

Chapter 5

Social Relationships Impact Collective Decision-Making in Tibetan Macaques



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5.1 Introduction

Group-living offers many benefits related to survival and reproduction for animals (Bertram 1978; van Schaik 1983; Zemel and Lubin 1995; Krause and Ruxton 2002). Nevertheless, it also involves some unavoidable costs, such as mate competition or interindividual conflict (Kappeler et al. 2015). Therefore, animals need to coordinate their actions and maintain group cohesion to gain the benefits of group-living (Conradt and Roper 2003; Fichtel et al. 2011). Group coordination is often difficult to achieve because individuals may differ in their needs and interests. When these differences cannot be reconciled, cohesiveness can be at risk (Rands et al. 2003,

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2008). How consensus is achieved and implemented at the behavioral level is often studied during natural group movements to and from specific resources and/or locations (e.g., sleeping and foraging sites). Such studies can provide an ecologically relevant context to probe into fundamental mechanisms of social coordination of collective actions (Boinski and Garber 2000; Fichtel et al. 2011).

Social interactions could affect the process of group movements. For example, in large anonymous groups, such as fish schools and bird flocks, in which members do not know each other individually, direction and action during movements are regulated by self-coordination by individuals following the simple rule of keeping a certain distance to the nearest neighbor (Parrish and Edelstein-Keshet 1999; Couzin et al. 2002; Hemelrijk 2002). In contrast, in primate groups, where members know each other individually, certain dominant or affiliated individuals may play specific roles in the context of collective behavior, such as initiating or terminating a group movement (Boinski and Garber 2000; King and Cowlshaw 2009; King and Sueur 2011).

In primate species, initiation of a group movements can be accompanied by notifying behaviors (Kummer 1968) or preliminary behaviors (Sueur and Petit 2008a) that are exhibited in the pre-departure period, directly preceding the group movement. This recruitment process often includes visual and acoustic communication, and which can influence the recruitment success of an initiation, i.e., whether the initiator is followed and, if so, by how many group members and how quickly (Sueur and Petit 2010; Selmann et al. 2016; Sperber et al. 2017).

A successful collective movement can be driven by an unshared decision-making mechanism, i.e., one individual leading all group movements and other members following it all the time (Conradt and Roper 2005). In this decision-making process, the highest-ranking male usually plays a major role in leadership in several species of Old World monkey (Sueur and Petit 2008a). Alternatively, shared or partially shared decision-making mechanism can also result in a collective movement. That is, all group members or a subgroup can lead the movement of the entire group on different occasions (Pyritz et al. 2011). In this case, individuals with better social connections enjoy higher rates of initiating group movements (Sueur and Petit 2008b; Strandburg-Peshkin et al. 2015; Fratellone et al. 2018).

A major focus in the study of collective decisions in primates is the joining process, which occurs once an individual has initiated a collective movement. Often, primates do not decide independently on activity changes, but, rather, base their choices on the actions of their group mates. This form of joining rule, when one individual taking an action makes it more likely for another to do so as well, has been termed mimetism (Deneubourg and Goss 1989). Mimetism can be further categorized as anonymous mimetism and selective mimetism. Anonymous mimetism refers to individuals being more likely to take the actions of other individuals irrespective of their identity, and thus group movements can simply depend on the number of individuals who have already left or performed a certain behavior (Petit et al. 2009). Selective mimetism refers to joining decisions based on some other

factors, such as distance, with individuals being more likely to join a movement when in close proximity (Ramseyer et al. 2009; Ward et al. 2013), and affiliation, with individuals being more likely to follow those group members with whom they have strong social bonds (King et al. 2011; Sueur et al. 2009, 2011; Seltnmann et al. 2013; Strandburg-Peshkin et al. 2015; Farine et al. 2016).

