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Female Social Connectivity through the Leadership and Movement Progression of Tibetan Macaques at Mt. Huangshan, China

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FEMALE SOCIAL CONNECTIVITY THROUGH THE LEADERSHIP AND

MOVEMENT PROGRESSION OF TIBETAN MACAQUES

AT MT. HUANGSHAN, CHINA

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A Thesis

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The Graduate Family

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Master of Science

Primate Behavior and Ecology

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by

Gregory Patrick Fratellone

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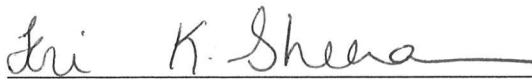
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ABSTRACT

FEMALE SOCIAL CONNECTIVITY THROUGH THE LEADERSHIP AND
MOVEMENT PROGRESSION OF TIBETAN MACAQUES
AT MT. HUANGSHAN, CHINA

by

Gregory Patrick Fratellone

June 2015

The present study investigates the leadership and progression of collective movements of Tibetan macaques (*Macaca thibetana*) found in Mt. Huangshan, China. I gathered information on their movements and social networks through all-occurrence, focal and scan sampling. I hypothesize that high-ranking females lead more collective movements than males as they have highly structured social bonds. I also predict that movements weighted by female presence are more efficient as societies are matrilineally structured and females are more socially connected. There were a total of 128 successful collective movements recorded over a 2-month period. There was no significant effect of sex, age or rank on the leadership frequency. The highest-ranking female (YH) and a young female (TXX) led more collective movements than expected by chance, which may be a consequence of the mating season. There was a significant difference in successful movement time between movements weighted by female presence and those unweighted, which may be due to the matrilineally-structured societies and strong female bonds present.

ACKNOWLEDGEMENTS

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CHAPTER I

INTRODUCTION

As a socially well-connected and cohesive species, people tend to make many

collective decisions about everyday activities such as where to go for dinner or how to

get to the new store in town. Due to advanced language and extraordinary cognitive

ability, most people do not find collective decision-making difficult. What is fascinating

is that nonhuman species whose communication skills we do not fully understand are still

able to participate in similar collective decision-making. The fundamental question

remains: How do nonhuman animals collectively reach a decision?

A collective movement can involve a group of hundreds or even thousands of

synchronously moving animals that go in the same direction, maintain cohesion and

reach a new location (Jacobs, Watanabe, & Petit, 2011; Fernandez, Kowalewski, &

Zunino, 2013). This phenomenon has been observed in a number of social organisms

(insects: Seeley, Camazine, & Sneyd, 1991; Mallon, Pratt, & Franks, 2001; Pratt, Mallon,

Sumpter, & Franks, 2002; Couzin & Franks, 2003; Collignon & Detrain, 2009; birds:

Ballerini et al., 2008; Daruka, 2009; Nagy, Akos, Biro, & Viscek, 2010; fish: Sumpter,

Krause, James, Couzin, & Ward, 2008; Ward, Sumpter, Couzin, Hart, & Krause, 2008;

humans: Dyer et. al., 2008; Faria, Codling, Dyer, Trillmich, & Krause, 2009; Moussaid,

Perozo, Garnier, Helbing, & Theraulaz, 2010). Collective movements incorporate

necessary decision-making skills, which include self-organization principles and

leadership (Sueur, Deneubourg, & Petit, 2011; Furrer, Kunc, & Manser, 2012; Fernandez

et al., 2013). The social network of the species also plays an important role in collective

decision-making as the connectivity and affiliation to other individuals in a group can

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lead to successful movements that benefit each member (King & Cowlishaw, 2007; Ramseyer, Boissy, Dumont, & Thierry, 2009).

A preliminary examination of the distribution of collective movements in a troop of Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan, China shows that high-ranking individuals initiate more successful movements than low-ranking individuals. The frequency of successful movements does not significantly differ between mature and immature monkeys, nor is there a significant difference between females and males (Lewis, 2013). These results seem contradictory to previous collective movement literature, suggesting mature individuals in many species tend to initiate more group movements than immature individuals (King, Douglas, Huchard, Isaac, & Cowlishaw, 2008; Lusseau & Conradt, 2009; Petit, Gautrais, Leca, Theraulaz, & Deneubourg, 2009; Nagy et al., 2010; van Belle, Estrada, & Garber, 2013; Fernandez et al., 2013). In most mammals, female reproductive strategies include gaining access to high quality food resources and using this food acquisition to provide energy-demanding care to their potential offspring (Zhao, 1994; Zhao, 1997; Petit et al., 2009; Furrer et al., 2012; Fernandez et al., 2013). In contrast, the reproductive success of males primarily depends on the availability of females to mate with. As a consequence, females often engage in food or range competition more frequently than males and select mates that contribute the most to their reproductive success. Conversely, males engage in competition with other males and put most of their efforts into gaining access to females (Zhao, 1993, 1994, 1997; Berman, Ionica, & Li, 2007). This female-male pattern is known as Bateman's rule, which simply states that "females need food and males need females" (Bateman, 1948). The theory suggests that females would lead more successful collective

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movements than males because they have a greater fitness stake and thus incentive to do so. In a study of Tibetan macaques, Lewis (2013) found that more females initiated successful movements than males and two of those females (i.e., TH and YZ) were the most successful leaders of the troop, although the patterns she described were not statistically significant.

The theory may also favor females who have stronger social ties than their male counterparts. Female interactions are extremely valuable as they act as buffer against female reproductive costs. These interactions allow females to form strong relationships that must be maintained and protected to serve their adaptive function (Henzi, Lusseau, Weingrill, van Schaik, & Barrett, 2009). In most primate societies, extensive maternal care tied with an extended juvenile life history stage tends to manifest into a highly complex social structure that greatly impacts an individual's reproductive success (Altmann & Alberts, 2003). Altmann and Alberts (2003) found that the social environment of savannah baboons (*Papio cynocephalus*) increases variability in reproductive success, with social skills leading to matings despite the influence of dominance. Females often remain in their natal groups whereas males disperse when they reach maturity in a number of primate species (*M. mulatta*: Chepko-Sade & Sade, 1979; McCowan, Anderson, Heagarty, & Cameron, 2008; *M. thibetana*: Zhao, 1996; Zhao, 1997; Berman et al., 2004; Li et al., 2007; Sueur, Petit, et al., 2011; Thierry, 2011; Xia, Li, Garber, et al., 2012; Xia, Li, Matheson, et al., 2012; Sheeran, 2013; *P. ursinus*: Henzi et al., 2009). Primate societies can also be matrilineally structured wherein mothers, daughters and sisters maintain preferential bonds through grooming, supporting each other during conflicts and possessing stable dominance relationships (Thierry et al., 2000;

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Berman, Ogawa, Ionica, Yin, & Li, 2008; Sueur, Petit, et al., 2011; Thierry, 2011; Xia, Li, Garber, et al., 2012). Therefore, females need to bond to certain, often related, conspecifics who tolerate one another during food acquisition and remain cooperative during foraging conflicts (Thierry, 2011). Generally speaking, females in societies characterized by strong within-group competition must be able to form coalitions with related and high-ranking conspecifics so that they may gain access to resources (Berman et al., 2008). Female social strategies such as this allow certain females to outrank some males even if those males are individually stronger (Berman et al., 2004; Drea, 2005). The strength of female social connections may also allow females to avoid unsolicited sexual interactions with male suitors and to enhance the survival of their infants (Drea, 2005). Another study on savannah baboons found that social connectivity in adult females is positively correlated with infant survival, independent of maternal dominance rank, group membership, and environmental conditions (Silk et al., 2003).

Although collective movement study in a variety of taxa is becoming increasingly popular in the literature, studies that use empirical data or theoretical data implemented into models tend to lack emphasis on crucial factors such as leadership dynamics or social connectivity. Models in particular tend to oversimplify the complex reality of social organisms (Jacobs & Petit, 2011). The same is true for social network analysis, as behavioral studies with animals have only focused on this method within the last decade (Lusseau & Newman, 2004; Flack et al., 2006; Whitehead, 2008; Kasper & Voelkl, 2009; Jacobs & Petit, 2011; Sueur, Jacobs, et al., 2011; Pinter-Wollman, 2015a). Even with an intricate examination of complex relationships, a recent study by Franz, Altmann and Alberts (2015) states that animal social networks are still poorly understood. The current

study will attempt to examine both collective movement and sociality, focusing on social networks in relation to leadership frequencies and movement progressions. This will yield an in-depth perspective on how primates use their affiliative and aggressive associations to determine the individuals who lead and join collective movements. The study will attempt to answer the following questions: Do females lead more successful collective movements than males? What factors allow an individual to become the initiator of a collective movement? How do females contribute to the efficiency of collective movement progressions? What factors contribute to the following behavior of conspecifics?

The purpose of this study is to determine whether or not selection pressure on females for higher levels of social connectivity result in a significant increase in leadership and significantly more efficient movement progressions. I hypothesize that females are more socially connected than their male counterparts. The reproductive success of females depends more on highly structured social bonds and food acquisition than that in males. To test this hypothesis, I predict that high-ranking females will lead more collective movements than other troop members as shown in the preliminary results from Lewis (2013). Because collective movements with more individuals will result in an increase in the time taken to successfully complete a movement, I also predict that movements containing more females than males will progress quicker, and are therefore more efficient, as a result of the strong social bonds between females.

CHAPTER II

LITERATURE REVIEW

Social Networks

The social structure or the network of social bonds incorporates the hierarchical

design, kin relations and affiliative behaviors of a species (Sueur & Petit, 2008) while

also taking into account individual knowledge and motivation or his or her tendency to

continue a current behavior (Petit et al., 2009; Bode et al., 2012). Unlike other analytical

techniques, social network analysis focuses on the patterns of relationships between

individuals by identifying key players in a group, examining each individual's structural

and functional influence, and investigating how he or she increases or decreases the

social structure's stability (McCowan et al., 2008; Pinter-Wollman, 2015a, 2015b).

Although human social networks are much easier to study, the direct observation of

associations and interactions between individuals makes social network analysis possible

in nonhuman animals (Lusseau & Newman, 2004). In fact, this analysis has been

increasingly applied to animal behavior and primatology studies within the last decade

(Lusseau & Newman, 2004; Flack et al., 2006; Whitehead, 2008; Kasper & Voelkl, 2009;

Jacobs & Petit, 2011; Sueur, Jacobs, et al., 2011; Pinter-Wollman, 2015a). Although

social network analysis is becoming more popular in the literature, animal social

networks are still poorly understood (Franz, Altmann & Alberts, 2015). The method of

social network analysis was originally developed through mathematical graph theory

(Kasper & Voelkl, 2009; Sueur, Jacobs, et al., 2011) and famously forms the basis for the

"small worlds" concept (i.e., the structure of a network that allows two individuals to be

connected via other key individuals)—an idea behind the phrase, "six degrees of

separation" (Milgram, 1967). Moreno (1946) introduced the social sciences to the idea of sociograms and social matrices and a social network renaissance began through the desire to investigate large, dynamic networks such as the Internet (Voelkl & Noë, 2008; Kasper & Voelkl, 2009).

Primate social organization has received a great deal of attention due to the unknown environmental and evolutionary effects on sociality as well as the trickle-down effect social behaviors may have on other, well-studied demographics, or behaviors such as mating and foraging (Kasper & Voelkl, 2009). A comparison between various primate species may also prove beneficial to reveal the ultimate consequences of sociality and the many environmental pressures that lead to various primate social structures (Pinter-Wollman, 2015a). For example, Voelkl and Noë (2008) used a network approach to examine information propagation among primate groups. Their simulation experiments resulted in the influence of association patterns on the speed of information transmission (Voelkl & Noë, 2008). Franz and Nunn (2009) used a network-based diffusion analysis on artificially created learning data based on an empirical network of co-feeding associations from a group of eight Japanese macaques (*M. fuscata*) to detect social learning (i.e., the acquisition of new behaviors from other group members). The study found that this analysis provides greater statistical power to infer social learning than the diffusion curve analysis, the statistics previously used by other researchers (Franz & Nunn, 2009). Another study conducted by Henzi et al. (2009) sought to detect strong and persistent relationships between females in two chacma baboon troops in South Africa with social network techniques. Surprisingly, females use a more cyclical mode of sociality, which is dependent upon resource availability. When resources are available,

female relationships are not maintained and only short-term companionships persist (Henzi et al., 2009).

