options (King et al. 2008). In general, a conflict of interest is regarded as a disadvantageous occurrence that raises obstacles to collective decision-making (Solum et al. 2014). Therefore, social animals have taken some actions to reduce conflicts within groups.

Conflicts can be resolved effectively through compromise, especially in cases of "when" and "where" decisions (Solum et al. 2014). Under such situations, some members must strike a balance between group and individual benefits by decreasing their optimal choices about direction and timing, thus they can be considered as compromisers. For example, Sankey et al. (2019) found that despite substantially lower body mass, female homing pigeons are not slower than the males in flocking, suggesting that both sexes coordinate their solo speed and then their groups fly at averaging speeds. Speed compromise can maintain cohesion for groups and reduce energetic costs for individuals (Sankey et al. 2019). Wild olive baboons *Papio anubis* move in the average of suggested destinations (i.e., compromise) when the angle between initiators' directions falls below 90° (Strandburg-Peshkin et al. 2015). Moreover, in European bison *Bison bonasus*, juvenile compromisers prefer to follow the direction of adult females even if this direction is not their optimal choice; compromisers allow adult females to initiate several successful group movements and direct most movements within the herd/group (Ramos et al. 2015). The compromising process generates stronger group vigilance (Janson and Goldsmith 1995) and reduces aggression by conspecifics (L'heureux et al. 1995). Generally, compromise processes are somewhat common in collective behavior and play a role in group consensus.

While previous studies highlighted the role of compromisers in group consensus, they provided little insight into why compromisers would allow others to initiate and lead group movements. Specifically, it is unclear how compromisers determine the trade-offs between gain and loss of individual benefits. Such analyses require experimental manipulation of animal groups, which is currently lacking in the field.

We conducted the present study on a group of free-ranging Tibetan macaques *Macaca thibetana* who often switch their location from a provisioning area (i.e., foraging site) to the forest (i.e., social arena). Monkeys have different directional options before the group departs (Figure 1). Some individuals follow a direction that other members might not (Wang et al. 2015). Consensus decisions may need group members to determine a common direction, timing, or destination of group travel. Potential conflicts of interest in Tibetan macaques represent consensus costs. Individuals must regularly negotiate conflicting interests among group mates that vary in their optimality criteria (Wang et al. 2020). This prerequisite requires the
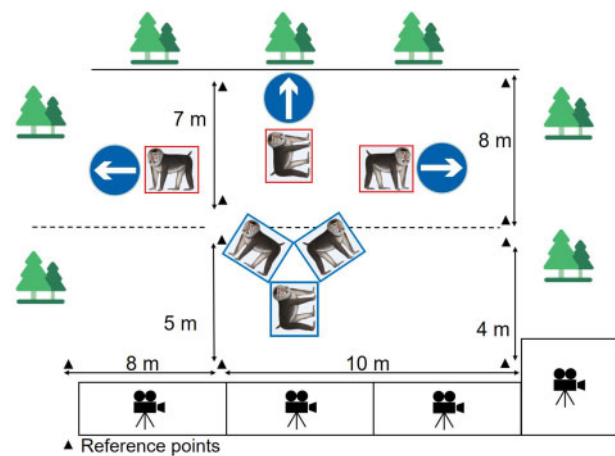

Figure 1. Diagram of the feeding site and 3 potential directions that the Tibetan macaques could take to reach the forest. Monkeys in the red box are the "front-runners" and individuals in the blue box are the "compromisers."

majority of group members to choose between collective decisions and individual choice, representing a compromising process.

Previous studies showed that all adult Tibetan macaques could successfully initiate group movements and distribute the leadership during group movements (Wang et al. 2016). However, the decision-making process not only refers to the first movers' initiation but also includes other participants' involvement in the movement. Thus, one needs to fully explore group movements in this species and understand the members (e.g., compromisers) that might influence the entire decision-making process.

During the study period (August to December of 2012) which coincided with the mating season, Tibetan macaques would compete over mates or social status (Li 1999). Monkeys showed intense aggressive events in the context of mating competition. Meanwhile, monkeys exhibit a series of conflict management behaviors, for example, conflict avoidance (Li 1999); hence, avoiding additional conflict caused by conflicts of interest in movement decisions could increase individual benefits. In this paper, we hypothesized that compromisers would forgo preferences of movement direction, and this trade-off would avoid attacks from opposers of direction in Tibetan macaques. Thus, different group members might play their corresponding roles within subgroups in a group movement. Hierarchical cluster analysis is particularly suitable when a social organization can be resolved into a structure of embedded hierarchical levels, such as "families" within "groups" (Whitehead 2009). Accordingly, using hierarchical cluster analysis, we provided some predictions as follows.