Individuals may also engage another joining process based on a quorum rule. This rule states that once a minimum number of group members joins a movement, group movement will occur all the time (Conradt and Roper 2003; Wang et al. 2015; Rowe et al. 2018). A response to a quorum is observed when the probability of members exhibiting a vote by joining a movement depends on the number of individuals already performing the voting behavior (Pratt et al. 2002; Seeley and Visscher 2004; Sumpter 2006; Ward et al. 2008).

Interestingly in macaques, social style appears to influence the organization of group movements (Sueur and Petit 2008a). Social styles of the species of *Macaca* have been divided into four grades (Thierry 2000), ranging from grade 1 (the most intolerant) to grade 4 (the most tolerant). These styles appear to influence the initiation and joining process of group movements (Sueur and Petit 2008a). In species with a more despotic dominance style, decision-making is more likely to be unshared and social rank determines leadership (Sueur and Petit 2008a, b). In contrast, in species exhibiting a more egalitarian style, decision-making is more likely to be shared and social relationships determine leadership (Sueur and Petit 2008a). For instance, in rhesus (*Macaca mulatta*) and Japanese macaques (*M. fuscata*), both of which have a despotic social style, movements are mainly initiated by dominant individuals, and joining processes are also determined by dominance order (Sueur et al. 2009; Jacobs et al. 2011). In contrast, in macaques with a more egalitarian social style, such as Tonkean (*M. tonkeana*) and Barbary macaques (*M. sylvanus*), decision-making is equally or partially shared, and joining processes are determined by affiliation (Sueur et al. 2009; Jacobs et al. 2011; Seltnmann et al. 2013).

Currently, the relationship between social style and leadership and other important aspects of collective decision-making has been investigated only in a limited number of macaque species. Therefore, detailed studies of collective movement in relatively less known species, such as the Tibetan macaque (*M. thibetana*), are of special interest for a better understanding of the link between social relationships and collective decision-making. We therefore take this opportunity to review and synthesize information based largely on our studies of Tibetan macaques. We hope that some of the findings and insights (including those that have not been fully developed in our publications) will enrich our understanding of decision-making processes in collective movement in primates in general and macaques in particular.

5.2 Collective Decision-Making in Tibetan Macaques

5.2.1 *A Macaque Species for Studying Decision-Making*

Because *Macaca* species vary in dominance style (Thierry et al. 2004), they serve as an interesting taxon to study how social relationship influences the process of group movements (Jacobs et al. 2011). Tibetan macaques are highly gregarious and live in cohesive groups (Li 1999). Similar to other macaques, Tibetan macaques show female philopatry, male dispersal, and linear dominance hierarchies (Berman et al. 2004).

The wild group of macaques we studied (YA1, see Chap. 2 for detailed information about the history, demography, and habitat of the study group) engaged in social activities in nearby forest during most of the day without any restriction on their home range. For the convenience of viewing by tourists, they were supplied with 3–4 kg of corn daily (Berman and Li 2002; Berman et al. 2008; Xia et al. 2012). After corn feeding, they regularly switched locations from the feeding site to the nearby forest. Collective movements often occurred at the time of the switch. We therefore investigated decision-making processes during group movements in this group from August to December of 2012.

5.2.2 *Decision-Making During the Initiation Process of Group Movements*

It is still debated whether Tibetan macaques exhibit a despotic or a tolerant dominance style (Thierry 2000; Berman et al. 2004). In accordance with a despotic dominance style (Berman et al. 2004), Tibetan macaques should be expected to show an unshared decision-making process when initiating group movements, i.e., a single, highest-ranking individual leads most movements. In reality, however, Tibetan macaques demonstrate a shared decision-making process with affiliative individuals more often initiating group movements than less sociable group members (Wang et al. 2016). Considering the above contradiction about dominance style in Tibetan macaques, we assume that there may be a potential connection between social rank/affiliative relationship and the initiation of group movement.