Chepko-Sade and Sade (1979) identified where female social bonds are likely to break during a fissioning event by creating a social network for a group of free-ranging rhesus macaques on Cayo Santiago, Puerto Rico. They found that the loss of the central female in a group increases the probability of a group division, because the primary tie of every female to her matrilineal group is through her mother, and the daughters of the central female may act as independent units following a division (Chepko-Sade & Sade, 1979). Watts (2000) investigated male-male grooming networks of chimpanzees at the Kibale National Park in Uganda to test whether or not opportunity costs limit the number of individuals who interact through grooming and lead males to only concentrate on certain, central partners. Male chimpanzees mostly groom an average of 8-12 other adult males, leading to the conclusion that male-male grooming reinforces the male bonds necessary to chimpanzee sociality (Watts, 2000). McCowan et al. (2008) examined the agonistic patterns of rhesus macaques over a three-year period at the California National Primate Research Center. They found that the degree of affiliative interactions such as grooming is significantly correlated with the rate of aggression and the occurrence of "cage wars" (i.e., severely aggressive outbreaks). They also found that a lower proportion of adult females within a group leads to increased social power, decreased fragmentation and decreased aggressive intensity, and that social cohesion prevails through higher rates of affiliative reciprocity. The study concludes that group composition and matrilineal structure may be manipulated to reduce morbidity and mortality through aggression in rhesus macaques (McCowan et al., 2008).

In the study of social networks, researchers typically focus on single individuals or dyads to make statements that characterize the group (Ogawa & Takahashi, 2003; Kasper & Voelkl, 2009; Jacobs & Petit, 2011; Sueur, Jacobs, et al., 2011) although it is vital to understand the benefits and costs of individual variation on biological systems such as social insect colonies (Pinter-Wollman, 2015b). However, it is necessary to examine interactions that involve three or more individuals to assess primate social structure (Ogawa & Takahashi, 2003). Also, researchers who have examined social organization and structure in the past used a traditional, categorical approach based on sex, hierarchy, ecological factors and life-history traits, which failed to capture specific aspects of sociality (Kasper & Voelkl, 2009). Kasper and Voelkl (2009) used a set of structural network metrics to describe primate social organization using 70 primate groups gathered from previously published and unpublished literature. They found that primate social organization is highly diverse, as indicated by the variation in the network metrics between the groups, and concluded that network analysis can quantitatively highlight important differences on the group level (Kasper & Voelkl, 2009). Using the same dataset, the researchers also examined the emergence of cooperation among interactional primate networks and found clear evidence of cooperative facilitation through social structure (Voelkl & Kasper, 2009).

The social network is strongly tied to the process of collective decision-making and movement, allowing individuals to maintain cohesion and control speed as well as group size (Moussaid et al., 2010; Bode et al., 2012; Zhang et al., 2012). In fact, group members may join the movement progression through kinship and affiliation to increase their own fitness (Ramseyer et al., 2009; Sueur et al., 2011). Social information is crucial

in human crowd dynamics (Moussaid et al., 2010) and serves as a great benefit to many group-living species (King & Cowlishaw, 2007). Using a collective movement model, King and Cowlishaw (2007) found that individuals gain their social information from the environment and from informed group members through signals (i.e., intentional communication) or cues (i.e., unintentional communication), both of which allow for quicker, more accurate decisions. Individuals may gather information from many group members to come to a correct conclusion and should avoid this information gathering when the knowledge is of poor quality or when the group is too large. Another model by Bode et al. (2012) examined the influence social preference has on leadership and the impact of social networks on these collective decisions. When a conflict arises between the informed individuals of the group, their social positions only need to be higher than average to achieve consensus among the other group members (Bode et al., 2012). A numerical, model-based study measuring bird positions has been attempted to examine simple interactive rules as the basis of collective behavior and to assess topological versus metric distance between birds in flight (Ballerini et al., 2008). European starlings (*Sturnus vulgaris*) interact with six to seven neighbors during collective flights to increase their anti-predatory response and utilize topological over metric distance to strengthen cohesion (Ballerini et al., 2008). In fact, social organization influenced by ecological conditions seems to serve as an anti-predation strategy in many animal species (Barelli et al., 2008; Sueur & Petit, 2008; Ramseyer et al., 2009; Jacobs et al., 2011). In a study on mixed-species flocking structure, researchers examined the species differences and social systems of jackdaws (*Corvus monedula*) and rooks (*C. frugilegus*) to understand how heterogeneous structure can influence movement rules. Using high-

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resolution photography and proximity to neighbors, they found that socially dominant rooks are at the front of flock movements, suggesting the presence of initiation or leadership among rooks, and both corvid species usually remain close to conspecifics, suggesting an importance of monogamous pair bonds. Flock structure cannot be understood or defined without the incorporation of social connectivity (Jolles, King, Manica, & Thornton, 2013). Using hierarchical cluster analysis, Zhang et al. (2012) found that the overall network connectivity of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) is sparse, indicative of a multilevel society. Betweenness and eigenvector centrality indices indicated strongly-linked female relationships in which females hold more important social roles than males. The female-bonded social organization is also more fluid than researchers expected, with smaller networks being less stable than larger ones. The researchers claimed the plasticity in network structure is due to ecological and social conditions (Zhang et al., 2012).

An important study on social connectivity in macaques attempted to examine the co-variation of social style by ranking each on a four-graded scale from despotic (grade 1) to egalitarian (grade 4). Overall, those categorized into grade 1 possess asymmetrical patterns of social interaction, intense dominance, strong kin bias and infrequent post-conflict affiliation whereas those belonging to grade 4 possess strong group cohesion and moderate levels of kin bias (Thierry, Iwaniuk, & Pellis, 2000; Berman, Ionica, & Li, 2004; Berman et al., 2008; McCowan et al., 2008). A follow-up study to the initial four-graded assessment tested the importance of phylogenetic lineage in social organization and categorized sixteen macaque species (Thierry et al., 2000). Grade 1 includes rhesus macaques, Japanese macaques and Taiwanese macaques (*M. cyclopis*); grade 2 includes

long-tailed macaques (*M. fascicularis*) and pig-tailed macaques (*M. nemestrina*); grade 3 includes stump-tailed macaques (*M. arctoides*), Assam macaques (*M. assamensis*), bonnet macaques (*M. radiata*), lion-tailed macaques (*M. silenus*), toque macaques (*M. sinica*), Barbary macaques (*M. sylvanus*) and Tibetan macaques; grade 4 includes moor macaques (*M. maura*), crested black macaques (*M. nigra*), booted macaques (*M. ochreata*) and Tonkean macaques. Grades 2 and 3 presented great difficulty for categorization. Although there is still debate, researchers confirm the phylogenetic influence of macaque social organization and certain conserved social features over time within each grade such as male-female dominance relationships and individual temperament. Traits such as aggression and conciliation were inconclusive and do not correlate with phylogeny, but traits such as male dispersion and dominance ranks do correlate and present interspecific variation. However, it is worth noting that ecological theories suggest a greater environmental influence on social organization and related traits. Therefore, the phylogenetic examination of social traits may be inappropriate for this genus (Thierry et al., 2000).

Sueur and Petit (2008) used this scale analysis to compare the social organization of semi-free ranging rhesus and Tonkean macaques when joining movements. Rhesus macaques structure their movements through dominance and kinship, as older and more dominant males possess the highest centrality and join movements based on kin relations. Tonkean macaques possess no specificity in their movement structure with dominance weakly influencing behaviors and the equal likelihood of an individual joining movements. Using the semi-free ranging rhesus macaque data (Sueur & Petit, 2008), Jacobs et al. (2011) compared those findings to the movement style of wild Japanese

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macaques, predicting that both would have the same social organization as both belong to the same grade. High-ranking Japanese macaque males and females initiate movements, and their associations are strongly dependent on kinship, which is similar to rhesus macaques. Sueur, Petit and colleagues (2011) conducted a comparative network analysis of 12 groups in four species of macaques (rhesus macaques, Japanese macaques, crested black macaques and Tonkean macaques) to show that top-ranking group members are more central in less tolerant species. The results did not confirm this statement but showed that rhesus and Japanese macaques (i.e., intolerant species) have more clustered networks than their tolerant counterparts. The results also showed that the centrality coefficient decreases as group size increases and that the kin-contact coefficient increases as the proportion of females in a group increases, both of which act in unison (i.e., the more related individuals present, the more central key individuals were). In conclusion, interspecific variation exists among macaque social structures and affiliative relationships underpin their collective movements (Sueur, Petit, et al., 2011).

Collective Decisions

Animal groups continuously shift from grooming to foraging or find new places to sleep or nest, both of which require decision-making mechanisms (Sueur, 2012). Self-organization principles seen at the individual level govern the local interactions of collective decision-making. The global structure of a collective movement is unknown; a lack of centralized control seems to persist (Sueur et al., 2011). There are two main self-organization principles, mimetism and quorum response. Mimetism is further divided into two types: anonymous and selective. Anonymous mimetism is when multiple individuals contribute to a decision by joining a movement according to the number of

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individuals who are already joining and is independent of rank or affiliation. Selective mimetism is when multiple individuals contribute to a decision by joining a movement according to the number of individuals who are already joining as well as the social or affiliative relationships they have with those individuals (Jacobs, Sueur, Deneubourg, & Petit, 2011; Lewis, 2013; Wang et al., in press). Quorum response (i.e., social amplification or majority rule) represents the threshold of individuals performing a behavior that is necessary for other conspecifics to display the same behavior (Kerth, Ebert & Schmidtke, 2006; Ward et al., 2008; Sumpter & Pratt, 2009; Pyritz, King, Sueur, & Fitchel, 2011; Sueur et al., 2011; Furrer et al., 2012; Fernandez et al., 2013; Lewis, 2013; Wang et al., in press).

Leadership (i.e., initiation) also governs decision-making, which may be defined as personal (i.e., unshared) or distributed (i.e., shared). Personal leadership means the movement occurs with one initiator where conspecifics benefit from that individual's knowledge and distributed leadership means the movement can occur with more than one initiator where individuals pool their knowledge (Barelli, Boesch, Heistermann, & Reichard, 2008; King et al., 2008; Petit et al., 2009; Ramseyer et al., 2009; Pyritz et al., 2011; Sueur et al., 2011; Furrer et al., 2012; Sueur, 2012; van Belle et al., 2013; Fernandez et al., 2013). Distributed leadership has another layer as it may be equally shared, meaning all individuals in the group can initiate, or partially shared, meaning only a certain number of individuals from the group can initiate (Pyritz et al., 2011; Sueur, 2012; van Belle et al., 2013; Fernandez et al., 2013).

Honeybees (*Apis* sp.) and several species of ants such as army ants (*Eciton burchelli*), pavement ants (*Tetramorium caespitum*) and *Lepthothorax albipennis* use a

quorum response to make decisions about foraging and nesting areas. Honeybee colonies select nectar sources by having a relatively small number of individuals "waggle dance" to recruit other members. The self-organized quorum rule occurs during both recruitment and abandonment of their food sources, allowing for quick responses that limit the presence of stress and damage (Seeley et al., 1991). Chemical trails and simple interactive rules govern the traffic flow of army and pavement ants (Couzin & Franks, 2003; Collignon & Detrain, 2009). Army ants create a three-lane structure where returning individuals occupy the middle lane and avoid collisions with conspecifics. The three-lane structure results in increased coordination and movement flow. These ants can move in the same direction as most of their conspecifics are moving in through the presence of pheromones (Couzin & Franks, 2003). Similarly, pavement ants have leaders who discover a food source and recruit members through a chemical trail. Once a sufficient number of group members follow the trail, this alone can ensure others find the food source without the presence of the initial leaders (Collignon & Detrain, 2009). *L. albipennis* uses tandem running (i.e., ant moves from the old nest site to the new one) to initially recruit subgroups and social carrying (i.e., carrying remaining group members and brood items to new nest site) to reliably choose a superior nesting site (Mallon et al., 2001; Pratt et al., 2002). Like honeybees, these ants also use a small number of individuals to examine potential nesting sites and recruit members who follow a quorum response (Mallon et al., 2001). The time spent to reach a quorum leads to efficient emigration by allowing followers to assess the picked site and reducing the chance of the group splitting up. The population sizes also weakly but significantly affect the necessary quorum size (Pratt et al., 2002).