P1a: Monkeys would form consistent clusters (tend to move together) during group movements. P1b: The individuals in the same cluster would share some tendencies, such as leadership success, following times, social centralities, social rank, or age. P2: The individuals in 1 cluster would engage in more proximity relations with another cluster to increase social affiliation. P3: The cluster following another on its group departure would decrease the risk of being attacked by that cluster and eventually increase individual benefits.

Materials and Methods

Study site and subjects

From August to December 2012, we investigated a group (Yulinkeng 1, YA1) of Tibetan macaque at Mt. Huangshan, China.

During our study, the YA1 group moved freely in the forest, but to facilitate sightseeing, monkeys were supplied daily with corn (the total amount was less than 4 kg) by park rangers at the provisioning area (Berman and Li 2002; Berman et al. 2008; Usui et al. 2014). When corn was consumed, Tibetan macaques could move their location from the feeding site to the surrounding forest. There were 3 potential directions before group departure (Figure 1).

The YA1 group consisted of 32 members, and we selected all adults as our focal animals (Table 1) including 4 adult males and 8 adult females. All 12 adults could be identified by their unique physical characteristics such as face shape, body appearance, or hair color (Li 1999; Xia et al. 2012).

Data collection

We observed the YA1 group for 7 h daily, which included provisioning activities. The total observation time was 104 days, with 219 observed cases of group departure. Once the macaques shifted from the provisioning area to the forest, we recorded group departures using video cameras (Canon EOS 550D, Canon, Tokyo, Japan) with an all occurrences sampling method (Altmann 1974). The provisioning area was marked with reference points (Figure 1). This allowed us to measure the exact movement distances of Tibetan macaques. The chaotic movements triggered by conflict events or sexual chases were not included in our data (Sueur and Petit 2008).

Initiation attempts were only recorded when two-thirds of the group members (i.e., the majority of group members) were present in the provisioning area. We used the following behavioral definitions for collecting data on group movement (Wang et al. 2015, 2016): 1) an initiation attempt: a situation where 1 individual rushed more than 10 m in less than 30 s from the provisioning area toward the surrounding forest. We called this first individual the "initiator"; 2) the following behavior: within 5 min of the initiator's first move, the action of any individual that walked more than 5 m and less than 45 degrees of the orientation proposed by the initiator (Sueur and Petit 2008). Individuals could start to follow in any position of the provisioning area. The same criterion of 5 min was used for the time limit of each successive joiner during group movements; and 3) a successful initiation of group movement: the movement included at least two-thirds of the YA1 group members.

To record conflict events among the 12 adults, we carried out 10-min focal samples (Altmann 1974) when they engaged in social activities in the forest. Aggressive acts included staring, chases, slaps, grabs, and bites, whereas submissive acts included displaying bared teeth, mock leave, avoidance, fleeing, and screaming (Li 1999;

Berman et al. 2004). To document social affiliation among the 12 adults, we also used a 10-min focal sampling method to record the duration of a focal subject's proximity to other adults within 1 m (Li 1999; Berman et al. 2008).

Data analysis

We measured leadership success and the following score using a standardized number of successful initiations and following behavior, respectively. The standardized number was calculated as: $X'_i = X_i/T_i \times 1{,}000$, where X'_i is the standardized number for leadership or following for individual i; T_i is the number of times individual i was recorded; and X_i is the number of successful initiations or following of individual i (Jacobs et al. 2011; Wang et al. 2016).

To test whether there were any clusters during group movements, we used SOCPROG 2.4 (Whitehead 2009; Funkhouser et al. 2018) to conduct a hierarchical cluster analysis based on the data of half-weight index (HWI) matrices (Borgatti et al. 2002). HWI is determined by dividing the number of times 2 individuals occurred in the same group movement with the total number of group movements (Cairns and Schwager 1987).

We also calculated the eigenvector centrality coefficient via HWI matrices using SOCPROG 2.4. Eigenvector centrality coefficient measures how closely associated an individual is to others in group movements (Wang et al. 2015, 2020). A higher score of the eigenvector centrality coefficient indicates that the individual possesses more movement partners (Newman 2004). The eigenvector centrality of each individual was calculated from a network based on HWI matrices every month (August–December 2012). If we eliminated 1 individual from the network and calculated centralities, the values would differ from previous ones. Thus, those matrices were not regarded as independent of each other. To compare the differences of eigenvector centralities of individuals from different clusters, we ran the permutational multivariate analysis of variance (PERMANOVA) in the vegan package (version 2.5-7) of R version 3.6.1.

We scored every adult's joining order by the following formula: $1 - [I - 1/N - 1]$, where I is the position of the joining process occupied by the individual and N is the number of movement participants (Barelli et al. 2008). The index ranges from 1 (first position) to 0 (last position).

The dominance rank of the 12 adults was based on a David's score (Gammell et al. 2003) which classifies aggressive/submissive interactions (Li 1999; Zhang et al. 2014). The individual with a higher David's score was more dominant in the group.