We observed initiation processes when Tibetan macaques returned from the feeding site to the nearby forest. Thus, an initiator was defined as the first individual that moved more than 10 m in less than 30 s from the provisioning area to the forest. Any individual walking more than 5 m and within 45° of the direction taken by the initiator was considered as a follower (Sueur and Petit 2008a). We used the criterion of 5 min for each successive follower who joined the movement after the first mover or previous follower (Wang et al. 2016). In our study, only those movements including at least two-thirds of group members were counted as successful group movements. To quantify leadership in group movements, we standardized initiation

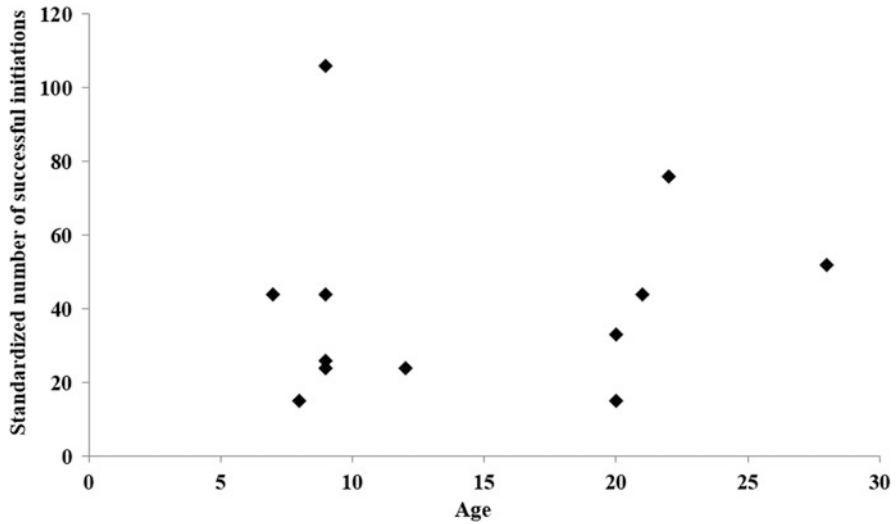


Fig. 5.1 Age of adults and their successful initiations of group movements in Tibetan macaques. There was no correlation between the two variables

data on the number of initiations of each individual by the number of times in which this individual was identified at the provisioning area (Wang et al. 2016).

During the 5 months of our observation period, we recorded more than 200 initiation attempts, all of them by adult members. Two-thirds of these initiations were considered as successful group movements. We found that all adults could initiate group movements, but that they differed significantly in the standardized number of successful initiations. This result clearly showed that decision-making during the initiation process of group movement was shared among adults.

To explore which factors might affect collective decision-making, we analyzed the relationship between several key biological/social attributes and the initiation of group movement. Interestingly, there was no significant difference in the standardized number of successful initiations between adult males and females. Second, there was neither a correlation between social rank and the standardized number of successful initiations nor with the success ratio of initiations. Also, age of adults was not correlated with the successful initiation of group movement (Fig. 5.1).

To evaluate the relationship between social affiliation of an adult and its leadership in group movements, we related the number and ratio of successful initiations of every subject in the provisioning area to its eigenvector centrality coefficient based on proximity relations among group members when they were in the forest (in comparison with the situations when they were in the feeding site). We used focal animal sampling method to collect proximity data for assessing affiliative relationships among group members (Altmann 1974; Li 1999; Berman et al. 2008). We found a positive correlation between the eigenvector centrality coefficient (based on proximity relations) and the standardized number of successful initiations