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Three-spined stickleback (*Gasterosteus aculteatus*) shoals have been studied extensively in regard to collective movements and their use of quorum response. By presenting the focal fish with two phenotypically different fish replicas, Sumpter et al. (2008) examined the quorum response strategy of the species and found that the subjects always follow the more attractive of the two replicas, with the proportion of followers positively correlated with group size. Using a constructed maze with replicated conspecifics and a simulation model, Ward et al. (2008) found that the fish go in the direction initiated by the majority independent of which fish initiates (i.e., conspecifics or replica fish). The results from the simulation model in particular showed how quorum response improves the accuracy of decisions as individuals use the decisions made by others to avoid flaws in their own decision-making abilities. This finding has led the researchers to discuss the information transfer hypothesis, which is when individuals join a group and respond to the actions of others by a quorum response so that they may gain an advantage over solitary individuals during information processing (Ward et al., 2008). This theory also plays a role in the fission-fusion societies of Bechstein's bats (*Myotis bechsteinii*). An experimental manipulation of roost suitability and conflicting information transfers tested the decision-making mechanisms used by females in this species. The bats make frequent collective decisions by considering both individual and conspecific information. Almost all individuals visit the roost, using a quorum threshold to later decide whether or not they should remain there. These female bats may avoid making the wrong choice and increase accuracy by forming subgroups and relying on the decisions of their conspecifics (Kerth et al., 2006).

Some primate species combine both quorum response and mimetism throughout the collective movement process. A semi-free ranging group of white-faced capuchins (*Cebus capucinus*) at the Primate Centre of Strasbourg University in France join movements using a mimetic process and then switch to a quorum rule to avoid the cancellation of a movement by the initiator (Petit et al., 2009). A semi-free ranging group of brown lemurs (*Eulemur fulvus fulvus*) at the same facility display a probability to join based on quorum response and selective mimetic behavior (Jacobs, Sueur, et al., 2011). Tonkean macaques (*M. tonkeana*) at this facility use mimetism for notifying behaviors during the pre-departure process (i.e., the decision to start a movement) and, like brown lemurs, switch to a combination of quorum response and selective mimetism based on affiliation with other group members when individuals want to join a movement. Incorporating a stochastic agent-based model with empirical data from two Tonkean macaque groups showed a link between the two processes through a voting mechanism and how quorum response and selective mimetism act together in departure (Sueur et al., 2011). A more recent study by Wang et al. (in press) examined the departure process in free-ranging Tibetan macaques at Huangshan, China to determine which self-organization principle governs their collective decisions during movement. Tibetan macaques adjust their joining rule based on the number of individuals involved in the movement. When there are three-six early joiners (i.e., an individual that moves within the first five minutes after the initiator's departure), individuals use selective mimetism. When there are seven or more early joiners, individuals use a quorum response. They concluded that early joiners play a central role in deciding which principle to use and that

their rank or social relationships may determine whether or not other group members join in the movement progression (Wang et al., in press).

The speed and accuracy of decisions being made and the trade-off between these two variables are vital to the success of collective movements (Franks, Dornhaus, Fitzsimmons, & Stevens, 2003; Sumpter & Pratt, 2009). Researchers have explored this concept by investigating the rate of nest choice in harsh versus normal conditions of ants to determine whether an increased speed reduces the accuracy of the decisions. In harsher conditions, recruitment for nest choice requires a lower quorum threshold, which quickly leads to error-prone decisions (Franks et al., 2003). The high quorum threshold in a normal environment allows for accuracy, which requires a higher quorum threshold and creates an extended time period to choose between alternative nesting sites (Franks et al., 2003; Sueur, 2012). A simple mathematical model developed by Sumpter and Pratt (2009) also makes this point, showing that quorum thresholds can tune the trade-off between decision speed and accuracy. The "wisdom of crowds" argument states that poorly informed individuals collectively make better decisions than a smaller collection of informed individuals, which is the premise of the Condorcet theorem (King & Cowlishaw, 2007; Sumpter & Pratt, 2009). The simulation model showed how a more accurate choice also results in an extended time period to make such a choice and how a faster decision results in more group members making error-prone decisions (Sumpter & Pratt, 2009). Group size is also a factor in speed and accuracy as the quorum threshold is usually smaller for larger groups (Sueur, 2012). In a recent study, Pinter-Wollman (2015b) investigated how individual variation affects social network structure by examining the spatial behavior of working harvester ants (*Pogonomyrmex barbatus*). The

study found that spatial behavior promotes frequent interactions in a network and facilitates the rapid information flow inside of the nest. The process of information transmission is negatively affected when certain individuals are lost (Pinter-Wollman, 2015b).

Leadership and self-organization principles act in unison with each another to produce a collective movement. Leaders may possess an advantage; they pull others into a direction they find beneficial for their individual fitness and potentially gain the respect of their following conspecifics. Leadership can also be costly as there is a higher energetic requirement as well as higher risks. Age, sex, dominance rank, nutritional needs and socialization patterns influence leadership roles (Petit et al., 2009). Studies show that adults tend to initiate more than their immature counterparts and relate this finding to greater experience and knowledge (Barelli et al., 2008; King et al., 2008; Lusseau & Conradt, 2009; Petit et al., 2009; Nagy et al., 2010; van Belle et al., 2013; Fernandez et al., 2013). However, one study on wild but habituated banded mongoose (*Mungo mungo*) in Uganda found that there is no influence of age on the initiation of morning group departures (Furrer et al., 2012). The influence of nutritional needs has been termed "leading according to need" in the literature and represents those individuals as having a greater incentive to move (Furrer et al., 2012; Sueur, 2012). According to Sumpter (2009), a small number of individuals who have stronger needs than others may become leaders over a larger group of less-needy individuals. Deprivation of food/feeding experiments in banded mongoose found that deprived individuals are more likely to initiate (Furrer et al., 2012). Sueur's (2012) model found that collective decisions are the most dependent on the needs of all individuals involved. "Leading according to need" is a

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viable method regardless of the five varying conditions (i.e., water availability, protein availability, energy expenditure, resting state and socialization), where personal leadership is best when there is little difference in the needs of individuals and distributed leadership is best when there is more of a difference (Sueur, 2012).

Different species also possess differences in how sex and dominance rank initiate a group movement. Females who lead gain access to more high quality food resources and may do so as a reproductive strategy, whereas males who lead maintain their dominance status or do so as a mating strategy, all of which represent the sexual selection theory (Zhao, 1997; Barelli et al., 2008; Petit et al., 2009; Furrer et al., 2012; Fernandez et al., 2013). Psychological theories have also found support for the leader-member exchange (LMX) theory, which states that leadership is affected by the relationships between dominant and subordinate individuals (van Vugt, 2009). Across taxa, females lead more group movements than males (Petit et al., 2009), but a model based on macaque data with manipulated conditions demonstrates how personal leadership favors males as their increased body mass requires more nutritional intake (Sueur, 2012). Groups of wild black howler monkeys (*Alouatta pigra*) have the highest-ranking females initiating and leading significantly more collective movements than males while using a partially shared leadership form. However, nutritional requirements and reproduction do not influence their roles in the group movements (van Belle et al., 2013). Groups of wild white-handed gibbons (*Hylobates lar*) in Thailand also have females initiate and lead significantly more movements than males but possess a distributed leadership form (Barelli et al., 2008). Sheep ewes (*Ovis aries*) show distributed leadership during continuous group departures, with the involvement of several individuals being resolved

through communication and social ties (Ramseyer et al., 2009). Banded mongoose show no significant influence of sex on leadership, although pregnant females tend to initiate more during synchronized breeding periods (Furrer et al., 2012). On the other hand, dominant males of wild chacma baboons (*Papio ursinus*) usually lead the group to experimental food patches and obtain the most food resources even though both sexes are just as likely to lead (King et al., 2008). Wild black and gold howler monkeys (*Alouatta caraya*) use distributed leadership, and males lead more often than females during intergroup encounters. Once again, females and males are equally likely to lead during other activities (Fernandez et al., 2013). An interesting species with regards to personal leadership is bottlenose dolphins (*Tursiops* sp.) in New Zealand, where males initiate travel with a side-flop and females end the movement with an upside-down lobtail (Lusseau & Conradt, 2009).

Leader-follower dynamics may result from a need for individuals to effectively coordinate with one another (van Vugt, 2009) and have been examined in a number of cases. First, the spatial position of leaders in a movement differs depending on the species and may affect the decision process (Ramseyer et al., 2009; Bode, Franks, & Wood, 2012). Female initiators in white-handed gibbons and pigeon (*Columba* sp.) flocks tend to remain in the front of the movement (Barelli et al., 2008; Nagy et al., 2010), whereas chacma baboons are not necessarily needed at the front for movement initiation (King et al., 2008). Similarly, the leader of group departures in sheep tends to participate from the edge of the group (Ramseyer et al., 2009). Second, leaders and followers may possess differences in physiology, temperament, intelligence, or personality. Generally, individuals who are more gregarious tend to take more initiative and emerge as leaders

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more often than those who are more reserved (van Vugt, 2009). For instance, stickleback leaders are bolder and display a greater initiative to move whereas followers are shy and only move when other individuals have moved (Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009). A follow-up study using continuous-time Markov models found that stickleback followers also alter the way in which they respond to their leaders (Nakayama, Harcourt, Johnstone, & Manica, 2012). Finally, the affiliation between leaders and followers determine how willing the followers are to come to a decision they did not make themselves (King et al., 2008; Ramseyer et al., 2009). Individual chacma baboons more affiliated to the leader follow more closely, and the following behavior in this species occurs through the combination of social rank and affiliation (King et al., 2008). Similarly, sheep ewes tend to remain close to one another during a movement based on their affiliative bonds (Ramseyer et al., 2009). These studies collectively demonstrate why the social network is pertinent to the success of joint movements (Bode et al., 2012; Zhang, Li, Qi, MacIntosh, & Watanabe, 2012).

<center>Tibetan Macaques</center>

There are 23 species of macaques, which belong to three distinct groups: *silenus-sylvanus*, *sinica-arctoides*, and *fascicularis* (Thierry et al., 2000; Thierry, 2011; Li, Zhao, & Fan, 2015). Tibetan macaques are also known as Milne-Edwards' or Pere David's macaques and belong to the *sinica-arctoides* lineage (Fooden, 1983; Fooden, Guoqiang, Yongzu, Mingchaun, & Monyuan, 1994; Yongcheng & Richardson, 2008; Thierry, 2011; Sheeran, 2013). They closely resemble stump-tailed macaques and Barbary macaques in appearance and Assam macaques genetically (Pan, Jablonski, Oxnard, & Freedman, 1998; Berman et al., 2004; Berman, Li, Ogawa, Ionica, & Yin, 2007). This near-

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threatened species is native to east-central China, ranging from Guangxi to Yangtze

Gorge and Sichuan (Fooden et al., 1994; Takahashi & Pan, 1994; Pan et al., 1998;

Yongcheng & Richardson, 2008; Sheeran, 2013), with daily movements of 100-3000 m

(Thierry et al., 2000). This terrestrial and diurnal species prefers forested areas,

particularly primary and secondary evergreen, subtropical and deciduous forests (Fooden,

1983; Zhao, 1999; Matheson, Sheeran, Li, & Wagner, 2006; Yongcheng & Richardson,

2008; McCarthy et al., 2009; Thierry, 2011; Sheeran, 2013). Dense forests are necessary

for obtaining suitable, relatively fixed sleeping sites (e.g., group of large trees or ledge in

the middle of a cliff) and accessing widely distributed food sources (Zhao & Deng,

1998). These macaques mostly feed on fruits and leaves but occasionally eat other plant

parts, flowers and prey such as invertebrates, snakes and birds (Takahashi & Pan, 1994;

Zhao, 1999; Thierry et al., 2000; Thierry, 2011; Sheeran, 2013). They are also the largest

of the genus (Takahashi & Pan, 1994; Pan et al., 1998; Berman, Li, et al., 2007; Li et al.,

2007) and the most derived species of the *sinica-arctoides* group (Fooden, 1983; Sheeran,

2013).

Tibetan macaques possess a diverse yet unified social organization structured

around dominance hierarchies and kin relations (Berman et al., 2008; Thierry, 2011).