Table 1. Characteristics of focal Tibetan macaques in the Yulinkeng 1 (YA1) group during observation

Individual	Sex	Dominance rank	David's score	Age	Leadership success	Focal duration (s)
TG	Male	1	64	9	44	55,200
ZL	Male	2	45.27	12[a]	24	55,200
GS	Male	3	44.63	28	52	54,600
YH	Female	4	26.04	9	26	55,200
BT	Male	5	9.96	20[a]	15	55,800
Hhui	Female	6	6	7	44	54,600
YM	Female	7	−6	22	76	55,800
TH	Female	8	−7.22	9	106	55,800
HH	Female	9	−26.35	9	24	55,800
TR	Female	10	−41	8	15	55,200
TT	Female	11	−53	21	44	55,200
YZ	Female	12	−62.33	20	33	54,600

[a] These 2 individuals were immigrants from other groups. Their ages were estimated based on physical features (Li 1999; Xia et al. 2012).

In addition, we used the Mann–Whitney U-test to compare the variation between 2 independent samples and Spearman rank correlation to analyze the relationship between 2 series of samples. These statistical analyses and calculations were performed using the SPSS 26.0 software (SPSS Inc., Chicago, IL, USA).

Results

We verified whether adults formed subgroups when they participated in collective movements. Accordingly, we drew a social network among individuals during group movements (Figure 2). A red line between 2 individuals indicates a closer association during group movements than a blue line.

A dendrogram was prepared with the 12 adults on the ordinate and the degree of associations between these individuals on the abscissa (Figure 3). Adults were divided into 2 subgroups: 1) cluster A (including individuals GS, YM, TG, TH, ZL, YH, and Hhui) and 2) cluster B (including individuals BT, YZ, TR, TT, and HH).

The mean joining order of the individuals in cluster A was more significant than that of individuals in cluster B (Mann–Whitney U-test: $N_A = 7$, $N_B = 5$, $Z = -2.937$, $P < 0.01$, Figure 4). The average value of joining orders (0.42 ± 0.13) was in between the 2 clusters. This indicated that individuals of cluster A were more often in the first half positions (i.e., front-runners) than those of cluster B (i.e., compromisers) during group departures.

Individuals in cluster A had higher leadership success than did those in cluster B (Mann–Whitney U-test: $N_A = 7$, $N_B = 5$, $Z = -1.970$, $P < 0.05$, Figure 5). Individuals in cluster A also had higher values of the eigenvector centrality coefficient (social centrality) than did those in cluster B (PERMANOVA: $F = 10.742$, $R^2 = 0.518$, $P < 0.001$). Moreover, individuals in cluster A were higher in social rank than were those in cluster B (Mann–Whitney U-test: $N_A = 7$, $N_B = 5$, $Z = -2.355$, $P < 0.05$). However, there was no significant difference in age between individuals of cluster A and B (Mann–Whitney U-test: $N_A = 7$, $N_B = 5$, $Z = -0.166$, $P > 0.05$).

Duration percentage of proximity between clusters A and B was more significant than that within cluster B (Mann–Whitney U-test: $N_{A\&B} = 12$, $N_B = 5$, $Z = -2.355$, $P < 0.05$). This indicated that individuals in cluster B (compromisers) increased social affiliation with cluster A (front-runners) more often, but not with group

members in their cluster. Moreover, the duration percentage of proximity of the 5 individuals in cluster B toward members of cluster A during the 5 months (August–December 2012) was positively correlated with the following score of cluster B (Spearman rank correlation: $r_s = 0.637$, $N = 25$, $P 0.01$, Figure 6). Individuals who were more likely to follow could stay closer to front-runners more often than those who were unwilling to follow.

The frequency of aggression of cluster A toward members of cluster B was negatively correlated with the leadership success of cluster A (Spearman rank correlation: $r_s = -0.623$, $N = 35$, $P < 0.01$, Figure 7). Additionally, there was a negative correlation between the following score and the frequency of being attacked when cluster B followed more group movements initiated by cluster A (Spearman rank correlation: $r_s = -0.568$, $N = 25$, $P < 0.01$, Figure 8). These results indicated that the whole aggression rate by individuals of cluster A toward those of cluster B decreased when individuals of cluster A had more successful initiations.

Discussion

In this study, we examined the role of compromisers in coordination and consensus using hierarchical cluster analyses in free-ranging and provisioned Tibetan macaques. We also answered why and how compromisers made a trade-off between direction preference and individual safety in the social contexts of group movement and conflict management.

Tibetan macaques in this study formed 2 subgroups during their group movements. The subgroup often ahead during group departure was called the front-runner cluster and the other following this subgroup was called the compromiser cluster. Our results are consistent with observations cited in previous studies. For example, in Pekin ducks *Anas platyrhynchos*, the same class of individuals initiates most group movements and group cohesion is high when another class of members preferentially follows them (Liste et al. 2015). Further, consistent controllers of movement direction are found in zebra finches *Taenopygia guttata*; however, this control is not static and it could be shifted to other foraging pairs (Beauchamp 2000). In the present study, we used a hierarchical cluster analysis to show that a group of Tibetan macaques moving together could make a collective decision on 3 directions of motion, even with a potential conflict between the directional preferences of 2 small subgroups of front-runners and compromisers.