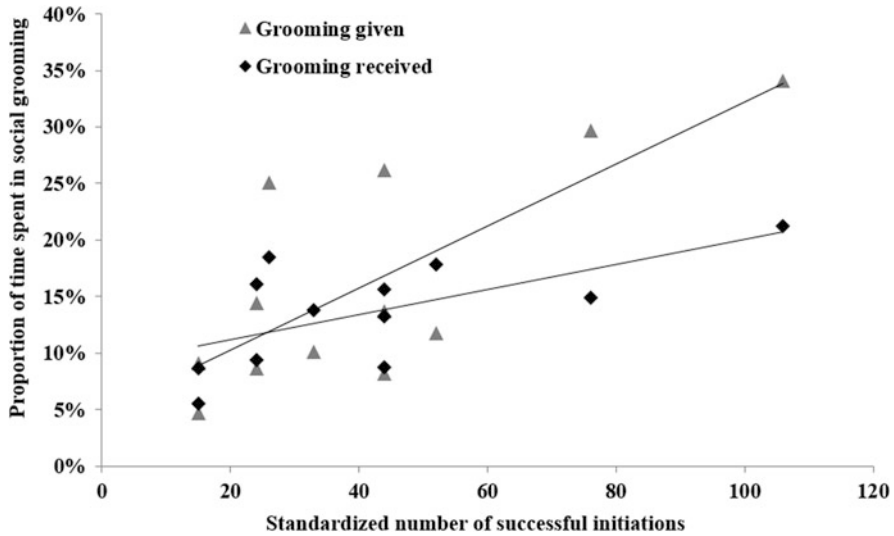


Fig. 5.2 Correlation between successful initiations of group movements and social grooming in Tibetan macaques. Proportion of time spent in social grooming indicates the duration of grooming of every subject divided by its total focal observation time. The two lines respectively represent positive correlations between grooming given/grooming received and successful initiations of group movements

across adults. Eigenvector centrality was also correlated positively with the success ratio of initiations.

Moreover, to further analyze the relationship between affiliated behavior and leadership of group movement, we correlated the initiation of group movement with social grooming among adults. Results showed that the standardized number of successful initiations was positively correlated with the duration of social grooming, including grooming given and grooming received (Fig. 5.2).

5.2.3 Decision-Making During the Joining Process of Group Movements

Joining processes were also observed when Tibetan macaques returned from the feeding site, where they were regularly provisioned, to the nearby forest. We tested whether joining occurs according to a quorum decision or mimetism as shown in a simple schematic to illustrate how the two responses would differ (Fig. 5.3).

During our preliminary observation of group YA1 (August 1–14, 2012), 5 min were used as the minimum duration of initiating a successful group movement. Therefore, an early joiner was defined as an individual that moved in the first 5 min after the initiator departed (Wang et al. 2015). According to this definition, an