These monkeys form multi-male, multi-female groups of 15-50 individuals (Ogawa,

1995; Thierry et al., 2000; Ogawa & Takahashi, 2003; Berman et al., 2004, 2007;

Berman, Li, et al., 2007; Li et al., 2007; Sueur, Petit, et al., 2011; Thierry, 2011; Xia, Li,

Matheson, et al., 2012; Sheeran, 2013). Although males seem to outnumber females with

a sex ratio of 1:1-9 in most troops (Sheeran, 2013), females are philopatric and males

disperse when they reach adulthood (Zhao, 1994, 1996, 1997; Ogawa, 1995; Ogawa &

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Takahashi, 2003; Berman et al., 2004, 2007, 2008; Li et al., 2007; Sueur, Petit, et al., 2011; Thierry, 2011; Xia, Li, Garber, et al., 2012; Xi, Li, Matheson, et al., 2012; Sheeran, 2013). Males tend to immigrate to sexually attract unfamiliar females or avoid competition with other males (Zhao, 1993, 1994). Males obtain the top dominance ranks as they compete for mates through rank competition (Berman et al., 2007), but some females outrank some males (Berman et al., 2004). Female macaques usually obtain a dominance rank right below their mothers and the youngest daughters outrank their older siblings, both of which result in linear hierarchy and intergroup competition among females (Chepko-Sade & Sade, 1979; Zhao, 1997; Berman et al., 2004; Li et al., 2007; McCowan et al., 2008; Thierry, 2011; Xia, Li, Garber, et al., 2012).

The kin bias appears to be strong in most macaque species with most related individuals remaining close to one another through proximity and grooming (Berman et al., 2008; Thierry, 2011). As such, the most persistent affiliation occurs between the mother and her infant (Deng & Zhao, 1991). Berman et al. (2008) found that kin bias examined through grooming is higher when the group is larger, that females are unable to maintain numerous grooming relationships as the group expands, and that the lower-ranking females almost always groom close kin. A study conducted by Xia et al. (2011a) found mother-daughter and sister-sister dyads prefer to groom each other more often than unrelated dyads do. Tibetan macaques are seasonal breeders that normally birth their offspring between January and April (Ogawa, 1995; Xia, Li, Matheson, et al., 2012) with their mating season beginning in July (Li et al., 2007; Berman, Li, et al., 2007; Berman et al., 2008). The societies are matrilineally structured as mothers, daughters and sisters maintain preferential bonds through grooming, supporting each other during conflicts and

possessing stable dominance relationships (Thierry et al., 2000; Sueur, Petit, et al., 2011; Thierry, 2011; Xia, Li, Garber, et al., 2012). Males can develop strong relationships through the handling of infants (Ogawa, 1995) and coalition conflict support (Thierry, 2011). In fact, males form triadic relationships with their infants as a cohesion tool or male consortship method (Ogawa, 1995; Zhao, 1996). They also tend to huddle together, indicative of their affiliative nature (Ogawa & Takahashi, 2003). The strong affiliation among Tibetan macaques may reduce the social tension present between males (Ogawa, 1995). High-ranking males may also support and tolerate other males when they find it necessary to do so to gain access to females during the mating season (Berman et al., 2007).

Over the past decade, the four-graded scale analysis has been controversial as applied to the Tibetan macaques. Thierry et al. (2000) first placed this species in the third level of the scale, as individuals possess more similarities with grade 4 than they do with grade 1. A study by Ogawa and Takahashi (2003) also states that Tibetan macaques are egalitarian and have a more relaxed dominance style based on their huddling behavior. However, Berman et al. (2004) found that Tibetan macaques at Mt. Huangshan, China are more despotic than previously thought. The levels of asymmetrical aggression, conciliatory tendency and affiliative kin bias more closely resemble those observed in other despotic macaque species (Berman et al., 2004, 2008). These measures are consistent across different partners, time periods and locations seen at Mt. Huangshan, China and, therefore, should be placed into the second grade on the scale (Berman et al., 2004). Berman et al. (2007) also made a distinction between males and females, stating that males tend to be more egalitarian than their female conspecifics as they possess

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higher conciliatory tendencies. Lewis (2013) also pointed out the difficulty in categorizing the YA1 troop into a grade during her study on their collective movements, stating that the four-graded analysis may not accurately measure the YA1 troop's social tolerance.

CHAPTER III

METHODS

Subjects and Study Site

Data collection occurred from July to September 2014 on a free-ranging group of

Tibetan macaques at Mt. Huangshan National Reserve located in Anhui province, China

(118.3E, 30.2N, elevation 1814m). This site is a UNESCO World Culture and Nature

Heritage site that allows tourism (Xia, Li, Garber, et al., 2012). More information about

the research site can be found elsewhere (e.g., Berman & Li, 2002; Li et al., 2007;

McCarthy et al., 2009).

There are two troops that reside here, Yulingkeng A1 (YA1) and Yulingkeng A2

(YA2). The YA1 group was the focus of this study. It consisted of 45 individuals (9

adults males and 11 adult females) as of July 2014 (Dao, personal communication). YA1

is a troop that has been monitored by researchers in China since 1986 (Ogawa, 1995;

Ogawa & Takahashi, 2003; Berman et. al., 2004, 2007, 2008; Berman, Li, et al., 2007;

McCarthy et al., 2009; Xia, Li, Garber, et al., 2012; Xia, Li, Matheson, et al., 2012). The

troop was driven into an unoccupied area in 1992 to make the troop more visible to

tourists (Berman & Li, 2002; Li et al., 2007; Berman et al., 2007, 2008) and is now seen

from several viewing platforms (Matheson et al., 2006). This led to the provisioning of

the macaques, who receive corn 3-4 times daily from park staff in an easily accessible

feeding area (Ogawa, 1995; Berman & Li, 2002; Li et al., 2007; Xia, Li, Garber, et al.,

2012; Xia, Li, Matheson, et al., 2012). The troop has become accustomed to a steady

food supply and therefore, collective movements often occurred during the switch

between feeding and resting periods. Collective movement data were mostly collected when the troop was leaving the feeding area.

The members of YA1 are particularly habituated to human presence and will interact with tourists (McCarthy et al., 2009). I only considered the adults in the troop for this study as juveniles and infants do not show tendencies to lead during collective movements (Wang et al., in press). The sociodemographic characteristics of the 20 adults included in this study are provided in Table 1 and kin relations are provided in Table 2. All adults were individually recognized based on unique physical features such as scars, injuries and hair color patterns (Li, 1999; Xia et al., 2012). An adult male immigrated into the troop during the study period and, therefore, behavioral data might not be comparable to the data collected for the other adults. Hence, the data collected about this

Table 1

Sociodemographic Characteristics of YA1 Adult Members in 2014

ID	Sex	Rank	Age	Focal Duration (s)	ID	Sex	Rank	Age	Focal Duration (s)
ZB	Male	1	14*	6250	YH	Female	1	11	5943
TG	Male	2	11	5073	YM	Female	2	24	6769
GS	Male	3	30	6328	YCY	Female	3	5	6977
ZL	Male	4	17*	6596	THY	Female	4	5	4758
YRB	Male	5	6	2887	TRY	Female	5	5	6860
BT	Male	6	26*	6035	HH	Female	6	11	5327
DS	Male	7	14*	6847	TH	Female	7	11	6686
HT	Male	8	24*	7481	TXX	Female	8	6	6387
TRB	Male	9	6	6612	TR	Female	9	10	5710
					TT	Female	10	23	7139
					YZ	Female	11	22	7410

*These individuals immigrated into the group. Therefore, their ages are estimated based on physical features (Sheeran, personal communication)

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adult male were excluded from analysis. An additional young adult female was identified during the study period and was also excluded from data collection based on the same principle. YeRongBing (YRB) was included in data collection but later excluded from social network analysis due to a focal duration period that was much lower than the other adults (see Table 1). A lack of observation for these three individuals could indicate that certain members never interact with each other even when that is not the case (Kasper & Voelkl, 2009). Researchers at Anhui University maintained the identities of the individuals, and they were available for identification throughout the study.

Table 2

Mothers and Their Adult, Juvenile and Infant Kin Relations

Mother	Kin					
	Adult		Juvenile		Infant	
	Male	Female	Male	Female	Male	Female
YM		YH YCY	YCLan	YCLong		
TT	TG TRB	TR TRY[a]	TRG TRY[b]	TRX*		
YZ	YRB		YRQ	YRX YRL*		
YH			YXK	YXX	X*	
HH			HXM HXH	HXW*		
TH		TXX[b]	TXH TXL		X*	
TR		THY	THH	THX		X*
TXX[a]				TQL*		

Note. Individuals marked with * represent juveniles or infants who are still weaning. Infants are marked with an X, as they were not given IDs at the time of study. Individuals are marked with an a or b to differentiate between two individuals who have the same ID initials.

Preliminary data collection and individual identification occurred from July 30, 2014 to August 9, 2014. A second researcher familiar with the study subjects assessed the reliability of individual identification during this time. Observations occurred from various viewing platforms near the feeding sites and at other locations that allow for visibility of the troop (see Figure 1).
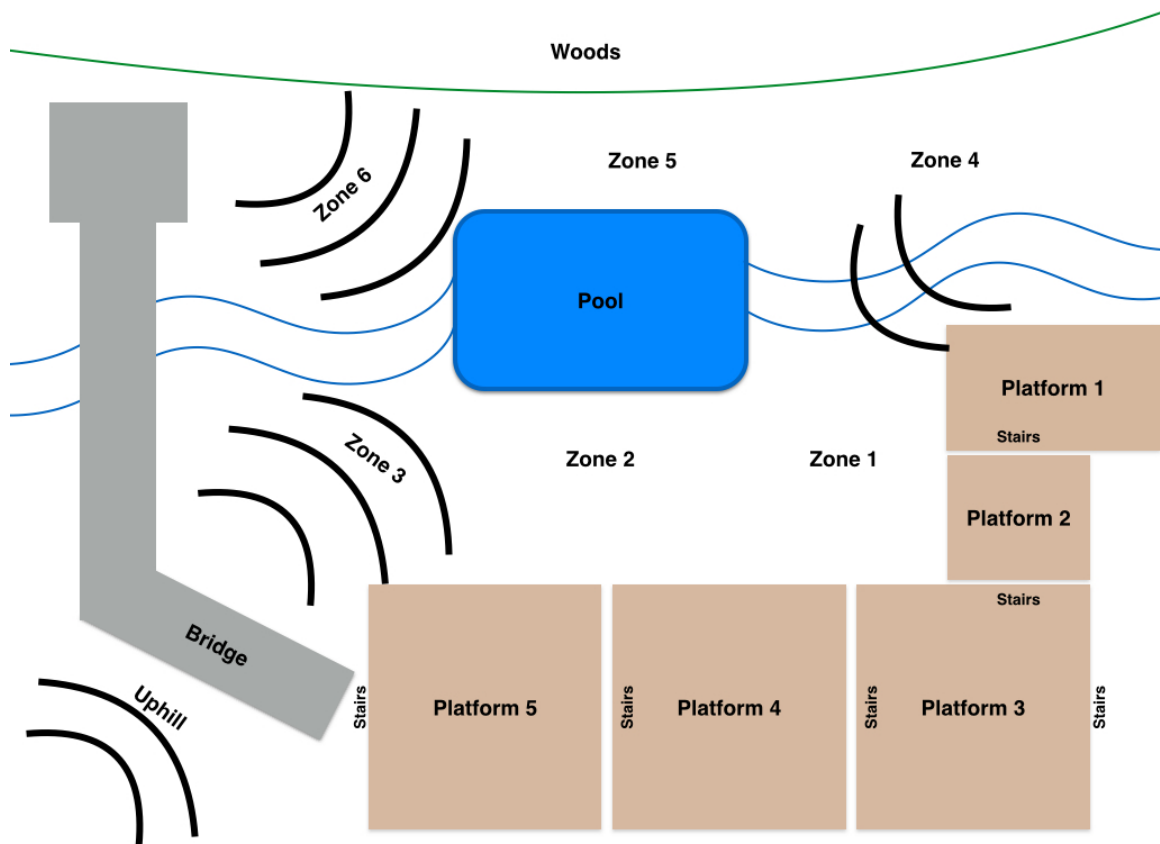
Figure 1. Diagram of the data collection area.