In our study, individuals who engaged in proximity relations with front-runners more often also followed more frequently. This could be an advantage for group cohesion. For social animals, it is widely recognized that collective decision-making arises from social interactions between group members (Dyer et al. 2009) and, therefore, the priority is to maintain affiliated relationships with controllers of group movement. For example, in free-ranging dogs *Canis lupus*, habitual followers develop significantly closer spatial associations with habitual leaders during resting, and group movements benefit from the effort of followers to maintain close proximity with specific valuable social partners (Bonanni et al. 2010). Moreover, before and during group progressions, Verreaux's sifakas *Propithecus verreauxi* followers often emit vocalizations to leaders at high frequencies that can provide information about spatial distances between individuals and help to maintain group cohesion (Trillmich et al. 2004). Here, Tibetan macaque compromisers were more often in proximity with front-runners than with other compromisers. We considered that in Tibetan macaques, group members in the
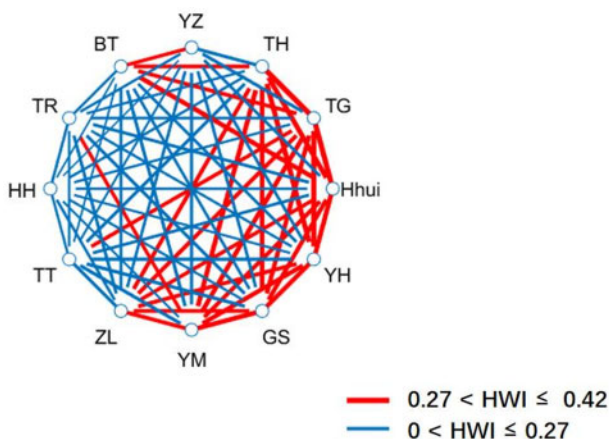

Figure 2. Social network among 12 Tibetan macaque adults during group movements. Line thickness is proportional to HWI values. The average value of HWI is 0.27 and the maximum value of HWI is 0.42. Lines are classified as blue color if $0 < HWI \leq 0.27$, and as red color if $0.27 < HWI \leq 0.42$.
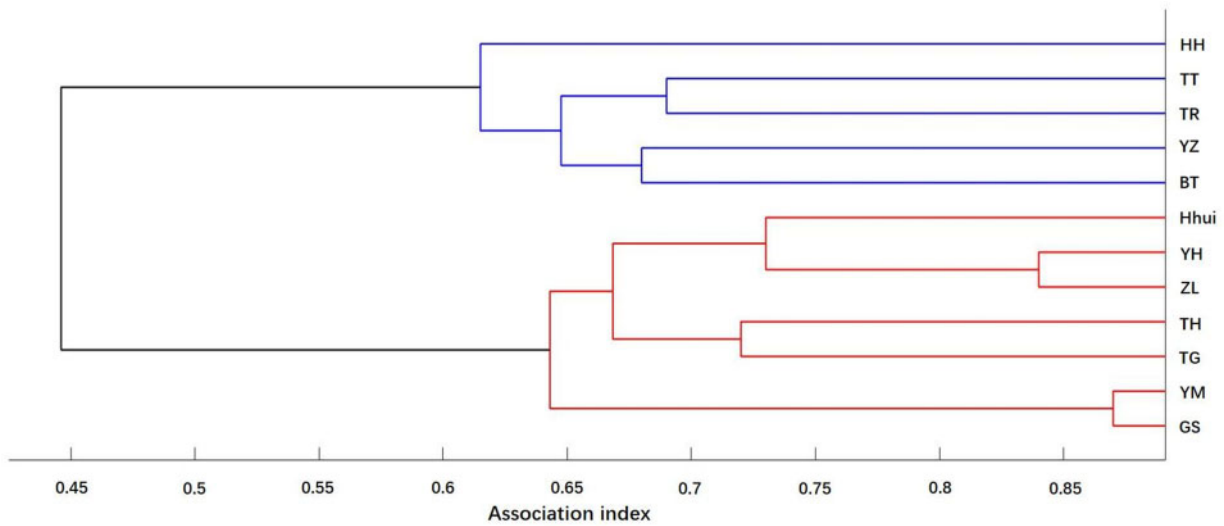
Figure 3. Hierarchical cluster analysis for 12 adult Tibetan macaque individuals during group movements (indicated on the ordinate). The association index estimates the proportion of time that 2 individuals spend together during group movements. The dendrogram indicates that all adult individuals can be divided into 2 clusters (i.e., 1 cluster in red and another in blue).
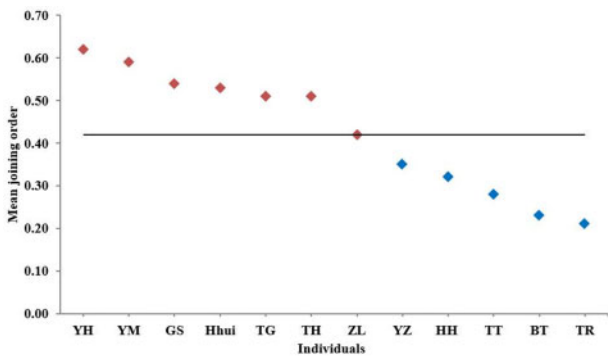