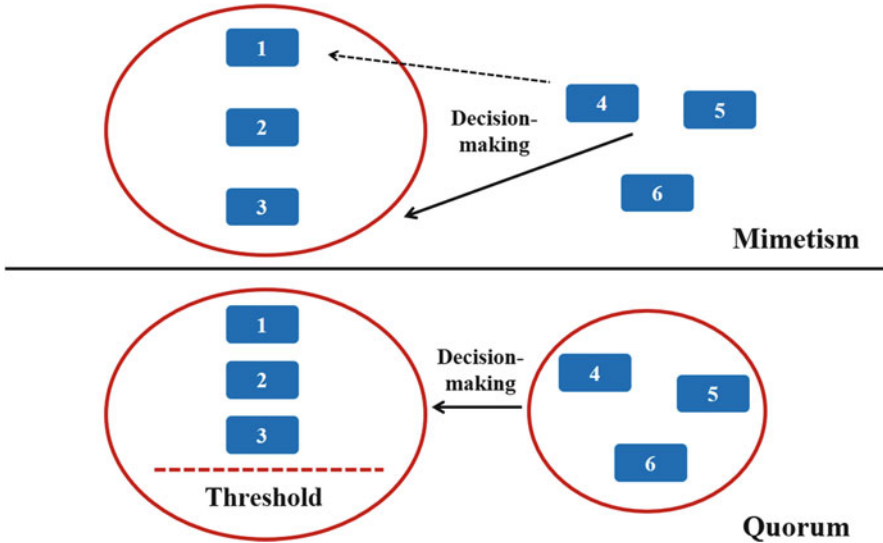


Fig. 5.3 A schematic depiction of mimetism and quorum. Nos. 1, 2, and 3 in red circles represent individuals who have joined the movement. Nos. 4, 5, and 6 are individuals waiting to join the movement. Dotted line of upper figure indicates selective mimetism: Nos. 4, 5, and 6 would join the movement based on the choice of specific members (e.g., No. 1 is the highest-ranking male). Solid line of upper figure indicates anonymous mimetism: Nos. 4, 5, and 6 would join the movement based on the number of joiners by linearly. Threshold of lower figure indicates quorum: for example, once half of the members (i.e., three individuals) have joined the movement, other individuals would follow the collective action all the time

initiator in our study was also considered as an early joiner because he/she left in the first 5 min.

We assessed the relationship between the number of adult early joiners and the probability of successful group movement. The results revealed that group movements were not successful unless three or more early joiners participated in the movement. When three to six early joiners participated, successful group movements occurred without a consistent pattern, showing some fluctuations in the probability of successful group movement. Nonetheless, once more than half of the early joiners participated in the movement, other group members followed the collective actions all the time.

To further study the role of early joiners in group movements, we performed a correlation analysis between the mean joining order and eigenvector centrality coefficient for adults in group movements (Wang et al. 2015). Results showed that the earlier an individual joined the movement, the higher its centrality was (Fig. 5.4). We then explored key attributes of early joiners in the social network of those in group movements. Our results showed that early joiners differed significantly in eigenvector centrality coefficient based on the half-weight index (HWI: co-occurrence index in group movements, Wang et al. 2015), but there was no difference between adult males and females. Also, age and eigenvector centrality

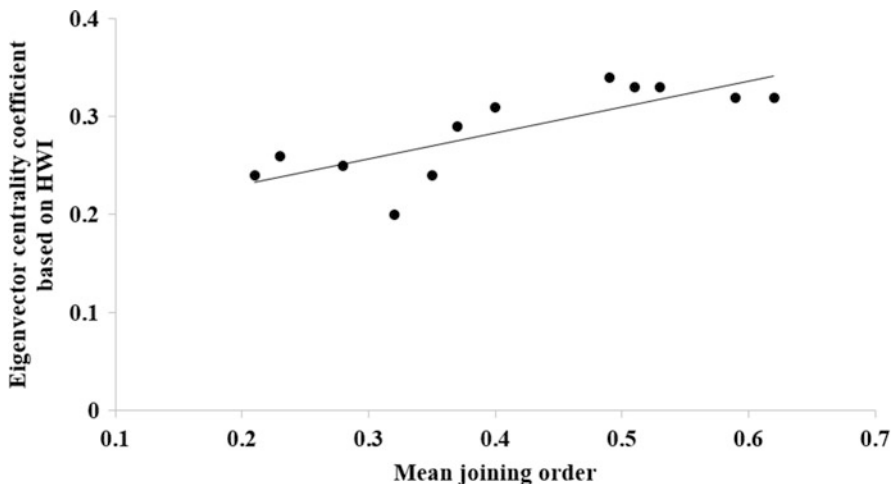


Fig. 5.4 Relationship between individuals' joining order of group movements and eigenvector centrality coefficient. HWI: co-occurrence index in group movements. The bigger the value of mean joining order was, the earlier an individual joined the movement