I recorded collective movements using an all-occurrence sampling method (Altmann, 1974). I based the analyses on 128 collective movements initiated by the 20 adult subjects. I collected data using a pen-and-paper method, later transferred to an Excel spreadsheet. A movement initiation began when one individual, the "initiator,"

moved approximately >10 m away from a stationary group in less than 40 s (Sueur &

Petit, 2008; Lusseau & Conradt, 2009; Petit et al., 2009; Jacobs, Sueur, et al., 2011;

Pyritz et al., 2011; Sueur et al., 2011). An individual who moved >5 m within a 45°angle

of the initiator's movement direction and within 5 min is a "follower" (Jacobs, Sueur, et

al., 2011; Sueur et. al., 2011; Sueur, Petit, et al., 2011). Each subsequent follower must

adhere to the same rules with the individual who moved previously. A successful

movement occurred when ≥2 individuals follow an initiator and an unsuccessful

movement occurred when no individual follows an initiator within a 5-min time period

(Jacobs, Sueur, et al., 2011; Pyritz et al., 2011). A movement finished when no other

individual joins within a 5-min time period (Jacobs, Sueur, et al., 2011). During each

collective movement, I identified all adult individuals (i.e., initiator, followers and those

who do not join) with a corresponding timestamp of when an individual began to move.

During periods when collective movements were not occurring, I collected data to

determine whether or not social connectivity had an influence on leadership frequency

and movement progression. I also collected this data using a pen-and-paper method, later

transferred to an Excel spreadsheet. If individuals moved further away from the viewing

platform, I used binoculars during observation. Using a focal animal sampling method

(Altmann, 1974) with a 5-min sample point, I gathered measures of affiliation and

aggression in a group. I examined affiliation through proximity, sitting near, co-feeding

and grooming. Individuals were in proximity with one another if they were ≤1 m away

from each other. In between focal samples, I used a scan sampling method (Altmann,

1974) with a 6-min sample point as another means of gathering proximity measures. I

collected agonistic data to determine the effect of social rank on leadership frequency,

which included threats, lunges, chases, grabs and bites defined by Berman et al. (2004, 2007). I considered an individual as a higher or lower rank based on the Clutton-Brock index of fighting success (Clutton-Brock et al., 1979). If at any point during either a focal or scan sample an individual initiates a collective movement, I switched back to an all-occurrence sampling method to capture movement data.

Statistical Analysis

I conducted a social network analysis for affiliation, aggression and collective movement to determine the social connections of the macaque troop. A node refers to each individual macaque in a network, where males are represented by squares and circles represent females. An edge represents an affiliative, aggressive or movement interaction/association and is represented by a line between two or more nodes. Both unweighted and weighted networks were constructed; an unweighted network displays the presence or absence of an interaction or association whereas the weighted network also includes the strength or frequency of each interaction or association. Only weighted networks are presented here (Hanneman & Riddle, 2005; Croft, James, & Krause, 2008; Kasper & Voelkl, 2009; Zhang et al., 2012). I conducted the network analysis with SOCPROG 2.4 and used NETDRAW to develop the visual representation.

I also calculated network metrics using SOCPROG 2.4. Degree or strength is the number of edges joined to a node, revealing the number of different connections and how well connected each individual is in a network (Croft et al., 2008; McCowan et al., 2008; Sueur & Petit, 2008; Whitehead, 2008; Henzi et al., 2009; Kasper & Voelkl, 2009; Sueur, Petit, et al., 2011). I used the dyadic association index (DAI) to measure the strength of

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association between two individuals (Croft et al., 2008). I calculated association by the

rates of affiliative behavior with the following equation:

$$\text{DAI}_{\text{AB}} = \frac{\Sigma(A+B)}{\Sigma A + \Sigma B - \Sigma(A+B)}$$

where *A* is the number of times individual A is seen, *B* is the number of times individual

B is seen and *A+B* is when both individuals are seen together, either in proximity,

grooming or co-feeding (Wittig & Boesch, 2003; Croft et al., 2008; Suer & Petit, 2008;

Sueur, Petit, et al., 2011). The half-weight index (HWI) also measured association in

terms of collective movement, which I calculated with the following equation:

$$\text{HWI}_{\text{AB}} = x/[x + y_{ab} + 0.5(y_a + y_b)]$$

where *x* is the association strength (i.e., the number of times individual A and individual

B both participate in a collective movement), y_{ab} is the number of times individual A and

B are observed where one participates in the movement and the other does not, y_a is the

number of times individual A participates in a movement and y_b is the number of times

individual B participates in a movement (Cairns & Schwager, 1987; Whitehead, 2003;

Croft et al., 2008). The thickness of the edge connecting nodes visually represents the

strength. The eigenvector centrality coefficient is another measure of social connectivity

between nodes, resulting in a number that indicates the degree of the individual as well as

the degree of those individuals the individual of interest is connected to (Sueur & Petit,

2008; Whitehead, 2008; Kasper & Voelkl, 2009; Sueur, Petit, et al., 2011; Zhang et al.,

2012). I indicated centrality by node size in the social network diagram. The clustering

coefficient represents the extent to which nodes are clustered in space. A high clustering

coefficient means the network is a highly structured and homogeneous unit (Whitehead,

2003; Hanneman & Riddle, 2005; Croft et al., 2008; Henzi et al., 2009; Kasper & Voelkl,

2009; Zhang et al., 2012). Nodes shown closer together in the social network have higher clustering coefficients. Spearman rank tests were used to analyze correlations between these social network properties (Zhang et al., 2012).

To further test the hypothesis of strong female social bonds, I conducted permutation tests for preferred/avoided associations with the collected affiliative data as described by Whitehead (2008). According to a commentary by Jacobs and Petit (2011), these preferred and avoided relationships may have an important impact on socially living organisms. Since the study period consisted of two months, I permuted groups within the sampling period, which is ideal for short-term studies (Whitehead, 2008). If individuals preferentially associate with specific group members, then the standard deviation (SD) and coefficient of variation (CV) of association indices should be greater in the real dataset than in the random dataset. On the other hand, if individuals tend to avoid specific group members, the proportion of non-zero association indices should be less in the real dataset than in the random datasets. With short-term studies, a significantly low mean of the real association indices is indicative of preferred associations (Whitehead, 2008). To decide how many permutations to run, I increased the number of permutations until the given p value stabilized (Bejder, Fletcher, & Bräger, 1998). I started with 1,000 permutations with 1,000 trials per permutation, which has proven to be optimal in most scenarios (Whitehead, 2008), and then conducted 2,000 permutations with 1,000 trials per permutation. Since the p values were similar, I stopped increasing the amount of permutations and ran 1,000 permutations with 1,000 trials per permutation for each randomization. To examine the difference between female and male

affiliation, I performed permutation tests on female-female associations and male-male associations separately.

To analyze the difference in leadership frequency between individuals, I used a chi-square test for categorical data. I reported standardized residuals • | 2 | as indicative of individuals who led significantly more or less often than expected. To analyze the difference in leadership between males and females, I used Mann-Whitney U test as the data was not normally distributed and a chi-square test. To examine the relationship between leadership frequency and rank, I used Spearman rank test to measure the nonparametric association between ranked variables and a chi-square test of independence. This is also the case for the relationship between leadership frequency and age.

To analyze the movement progression tied to female joiners, I first examined the relationship between successful movement time and the number of individuals in a movement (i.e., unweighted). I then examined the relationship between the proportion of females in each movement (i.e., weighted) to successful movement time. The movements are weighted as the number of individuals involved in each movement differs, ranging from three to ten individuals. I then compared the slopes of both unweighted and weighted movements using a t test to see whether or not more females involved in a collective movement significantly differ from those with less females involved. I then examined whether individuals preferred front or back positions during collective movements by utilizing the progression order index proposed by van Belle, Estrada and Garber (2013):

$$\text{Progression Order Index} = 1 - (I - 1)/(N - 1)$$

where I is the individual's position in a single movement progression and N is the number of group members involved in a single movement (Barelli et al., 2008). The index ranges from 1 (i.e., leader) to 0 (i.e., last follower). I used single sample t tests to examine whether each individual's mean progression order index was significantly different from an expected population mean of 0.5 (i.e., a consistent middle position in the collective movements, see van Belle et al., 2013).

CHAPTER IV

RESULTS

Social Network Analysis

To determine whether or not the social connections between females are stronger

than those between males, I conducted a social network analysis on affiliative, aggressive

and movement behavior. The weighted affiliative social network of the adults is shown in

Figure 2. The estimate of correlation between true and estimated association indices
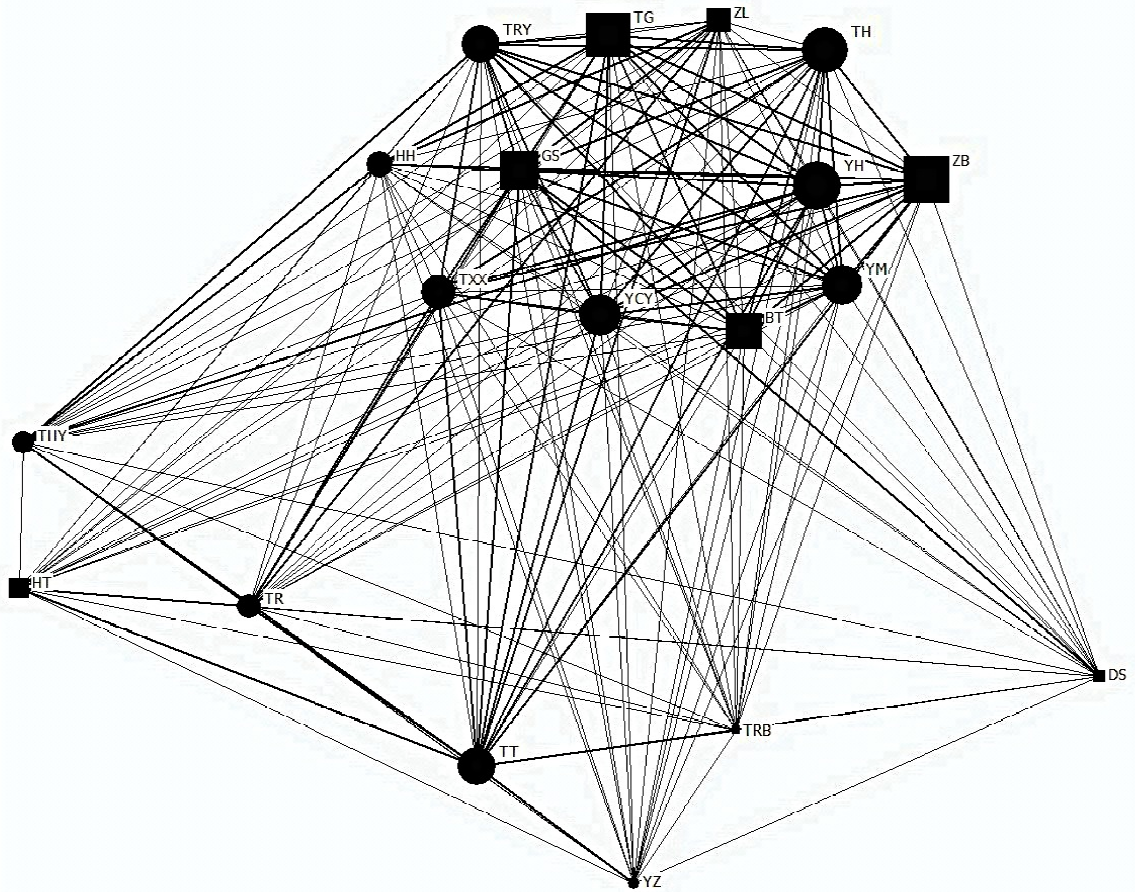
Figure 2. Weighted social network of affiliation. Nodes represent individuals with their
name abbreviations above each. Distances between individuals represent their
relationships in term of proximity and grooming. Circles represent females and squares
represent males. The size of a node is directly related to the individual eigenvector
centrality coefficient. Individuals are clustered in space based on clustering coefficients.

using Poisson approximation is 0.87. The mean affiliative associations equal 217.90 per individual and 11.47 per dyad. YH associated with individuals the most (sum of associations = 10.00) whereas TRB associated the least (4.69). The dyadic association index yielded the highest strength for YH (9.00) and the lowest for TRB (3.69). The eigenvector centrality coefficient revealed similar results (YH = 0.30, TRB = 0.11). There is a single cluster based on their individual clustering coefficients. However, some adult troop members did not belong to a single cluster. There was a significant correlation between affiliative strength and eigenvector centrality coefficients (Spearman rank correlation $r_s = 0.9887$, $N = 20$, $p < 0.001$), eigenvector centrality coefficients and clustering coefficients ($r_s = 0.7814$, $N = 20$, $p < 0.001$) and strength and clustering coefficients ($r_s = 0.6957$, N = 20, $p < 0.001$).