Figure 4. Mean joining order of the 12 Tibetan macaque adults during group movements. Red color indicates the individuals from cluster A and blue indicates those from cluster B. The black parallel line indicates the average value of joining orders among the 12 adults. Individuals are presented from left to right in descending joining order.
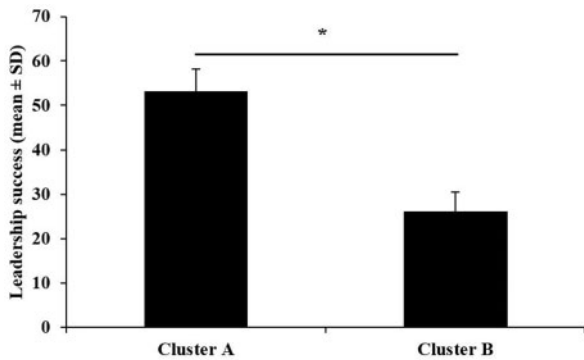

Figure 6. Correlation between proximity relations and following scores in Tibetan macaques of cluster B.

Figure 5. Leadership success between the 2 clusters of Tibetan macaques. *$P < 0.05$.
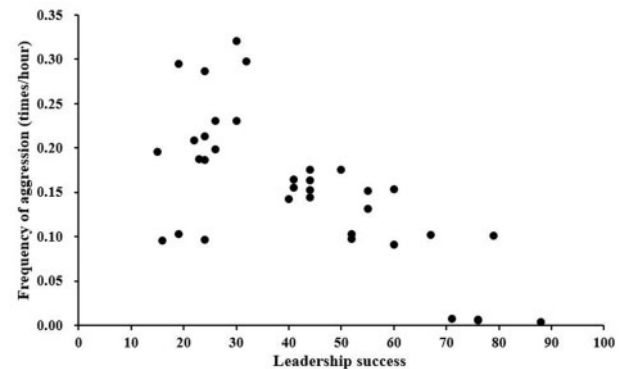
Figure 7. Correlation between leadership and aggression in Tibetan macaques of cluster A.

compromiser cluster might not maintain close social relationships with every single member of their cluster, but they would rather engage in proximity relations with front-runners. This
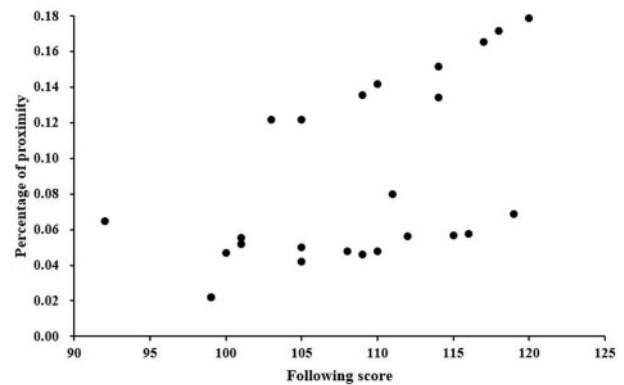
suggested that Tibetan macaque compromisers might develop strong affiliative relationships with front-runners, that is, regard front-runners as their preferred social partners.
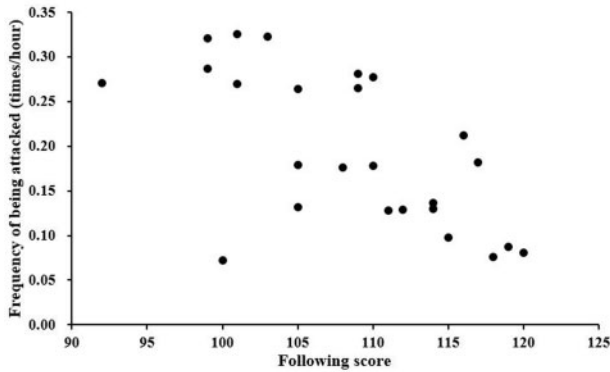
Figure 8. Relationship between "following" and "being attacked" in Cluster B of Tibetan macaques.