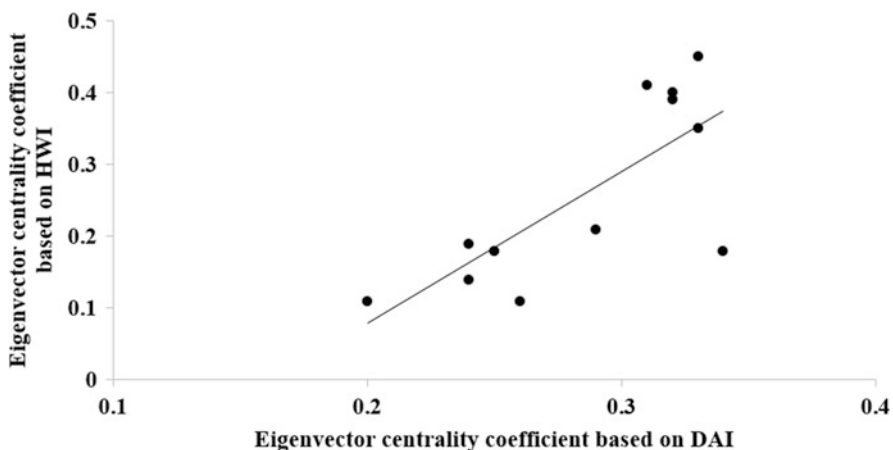


Fig. 5.5 Eigenvector centrality coefficients of individuals based on HWI and DAI. HWI: co-occurrence index in group movements. DAI: dyadic association index in proximity relations

coefficients were not correlated. However, social rank was positively correlated with eigenvector centrality coefficients in both adult males and females.

Finally, we compared two eigenvector centrality coefficients of individuals in group movements and in proximity relations (Wang et al. 2015). We found a positive correlation between the two coefficients (Fig. 5.5). This result indicates a close relation between affiliative behavior and the joining process of group movements.

5.3 Social Relationship and Collective Decision-Making

Our collection of studies revealed that all adult Tibetan macaques had opportunities to successfully initiate group movements. This result is consistent with studies in Barbary macaques (Seltmann et al. 2013) and Tonkean macaques (Sueur and Petit 2008a), both of which have a tolerant social style. However, different adults had varying times of success in initiating group movements across the study period. Eigenvector centrality coefficients were positively correlated with the number of successful initiation of group movements.

Our data demonstrate that more affiliative individuals were more likely to assume leadership roles. The importance of social relationship is consistent with the results of several other studies (e.g., Tonkean macaques: Sueur and Petit 2008a, b; Sueur et al. 2009). King et al. (2011) suggested that chacma baboons (*Papio ursinus*) with higher eigenvector centrality coefficients in their social network were more likely to attract partners to follow their initiations. We assume that individuals preferentially followed “friends” because following friends may be associated with benefits. For instance, female baboons (*P. cynocephalus*) that had closer bonds with others lived longer and their offspring also had a higher probability to survive (Silk et al. 2010), but in Tibetan macaques neither these friendships nor their potential consequences have been studied yet.

We found a positive correlation between the number of successful initiations and the amount of time spent grooming given/received, suggesting that the motivation to move may lay in staying away from the provisioning area and moving to the relatively calm forest, where animals could engage in social grooming. We carried out our study at a tourist site (Wang et al. 2016), and adult Tibetan macaques at our study site had indeed higher rates of aggression in the provisioning area than in the forest (Berman et al. 2007). Moreover, as no large predators were present at the study site in recent decades (Li 1999), the forest was supposed to be a safer and less stressful location for monkeys to engage in affiliative behaviors such as grooming. We see the location change from the provisioning area to forest as an adaptive response to the socioecological conditions experienced by our study group.

Our work on the joining process of group movements has provided several important insights into which rules might be used by Tibetan macaques in decision-making during collective movement. First, we found that the more central a group member was in the social network, the earlier it participated in a movement, as shown by the positive correlation between the mean joining order of every joiner and its eigenvector centrality coefficient (Wang et al. 2015). This result is comparable with situations in black howler monkeys (*Alouatta pigra*), where females at the front of a group movement have the highest centrality eigenvectors among the adult group members (Belle et al. 2013). Our results demonstrate the importance of early joiners in the decision-making process and indicate that the initiator was not always the only decision-maker. Other joiners in the first 5 min might also play a key role in decision-making.