The weighted agonistic social network of the YA1 adults is shown in Figure 3. The estimate of correlation between true and estimated association indices using Poisson approximation is 0.86. The mean agonistic interactions equal 40.50 per individual and 2.13 per dyad. ZB engaged in most aggressive interactions (sum of associations = 1.76) whereas YZ engaged the least (1.25). The simple ratio index for aggression yielded the highest strength for ZB (0.76) and the lowest for YZ (0.25). The eigenvector centrality coefficient revealed ZB as the highest (0.35) and YZ and TRB the lowest (0.13). There are three clusters of agonistic interaction based on individual clustering coefficients and all adults belonged to one of the three clusters (see Figure 3). There was a significant correlation between agonistic strength and eigenvector centrality coefficients (Spearman rank correlation $r_s = 0.9562$, $N = 20$, $p < 0.001$). However, the relationships between eigenvector centrality coefficients and clustering coefficients ($r_s = -0.18$, $N = 20$, $p >$

0.05) and strength and clustering coefficients ($r_s = -0.2937$, $N = 20$, $p > 0.05$) were
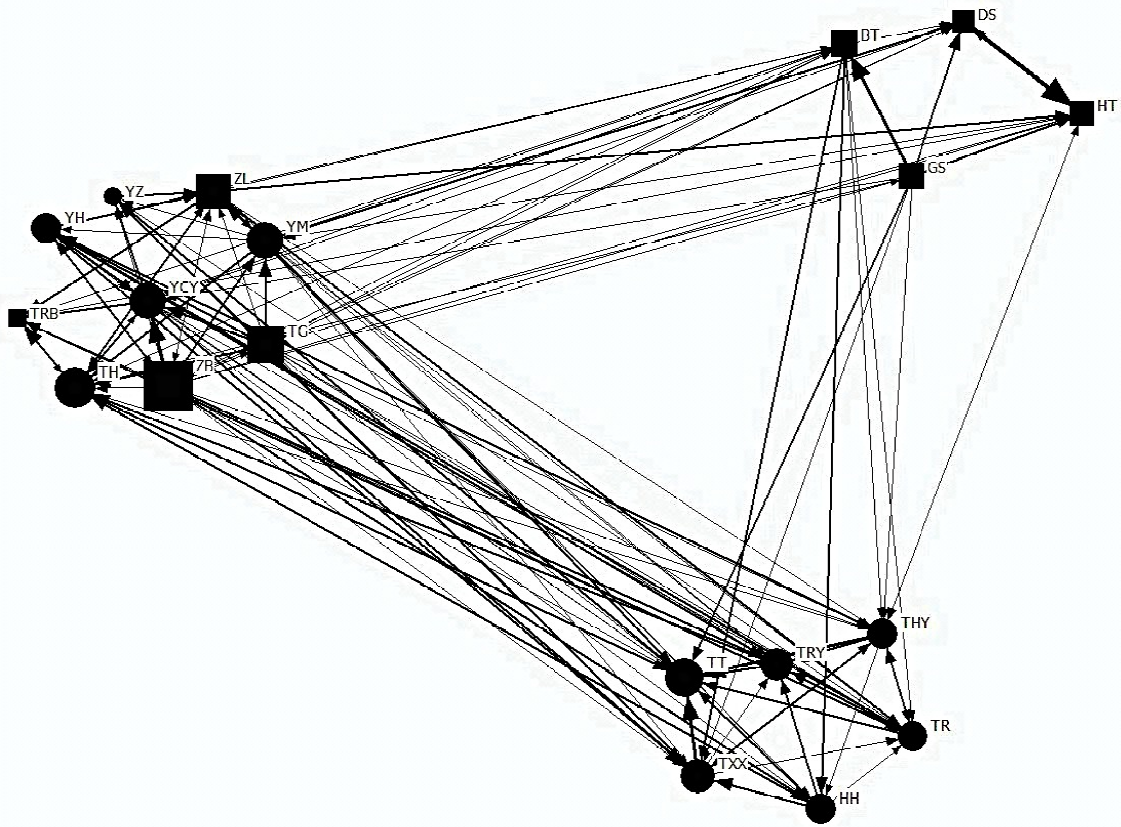
insignificant.

Figure 3. Weighted social network of aggression. Nodes represent individuals with their name abbreviations above each. Distances between individuals represent their relationships in term of proximity and grooming. Circles represent females and squares represent males. The size of a node is directly related to the individual eigenvector centrality coefficient. Individuals are clustered in space based on clustering coefficients.

The weighted collective movement social network is illustrated below (Figure 4). The estimate of correlation between true and estimated association indices using Poisson approximation is 0.86. The mean movement associations per individual equal 108.19 and 5.41 per dyad. ZB participated in collective movements the most (sum of associations = 6.14) whereas DS participated the least (3.14). The half-weighted index for collective

movement yielded the highest strength for ZB (5.14) and the lowest strength for DS

(2.14). The eigenvector centrality coefficients yielded similar results (ZB = 0.29, DS =
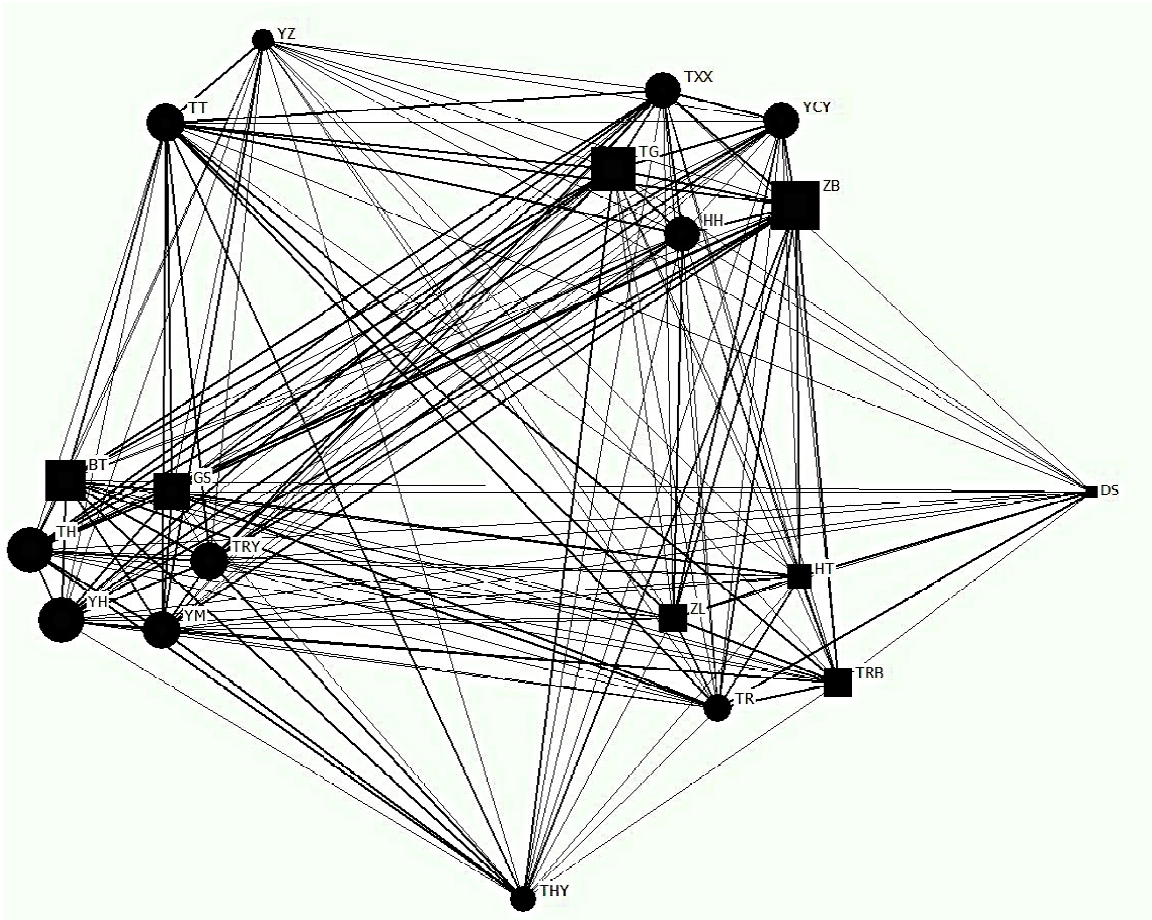
Figure 4. Weighted social network of half-weighted collective movements. Nodes represent individuals with their name abbreviations above each. Distances between individuals represent their relationships in terms of collective movement. Circles represent females and squares represent males. The size of a node is directly related to the individual eigenvector centrality coefficient. Individuals are clustered in space based on clustering coefficients.

0.12). There are four clusters of collective movement based on individual clustering

coefficients (see Figure 4). However, there are individuals who did not belong to any of

the four clusters. There was a significant correlation between collective movement

strength and eigenvector centrality coefficients (Spearman rank correlation r_s = 0.9883, *N*

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= 20, $p < 0.001$). However, the relationships between eigenvector centrality coefficients and clustering coefficients ($r_s = 0.2319$, $N = 20$, $p > 0.05$) and strength and clustering coefficients ($r_s = -0.1533$, $N = 20$, $p > 0.05$) were not significant.

The affiliative and collective movement networks were significantly correlated with each other in regards to strength (Spearman rank correlation $r_s = 0.9462$, $N = 20$, $p < 0.001$), eigenvector centrality coefficients ($r_s = 0.9229$, $N = 20$, $p < 0.001$) and clustering coefficients ($r_s = 0.4912$, $N = 20$, $p < 0.05$). The agonistic and collective movement networks were also significantly correlated with each other in regards to strength ($r_s = 0.6589$, $N = 20$, $p < 0.05$) and eigenvector centrality coefficients ($r_s = 0.721$, $N = 20$, $p < 0.001$). However, the clustering coefficients were not significantly correlated ($r_s = 0.1043$, $N = 20$, $p > 0.05$).

Since the social network analysis alone did not reveal high levels of female social connectivity, I analyzed female-female and male-male affiliative associations using permutations tests (see Table 3). The permutation tests of female-female affiliative behavior revealed 21 preferred associations that significantly differ with 9 significant individuals (see Figure 5). The real association indices significantly differed from the random dataset, both of which were low (Real: $M = 0.40$, Random: $M = 0.48$, $p < 0.001$). Both the standard deviation and coefficient of variation were significantly greater in the real dataset than in the random dataset (Real: $SD = 0.19$, Random: $SD = 0.16$, $p < 0.05$; Real: $CV = 0.47$, Random: $CV = 0.34$, $p < 0.001$). The permutation tests of male-male affiliative behavior revealed 9 preferred associations that significantly differ with no significant individuals (see Figure 6). The real association indices significantly differed from the random dataset, both of which were low (Real: $M = 0.25$, Random: $M = 0.30$, p

Table 3

Permutation Test Results of Preferred Affiliative Associations

Female[1]	Preferred Association[2]	Index[3]	Male[1]	Preferred Association[2]	Index[3]
YH ($p < 0.05$)	TRY ($p < 0.05$)	0.82	ZB ($p > 0.05$)	NA	NA
	HH ($p < 0.05$)	0.37			
	TXX ($p < 0.05$)	0.47			
	TR ($p = 0.001$)	0.21			
	TT ($p < 0.05$)	0.41			
	YZ ($p < 0.001$)	0.18			
YM ($p < 0.001$)	HH ($p < 0.05$)	0.26	TG ($p > 0.05$)	DS ($p = 0.001$)	0.12
	TXX ($p < 0.05$)	0.24			
	TR ($p < 0.05$)	0.24			
	TT ($p = 0.001$)	0.39			
	YZ ($p < 0.001$)	0.06			
YCY ($p < 0.05$)	THY ($p < 0.05$)	0.30	GS ($p > 0.05$)	TG ($p < 0.05$)	0.41
	TRY ($p < 0.05$)	0.44			
	HH ($p < 0.05$)	0.34			
	TT ($p < 0.05$)	0.41			
	YZ ($p < 0.05$)	0.12			
THY ($p < 0.05$)	NA	NA	ZL ($p > 0.05$)	ZB ($p < 0.05$)	0.40
				TG ($p < 0.05$)	0.26
TRY ($p < 0.05$)	NA	NA	YRB ($p > 0.05$)	NA	NA
HH ($p < 0.05$)	NA	NA	BT ($p > 0.05$)	HT ($p < 0.05$)	0.21
TH ($p < 0.05$)	HH ($p < 0.05$)	0.29	DS ($p > 0.05$)	ZB ($p = 0.001$)	0.14
TXX ($p > 0.05$)	NA	NA	HT ($p > 0.05$)	ZB ($p < 0.05$)	0.20
TR ($p < 0.05$)	TH ($p < 0.05$)	0.24	TRB ($p > 0.05$)	ZB ($p < 0.05$)	0.23
				HT ($p < 0.05$)	0.34
TT ($p > 0.05$)	TRY ($p < 0.05$)	0.33			
YZ ($p < 0.05$)	TH ($p < 0.05$)	0.09			
	TT ($p < 0.05$)	0.58			

[1]Individuals are listed in descending hierarchy with *p*-values indicative of their significance among others of the same sex. [2]Preferred association indicates which other individual of the same sex the individual of interest prefers to associate with, as well as a *p*-value indicative of the strength of association between the two. [3]Index refers to the association between two individuals based on the simple association index (Whitehead, 2008).