Our results showed that the front-runner cluster had higher leadership success and social centrality than other members outside the cluster. A higher score of the eigenvector centrality coefficient indicated that front-runners possess more followers during group movements. We believe that leadership success can be maintained when compromisers follow front-runners' decision-making. Some studies also demonstrated that following or compromise can affect group movements. For example, in chacma baboons, if less than 5 individuals join the movement, the initiator normally moves back to the group until a second attempt is made (Stueckle and Zinner 2008). Additionally, Strandburg-Peshkin et al. (2015) found that olive baboon followers are more likely to move toward the average preferred direction; they exhibit a compromise rule during group movement. It is critical to consider the perspective of the following individuals because group cohesion does not exist without them: all the group members must cooperate when choosing movement direction. Thus, Tibetan macaque compromisers might obtain some benefits (e.g., individual safety) derived by maintaining close associations with front-runners while forgoing their direction preference.

Tibetan macaques in the front-runner cluster were higher in social rank than were those in the compromiser cluster. Thus, subordinate compromisers would receive more individual safety by following the movements of front-runners because these are usually high-ranking individuals. In fact, Tibetan macaques in the front-runner cluster had lower aggressiveness when they initiated more successful group departures. Meanwhile, the compromiser cluster underwent fewer events of being attacked when they followed more group movements initiated by the front-runner cluster. Adult Tibetan macaques of the Yulinkeng 1 group potentially engaged in extensive conflicts in the mating season (Li 1999; Berman et al. 2007). Thus, maintenance of group cohesion also requires conflict management (Trillmich et al. 2004). Compromise can provide individual safety for Tibetan macaque followers, including a decrease in aggression from dominating front-runners. Individual safety to compromisers has been found in other studies. For example, in chacma baboons, female compromisers often keep close affiliation with male-dominant leaders; this enables them to increase protection from predators and infanticidal males (King et al. 2008; Stueckle and Zinner 2008). The orb spider (*Argiope keyserlingi*) appears to avoid predators by compromising on foraging profitability (Blamires et al. 2007). We suggest that the long-term benefits of association with dominant front-runners may often outweigh

consensus costs and, thus, result in subordinates accepting front-runners' decisions and following their movements.

Furthermore, subordinate compromisers might not benefit by accepting the despotic decisions of a single dominant decision-maker (Conradt and Roper 2003; Lusseau and Conradt 2009). In the present study, we found that individuals in group movements can be classified into a front-runner cluster and a compromiser cluster using the hierarchical cluster analysis. Thus, we consider that subordinate compromisers are willing to follow the front-runners' clique instead of a single leader consistently. In a previous study, we demonstrated that Tibetan macaques do not follow a single leader's decision, but they were more likely to follow different members' decisions (Wang et al. 2016). Our results further confirmed that decision-makers of group movements not only relate to leaders or front-runners but also include compromisers. Thus, this study extends the previous argument that the Tibetan macaque group had a distributed leadership rather than a personal leadership (Wang et al. 2016).

In conclusion, our study supported the hypothesis that Tibetan macaque compromisers can make a trade-off in coordination and consensus scenarios among social animals. Compromisers increase individual safety by forgoing their direction preference. Moreover, the results seem to indicate that adult males tend to be included in the front-runner cluster than in the compromiser cluster (3 vs. 1) while there was no difference in the number of adult females between the 2 clusters (4 vs. 4). Future works can quantify the possible differences in benefits and costs between males and females in the context of collective behavior.

Ethical Statement

All research protocols reported in this manuscript were approved by the Chinese Wildlife Management Authority. The study was completely observational in nature and did not involve invasive experimentation on wild primates. Thus, no review from an institutional ethics committee in China was required. This research followed the Wildlife Protection Law of the People's Republic of China. All research reported here adhered to the regulatory requirements of Huangshan Garden Forest Bureau, China, where the study took place.

Author Contributions

X.W.: original concept and analysis. All authors: planning and review and editing. All authors have read and agreed to the published version of the manuscript.

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Conflict of interest statement

The authors declare that they have no conflict of interest.

References

Alexander RD, 1974. The evolution of social behavior. *Annu Rev Ecol Evol Syst* 5:325–383.

Altmann J, 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–267.

Barelli C, Boesch C, Heistermann M, Reichard UH, 2008. Female white-handed gibbons *Hylobates lar* lead group movements and have priority of access to food resources. *Behaviour* 145:965–981.

Berman CM, Ionica C, Li JH, 2004. Dominance style among *Macaca thibetana* on Mt. Huangshan, China. *Int J Primatol* 25:1283–1312.

Berman CM, Li JH, 2002. Impact of translocation, provisioning and range restriction on a group of *Macaca thibetana*. *Int J Primatol* 23:383–397.

Berman CM, Li JH, Ogawa H, Ionica C, Yin HB, 2007. Primate tourism, range restriction, and infant risk among *Macaca thibetana* at Mt. Huangshan, China. *Int J Primatol* 28:1123–1141.