Second, we found that higher-ranking early joiners tended to have higher eigenvector centrality coefficients. Because the eigenvector centrality coefficient can quantify the attraction of early joiners to other members during the joining process (Newman 2004), our data (Wang et al. 2015) showed the role of social rank in early joiners. That is, higher-ranking joiners could have more companions in group movements. A similar influence of social rank on decision-making has also been reported in other species. For instance, alpha males have been reported to be the consistent decision-makers in group movements in mountain gorillas, *Gorilla gorilla* (Watts 2000).

Third, we found that early joiners who had higher centrality coefficients in proximity activities also had higher centrality coefficients during collective movements. This means that early joiners with frequent social interactions could also attract more members during the joining process. This result is comparable to findings in chacma baboons and red-fronted lemurs, *Eulemur rufifrons* (Stueckle and Zinner 2008; King et al. 2011; Sperber et al. 2019).

Our data also showed that when the number of early joiners in a group was below seven, group members preferred to follow higher-ranking or affiliative early joiners during the joining process of group movements. By this time, selective mimetism had most likely been used as the joining rule. Apart from our study, selective mimetism has also been suggested in several other studies (Detrain et al. 1999; Camazine et al. 2001; Couzin and Krause 2003; Sumpter 2006; Gautrais et al. 2007; Sperber et al. 2019). In Tonkean macaques, for instance, how an individual decides to join a collective movement depends on whether it is strongly affiliated to departing individuals (Sueur et al. 2009).

We can explain selective mimetism in Tibetan macaques with respect to their social style. For example, Tonkean macaques exhibit an egalitarian social structure (Sueur and Petit 2008b). In this species, individuals decide when to move via a quorum. The lack of centrality for dominant or old Tonkean macaques suggests that all individuals may have equal weight in the voting process and interactions are not constrained by individual status (Sueur and Petit 2008b). However, rhesus macaques, with a despotic style, prefer to join high-ranking or related individuals during collective movements, showing selective mimetism (Sueur and Petit 2008a, b; Sueur et al. 2010). In Tibetan macaques, higher-ranking early joiners were socially connected to more individuals than lower-ranking group members, both in collective movements and during proximity activities. As our results showed that high-ranking individuals had high centrality coefficients based on the co-occurrence index in group movements, they were more attractive to other members than low-ranking individuals during the joining process.

Our data also showed that when the number of early joiners had accumulated to more than half of the adults in our study group, all group members would participate in group movement all the time. Clearly, this threshold of “>50% adult members” indicates the existence of another joining rule, the quorum rule, during collective movements in Tibetan macaques. The voting process in the group of Tibetan macaques we studied may be explained by the reduction in the risk of being left behind from the group (Wang et al. 2015). A similar joining rule has also been found

in white-faced capuchins (*Cebus capucinus*), rhesus macaques, and Tonkean macaques, all of which use the threshold of four in collective movements (Petit et al. 2009; Sueur and Petit 2010).

5.4 Conclusions

In this chapter, we reviewed and synthesized studies of collective movement and decision-making in Tibetan macaques. We suggest that leadership of group movements in Tibetan macaques was distributed among adults rather than exclusively taken by a single, high-ranking individual. Different members led the group on different occasions, and social relationships were more related to leadership than social rank, age, or sex. Performing group movement presumably produced opportunities to switch locations for adults to participate in other social activities, including social grooming. Moreover, social relationship also mattered for the joining process. Tibetan macaques used selective mimetism and a quorum process in collective decision-making, and early joiners with closer affiliation played a critical role as to which rule was used. Thus, our study provided further evidence for the link between social relationships and collective decision-making in a little known macaque species. Future studies can examine whether social relationships affect the decision-making process in Tibetan macaques at the same level when group size varies. This will lead us to a better understanding as to whether a general pattern exists for group coordination and social cohesion through collective decision-making.

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