< 0.05). The coefficient of variation was significantly greater in the real dataset than in the random dataset (Real: $CV = 0.76$, Random: $CV = 0.69$, $p < 0.05$). However, the

standard deviations did not differ significantly (Real: *SD* = 0.19, Random: *SD* = 0.21, *p* >

0.05).

Leadership

To determine if high-ranking females led more successful collective movements

than other adult group members, I recorded 128 successful collective movements and

examined the difference in leadership frequency between individuals with regard to sex,

age and rank. All adults participated in the initiation of collective movements, with TXX

leading the most movements and YRB leading the least (see Figure 5).
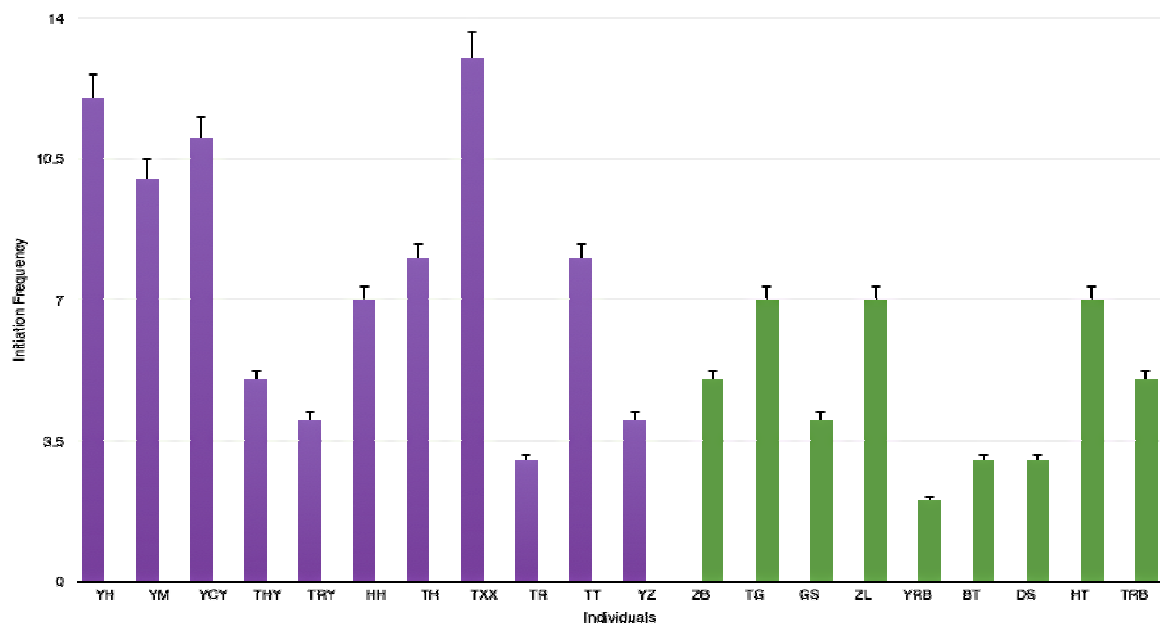
Figure 5. Distribution of initiation frequency among 20 adults. Gray bars indicate
females and black bars indicate males. Individuals of the same sex are presented from left
to right (females for the first eleven and males for the next nine) in descending order in
hierarchy.

The difference between male and female leadership frequency was not significant

(Mann-Whitney *U* test: Z = 1.14, *p* > 0.05, see Figure 6). However, two females—YH

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(SR = 2.21) and TXX (SR = 2.61)—significantly led movements more than expected by chance (χ^2 = 30.13, N = 20, p = 0.05).
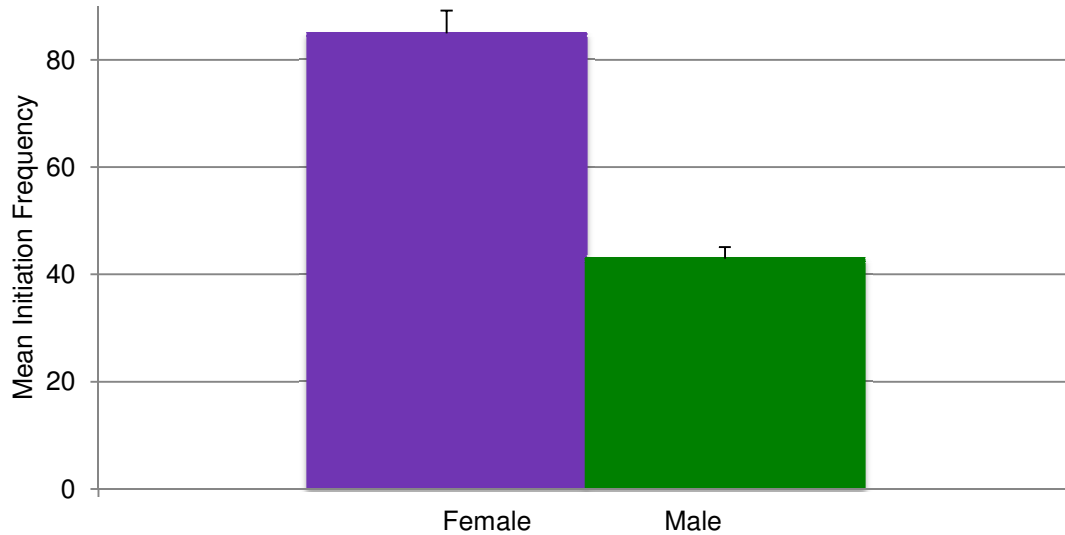
Figure 6. Difference of mean initiation frequencies between females and males.

There was no overall correlation between leadership frequency and rank among the group (Spearman rank correlation r_s = -0.0713, N = 20, p > 0.05). There was no relationship found, χ^2 (1, N = 2) = 0.08, p > 0.05. However, the highest-ranking female initiated more movements than expected by chance (SR YH = 2.21). There was also no correlation between leadership frequency and age among the group members (Spearman rank correlation r_s = -0.0711, N = 20, p > 0.05). There was no relationship found, χ^2 (1, N = 2) = 0.13, p > 0.05.

Movement Progression

To determine if successful collective movements with more females involved resulted in a quicker movement progression, I first examined the relationship between successful movement time and the number of individuals involved and then compared this to the movements weighted by female presence. All adults participated in a

movement at least once. The average time for successful movement completion per the

number of individuals involved was calculated, resulting in movement progression

occurring at a faster pace when there were fewer individuals participating (see Figure 7).
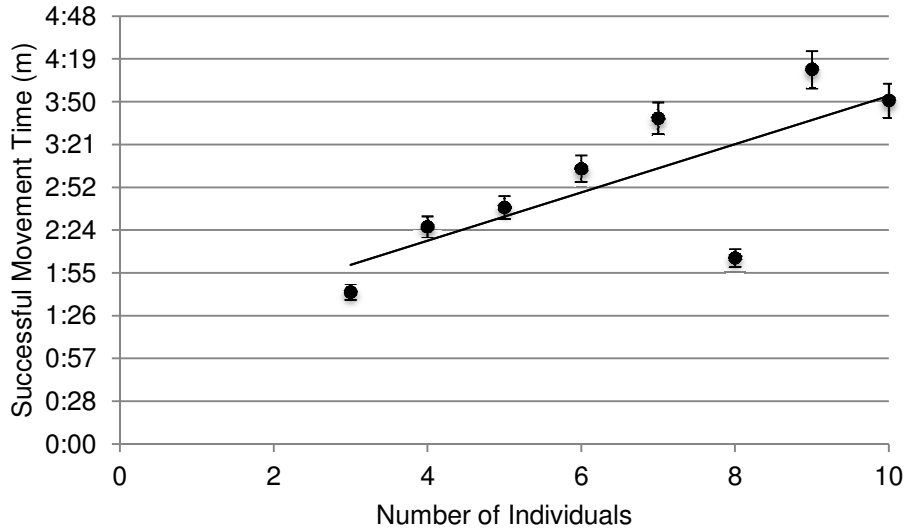
Figure 7. Mean duration of successful movements per number of individuals.

I calculated the slope of both unweighted and weighted collective movements in

relation to successful movement time and then tested the difference between the two

slopes. There was a significant difference between the movement progression in weighted

and unweighted movements ($t = 3.87$, $df = 253$, $p < 0.001$, see Figures 8 and 9).

The progression order index of all individuals revealed an insignificant result,

meaning no individual showed a preference for frontward or backward movement

positions ($t = 0.40$, $df = 19$, $p > 0.05$).

Figure 8. Duration of successful movements per number of individuals.
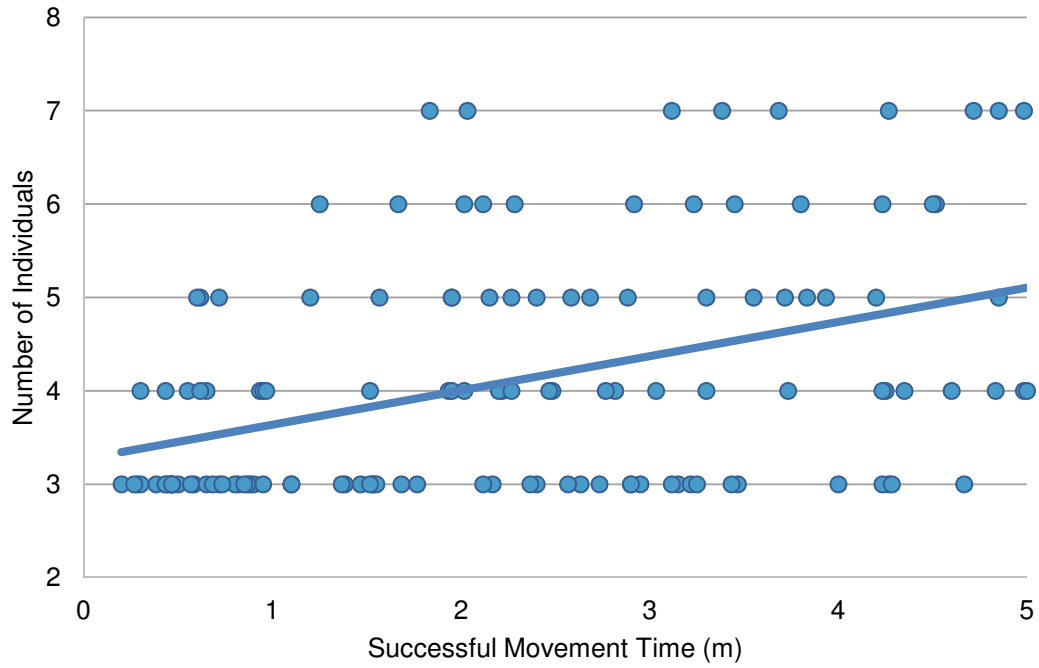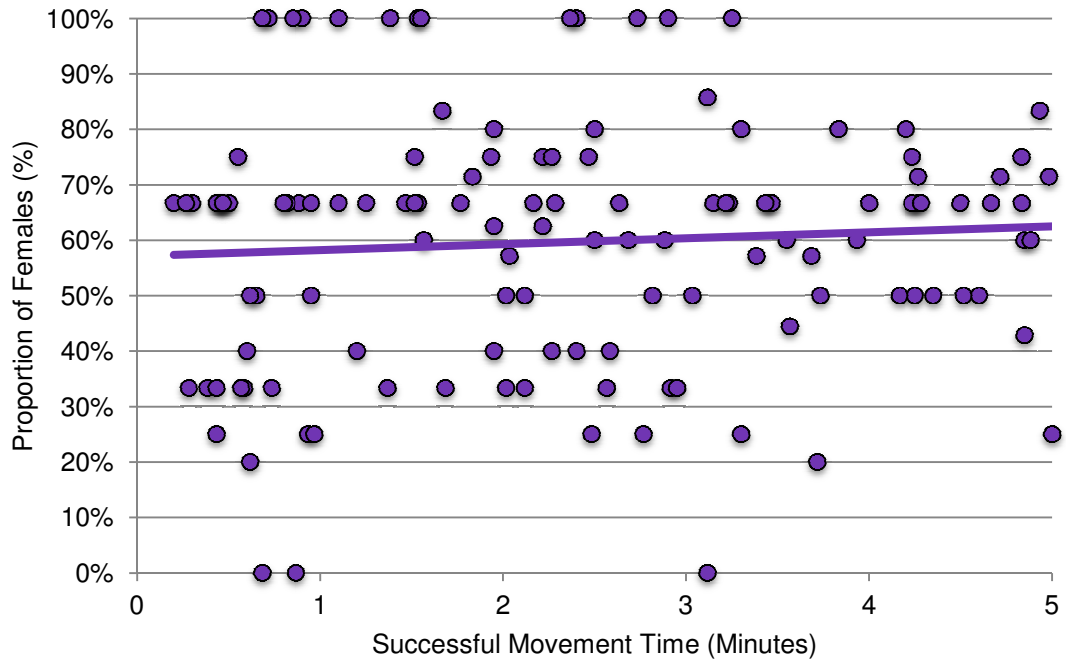

Figure 9. Duration of successful movements per proportion of females.