Berman CM, Ogawa H, Ionica C, Yin HB, Li JH, 2008. Variation in kin bias over time in a group of Tibetan macaques at Huangshan, China: contest competition, time constraints or risk response? *Behaviour* 145:863–896.

Beauchamp G, 2000. Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour* 137:301–314.

Blamires SJ, Thompson MB, Hochuli DF, 2007. Habitat selection and web plasticity by the orb spider *Argiope keyserlingi* (Argiopidae): do they compromise foraging success for predator avoidance? *Austral Ecol* 32:551–563.

Bonanni R, Cafazzo S, Valsecchi P, Natoli E, 2010. Effect of affiliative and agonistic relationships on leadership behaviour in free-ranging dogs. *Anim Behav* 79:981–991.

Borgatti SP, Everett MG, Freeman LC, 2002. *UCINET 6 for Windows: Software for Social Network Analysis*. Harvard: Analytic Technologies.

Boydston EE, Morelli TL, Holekamp KE, 2001. Sex differences in territorial behavior exhibited by the spotted hyena (Hyaenidae, *Crocuta crocuta*). *Ethology* 107:369–385.

Cairns SJ, Schwager SJ, 1987. A comparison of association indices. *Anim Behav* 35:1454–1469.

Chapman CA, Chapman LJ, 2000. Determinants of group size in primates: the importance of travel costs. In: Boinski S, Garber PA, editors. *On the Move*. Chicago: University of Chicago Press. 24–41.

Conradt L, Roper TJ, 2003. Group decision-making in animals. *Nature* 421: 155–158.

Conradt L, Roper TJ, 2005. Consensus decision making in animals. *Trends Ecol Evol* 20:449–456.

Conradt L, Roper TJ, 2009. Conflicts of interest and the evolution of decision sharing. *Phil Trans R Soc B* 364:807–819.

Dorning J, Stephen H, 2017. Dominance, gender, and season influence food patch use in a group-living, solitary foraging canid. *Behav Ecol* 28: 1302–1313.

Dyer JRG, Johansson A, Helbing D, Couzin ID, Krause J, 2009. Leadership, consensus decision making and collective behaviour in humans. *Phil Trans R Soc B* 364:781–789.

Funkhouser JA, Mayhew JA, Mulcahy JB, 2018. Social network and dominance hierarchy analyses at Chimpanzee Sanctuary Northwest. *PLoS ONE* 13:e0191898.

Gammell MP, de Vries H, Jennings DJ, Carlin CM, Hayden TJ, 2003. David's score: a more appropriate social ranking method than Clutton-Brock et al.'s index. *Anim Behav* 66:601–605.

Hansen MJ, Schaerf TM, Ward AJ, 2015a. The effect of hunger on the exploratory behaviour of shoals of mosquitofish *Gambusia holbrooki*. *Behaviour* 152:1659–1677.

Hansen MJ, Schaerf TM, Ward AJ, 2015b. The influence of nutritional state on individual and group movement behaviour in shoals of crimson-spotted rainbow fish *Melanotaenia duboulayi*. *Behav Ecol Sociobiol* 69:1713–1722.

Jacobs A, Watanabe K, Petit O, 2011. Social structure affects initiations of group movements but not recruitment success in Japanese macaques *Macaca fuscata*. *Int J Primatol* 32:1311–1324.

Janson CH, Goldsmith ML, 1995. Predicting group size in primates: foraging costs and predation risks. *Behav Ecol* 6:326–336.

King AJ, Douglas CMS, Huchard E, Isaac NJB, Cowlishaw G, 2008. Dominance and affiliation mediate despotism in a social primate. *Curr Biol* 18:1833–1838.

Kingma SA, 2018. Food, friends or family: what drives delayed dispersal in group-living animals? *J Anim Ecol* 87:1205–1208.

L'heureux N, Lucherini M, Festa-Bianchet M, Jorgenson JT, 1995. Density-dependent mother-yearling association in bighorn sheep. *Anim Behav* 49:901–910.

Li JH, 1999. *The Tibetan Macaque Society: A Field Study*. Hefei: Anhui University Press.

Lihoreau M, Buhl J, Charleston MA, Sword GA, Raubenheimer D, Simpson SJ, 2015. Nutritional ecology beyond the individual: a conceptual framework for integrating nutrition and social interactions. *Ecol Lett* 18:273–286.

Liste G, Asher L, Broom DM, Fusani L, 2015. When a duck initiates movement, do others follow? Testing preference in groups. *Ethology* 120:1199–1206.

Lusseau D, Conradt L, 2009. The emergence of unshared consensus decisions in bottlenose dolphins. *Behav Ecol Sociobiol* 63:1067–1077.

Majolo B, de Bortoli Vizioli A, Schino G, 2008. Costs and benefits of group living in primates: group size effects on behaviour and demography. *Anim Behav* 76:1235–1247.