CHAPTER V

DISCUSSION

Social network analysis focuses on relationships between individuals, revealing the central individuals and the social stability in an animal group (McCowan et al., 2008; Pinter-Wollman, 2015a, 2015b). In my study, the affiliative and agonistic social networks were significantly correlated with the one depicting collective movement data in regard to strength and eigenvector centrality, indicating that the social ties present in these different contexts are related to one another. Also, my estimate of correlation through Poisson approximation for each of the social networks indicated a high power of analysis, making it possible to examine the true social structure of the YA1 troop (Whitehead, 2008). In the affiliative network (see Figure 2), the social network metrics were significantly correlated with one another and therefore indicate a strong relatedness. The affiliative social network of my study group showed that high-ranking individuals are more central to the network than low-ranking individuals. This is consistent with findings by Flack et al. (2006) and Barrett et al. (2012), both of whom found that social structures change with the removal of high-ranking individuals as they are important drivers in animal social networks. A recent study calls this phenomenon into question, as they found no support for the idea that the removal of an alpha or beta male resulted in changes in total grooming or association rates of adult females in baboons (Franz et al., 2015). In my agonistic social network (see Figure 3), the clustering coefficients were not significantly correlated with the other two social network metrics in my dataset. The clustering coefficients of the collective movement social network (see Figure 4) were also not significantly correlated with the other two social network metrics in my dataset.

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Clustering can be more informative with larger animal groups containing millions of individuals over a long period of time and may even make little sense with regard to aggressive encounters in particular (Hanneman & Riddle, 2005; Kasper & Voelkl, 2009). Recent work on baboon social networks found that the removal of key individuals did not significantly affect the clustering coefficients of grooming and association networks. This suggests that clusters are not indicative of the social ties present (Franz et al., 2015). Other means of measuring clusters applied to a larger dataset may have revealed relatedness to strength and centrality, such as community modularity (Kasper & Voelkl, 2009; Lusseau & Conradt, 2009).

The affiliative social network analysis alone did not reveal a sex difference in the social bonding of individuals. However, permutation tests in my study resulted in an increased female social connectivity in comparison to males. Therefore, my hypothesis that females are more socially connected than their male counterparts is accepted. The female-female affiliative network showcased significant individuals and more significant social ties whereas the male-male affiliative network had no significant individuals present. Also, the standard deviation of male-male association indices was not significant, which may indicate that males do not preferentially associate with specific group members. It is important to note that the majority of collected affiliative data are proximity measures. Sueur et al. (2011) argued that more complex interactions should be used to define groups. Passively spending time together and sharing space may be informative since association data is easier to collect, but researchers should rely on interactional data more (Sueur et al., 2011). Future studies on Tibetan macaques could focus on affiliative interactions such as grooming and bridging to conduct social network

analyses and examine whether or not these measures also result in strong female social bonding.

The presence of social bonds may lead to reduced predation risks, increased resource availability and more mating opportunities on an individual level (Sterck, Watts, & van Schaik, 1997; Silk, Seyfarth, & Cheney, 1999; Silk, 2007). Female sociality in particular may also serve as a counterstrategy to infanticide (Treves & Chapman, 1996; Sterck et al., 1997; Soltis, Thomsen, Matsubayashi, & Takenaka, 2000; Cords, 2002; Henzi & Barrett, 2007; Silk, 2007). Infanticide has been found to influence social organization and has been reported in many animal species, particularly those that have a one-male social system and a lack of seasonal breeding (Treves & Chapman, 1996; Soltis et al., 2000). Although the costs of infanticide in multi-male groups are high (Soltis et al., 2000; van Schaik, Pradhan, & van Noordwijk, 2004) and seasonal breeding tends to reduce the likelihood of this event, there have been reports of infanticide in both scenarios. The lack of reported infanticide in this troop of Tibetan macaques may be due to unmet conditions for the killing of infants as an effective strategy, especially in a provisioned habitat (Soltis et al., 2000). Because infanticide serves as a selective force on the social strategies of females due to its detrimental effects on their reproductive success (Sterck et al., 1997), the potential alone could be enough to force females to band together (Cords, 2002). The collective movement network shows that two females with infants during the study period (TH and YH) preferred to move with one another and lower-ranking males such as BT (see Figure 4). Cords (2002) reported that female blue monkeys (*Cercopithecus mitis*) seek protection with other adult females when adult males aggress towards them in the context of infanticide. Female baboons also create

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strong, persistent bonds with other females in their group, especially with related peers (Silk et al., 1999, 2003, 2009), and increase their reproductive success by doing so (Silk et al., 2003; Silk, Altmann, & Alberts, 2006). Silk et al. (2003) found that female baboons who associate with each other increase the survival rate of their infants. Future studies on the social connectivity of the YA1 troop should also measure the survival rate of infants to address female sociality as a means of social strategy against male aggression.

To study the leadership patterns in collective movements, I analyzed the effects of demographics (i.e., age, sex and rank) on the frequency of leadership among adult individuals. According to Petit et al. (2009), the demographics analyzed in my study should influence leadership roles. However, my results show that there were no significant effects of these demographics on leadership frequency. Therefore, my first prediction that high-ranking females will lead more collective movements than other adult members was not supported. Many studies have found that adults tend to lead more movements than their immature conspecifics (Barelli et al., 2008; King et al., 2008; Lusseau & Conradt, 2009; Petit et al., 2009; Nagy et al., 2010; van Belle et al., 2013; Fernandez et al., 2013), yet a study by Furrer et al. (2012) found no age influence on morning group departure initiations in wild banded mongoose. The lack of age influence may be due to mongoose social organization, as females breed in synchrony and groups do not possess a linear dominance hierarchy (Furrer et al., 2012). Failure to find an impact of age on leadership in my study may be due to a lack of comparison between matures and immatures. It is also possible that a lack of significance means all adult individuals in the troop have equal likelihood of leading independent of their individual ages.

The sexual selection theory predicts that females who lead may gain access to more high quality food resources and may do so as a reproductive strategy, whereas males who lead may do so to maintain their dominance status or as a mating strategy (Zhao, 1997; Barelli et al., 2008; Petit et al., 2009; Furrer et al., 2012; Fernandez et al., 2013). Across taxa, females tend to lead more group movements than males (Petit et al., 2009). Female leadership has been observed in black howler monkeys (van Belle et al., 2013) and white-handed gibbons (Barelli et al., 2008). On the other hand, a model developed by Sueur (2012) with manipulation of certain conditions demonstrated how personal leadership could favor males. Male leadership has been observed in chacma baboons (King et al., 2008) and black and gold howler monkeys (Fernandez et al., 2013). According to calculated standardized residuals, two females in my study led more collective movements than expected by chance, suggesting the important role of these females during the study period. Studies that examined leadership found an influence of dominance (King et al., 2008; van Belle et al., 2013) even though this was not the case in my study. One female who led more collective movements than expected by chance was the highest ranking female (YH) but the other female (TXX) was ranked much lower (see Table 1). Similar to age, dominance rank may not have an effect on the leadership frequency if all individuals are just as likely to lead independent of their status. This would differ from rhesus macaques, who possess a more pronounced dominance hierarchy and prefer to move with high-ranking, related conspecifics (Sueur & Petit, 2008).

Social network analysis may help to explain my finding of significant leadership roles of these two females. First, YH has the most affiliative connections and is the most

central individual within the affiliative social network. However, the network does not yield explanatory results pertaining to the significant leadership of TXX. Second, both females appear to have different social ties in the agonistic network. Most aggressive interactions with YH involved the two highest-ranking males (ZB and TG), whereas TXX mostly aggressed with other mid-ranking females such as TH and HH. Finally, both females also belonged to different clusters in the collective movement social network. YH tended to participate in movements with mid-ranking females such as TH and TRY and lower-ranking males such as BT and DS. The two high-ranking males were more likely to participate in collective movements with young females such as TXX and YCY. This result could be explained by the mating season that encompassed the study period. Males tend to follow young, receptive females, inspecting their genitalia and copulating with them. Socioecological factors such as mating could affect our results, similar to results obtained by Ogawa and Takahashi (2003) investigating the huddling group size of Tibetan macaques. Further studies at Mt. Huangshan could conduct collective movement comparisons between the mating and non-mating seasons while collecting data on individuals involved with copulations.

To analyze movement progressions, I examined the relationship between successful movement time and the number of individuals in a movement. I found that movements with fewer individuals progressed faster than those with more individuals. I also examined the relationship between the proportion of females in each movement to successful movement time and compared the slopes of both unweighted and weighted movements. There was a significant difference in successful movement time between collective movements weighted by female presence and those unweighted. Therefore, the

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second prediction was supported: movements containing more females than males will progress quicker. The speed and accuracy of decisions being made and the trade-off between these two variables are vital to the success of collective movements (Franks, Dornhaus, Fitzsimmons, & Stevens, 2003; Sumpter & Pratt, 2009). Increased speed tends to decrease the accuracy of collective decisions in terms of environmental quality (Franks et al., 2003), which most likely does not apply in a provisioned, ecotourism site such as Mt. Huangshan. Quorum thresholds are another aspect of the speed and accuracy trade-off (Franks et al., 2003; Sumpter & Pratt, 2009; Sueur, 2012), but those were not examined here as movements with a greater majority of members involved would be necessary to complete such an analysis.

A study by Wang et al. (in press) examined the joining rules used in collective movements of the YA1 troop. They found that Tibetan macaques participate in a combination of selective mimetism and quorum response depending on the number of individuals involved (Wang et al., in press). Future studies on the collective movement progressions of Tibetan macaques should work toward operationally defining different movement types (i.e., directed vs. passive movements), mean travel distances, ecological conditions, and recruitment techniques (i.e., back glances, interindividual distances between movement followers, etc.; see Pyritz et al., 2009 & Ramseyer et al., 2009). They should also focus on entire group movements (e.g., movements that have at least two thirds of the group members join before termination), make distinctions between initiation and termination, and integrate social network metrics to thoroughly examine the successful movement time and social connectivity (Pyritz et al., 2009).

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In conclusion, the selection pressure on females for higher levels of social connectivity did not result in an increase in their leadership role but did result in more efficient collective movement progressions. I propose that females enhance the efficiency of collective movements through increased social connectivity. Social bonds may also influence leadership frequency outside of the mating season. I propose that age, sex and rank have no influence on the leadership capabilities of Tibetan macaques during the mating season. The physiological status, reproductive activities and social bonds of both females and males may vary through different seasons. A longitudinal study on the leadership and collective movements of Tibetan macaques at this site would further enhance our knowledge of their selection pressures.

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