Markham AC, Gesquiere LR, 2017. Costs and benefits of group living in primates: an energetic perspective. *Phil Trans R Soc B* 372:20160239.

Miller A, Judge DS, Uwingeneye G, Ndayishimiye D, Kaplin BA, Grueter CC, 2020. Feeding competition inferred from patch depletion in a supergroup of Rwenzori black-and-white colobus monkeys *Colobus angolensis ruwenzorii* in Rwanda. *Behaviour* 157:731–760.

Muller Z, Cuthill IC, Harris S, 2018. Group sizes of giraffes in Kenya: the influence of habitat, predation and the age and sex of individuals. *J Zool* 306: 77–87.

Newman MEJ, 2004. Analysis of weighted networks. *Phys Rev E* 70:056131.

Paukner A, Suomi SJ, 2012. Social after-effects of fur rubbing in tufted capuchin monkeys *Cebus apella*: increased antagonism and reduced affiliation. *Primates* 53:297–301.

Pyritz LW, Kappeler PM, Fichtel C, 2011. Coordination of group movements in wild red-fronted lemurs *Eulemur rufifrons*: processes and influence of ecological and reproductive seasonality. *Int J Primatol* 32:1325–1347.

Ramos A, Petit O, Longour P, Pasquaretta C, Sueur C, 2015. Collective decision making during group movements in European bison, *Bison bonasus*. *Anim Behav* 109:149–160.

Sankey DWE, Shepard ELC, Biro D, Portugal SJ, 2019. Speed consensus and the 'goldilocks principle' in flocking birds *Columba livia*. *Anim Behav* 157: 105–119.

Sasaki T, Mann RP, Warren KN, Herbert T, Wilson T, Biro D, 2018. Personality and the collective: bold homing pigeons occupy higher leadership ranks in flocks. *Phil Trans R Soc B* 373:20170038.

Smith JE, Estrada JR, Richards HR, Dawes SE, Mitsos K, Holekamp KE, 2015. Collective movements, leadership and consensus costs at reunions in spotted hyenas. *Anim Behav* 105:187–200.

Solum T, Eskridge BE, Schlupp I, 2014. Consensus costs and conflict in a collective movement. Proceedings of the 2014 Annual Conference on Genetic and Evolutionary Computation. New York: Assoc Computing Machinery. 49–56.

Strandburg-Peshkin A, Farine DR, Couzin ID, Crofoot MC, 2015. Shared decision-making drives collective movement in wild baboons. *Science* 348: 1358–1361.

Stueckle S, Zinner D, 2008. To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. *Anim Behav* 75:1995–2004.

Sueur C, Petit O, 2008. Shared or unshared consensus decision in macaques? *Behav Process* **78**:84–92.

Thompson CL, 2013. Non-monogamous copulations and potential within-group mating competition in white-faced saki monkeys *Pithecia pithecia*. *Am J Primatol* **75**:817–824.

Trillmich J, Fichtel C, Kappeler PM, 2004. Coordination of group movements in wild Verreaux's sifakas (*Propithecus verreauxi*). *Behaviour* **141**: 1103–1120.

Usui R, Sheeran LK, Li JH, Sun L, Wang X et al., 2014. Park rangers' behaviors and their effects on tourists and Tibetan macaques *Macaca thibetana* at Mt. Huangshan, China. *Animals* **4**:546–561.

Wang X, Sun L, Li JH, Xia DP, Sun BH et al., 2015. Collective movement in the Tibetan macaques *Macaca thibetana*: early joiners write the rule of the game. *PLoS ONE* **10**:e0127459.

Wang X, Sun L, Sheeran LK, Sun BH, Zhang QX et al., 2016. Social rank versus affiliation: which is more closely related to leadership of group

movements in Tibetan macaques *Macaca thibetana*? *Am J Primatol* **78**: 816–824.

Wang X, Xia DP, Sun L, Garber PA, Kyes RC et al., 2020. Infant attraction: why social bridging matters for female leadership in Tibetan macaques. *Curr Zool* **66**:635–642.

Ward AJW, Herbert-Read JE, Schaerf TM, Seebacher F, 2018. The physiology of leadership in fish shoals: leaders have lower maximal metabolic rates and lower aerobic scope. *J Zool* **305**:73–81.

Whitehead H, 2009. SOCPROG programs: analysing animal social structures. *Bahav Ecol Sociobiol* **63**:765–778.

Xia DP, Li JH, Garber PA, Sun LX, Zhu Y et al., 2012. Grooming reciprocity in female Tibetan macaques *Macaca thibetana*. *Am J Primatol* **74**: 569–579.

Zhang QX, Li JH, Xia DP, Zhu Y, Wang X et al., 2014. Influence of dominance rank and affiliation relationships on self-directed behavior in female Tibetan macaques *Macaca thibetana*. *Zool Res* **35**:214–221.