Spring 2017

Collective Decision Making in Tibetan Macaques: How Followers Affect the Rules and Efficiency of Group Movement

Amanda Rowe
Central Washington University, amanda.rowe@stonybrook.edu

Recommended Citation

COLLECTIVE DECISION MAKING IN TIBETAN MACAQUES: HOW

FOLLOWERS AFFECT THE RULES AND EFFICIENCY

OF GROUP MOVEMENT

_____

A Thesis

Presented to

The Graduate Faculty

Central Washington University

_____

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

Primate Behavior

_____

by

Amanda Kathryn Rowe

May 2017

1

CENTRAL WASHINGTON UNIVERSITY

Graduate Studies

We hereby approve the thesis of

Amanda Kathryn Rowe

Candidate for the degree of Master of Science

APPROVED FOR THE GRADUATE FACULTY

_____   _____
                    Dr. Lixing Sun, Committee Chair

_____   _____
                    Dr. Lori Sheeran

_____   _____
                    Dr. Steven Wagner

_____   _____
                    Dean of Graduate Studies

ABSTRACT

COLLECTIVE DECISION MAKING IN TIBETAN MACAQUES: HOW

FOLLOWERS AFFECT THE RULES AND EFFICIENCY

OF GROUP MOVEMENT

by

Amanda Kathryn Rowe

May 2017

Primate societies must undergo successful collective decision making during group movement to stay cohesive and provide ecological and evolutionary benefits of sociality. This study investigates how a fan structure facilitates successful group movement in the YA1 group of Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan National Reserve in Anhui, China. We used structural equation modeling (SEM) to determine the relative influences of sex, age, maternal kinship, dominance, and social network centrality on the number of fans (consistent followers) an individual had, and the number of group members an individual was a fan of (fandom). SEM revealed that dominant females had more fans, while younger, dominant individuals with more maternal kin were fans of more individuals. Fans and fandom were most strongly influenced by dominance, mostly displaying a strong network of females occupying top positions in the hierarchy who consistently followed each other. Rules used in affiliative interactions were maintained during movement to aid in successful collective decision making. In addition, we examined the relationship between the fan structure and movement efficiency. A positive regression between fans and efficiency ($R^2 = 0.402$) and conversely a negative correlation between fans and number of

unsuccessful movements (Rs = -0.367) was found, suggesting a link between social connections maintained in a movement and the efficiency of movement. Dominant females with more fans initiated less efficient movements because their complex fan structure slowed the joining process. However, individuals with more fans led fewer unsuccessful movements, suggesting a relationship between fans and initiation success. These findings displayed a complex network of social relationships within Tibetan macaque societies that were used during group movement organization to maintain cohesion and provide the benefits of sociality.

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (CONTINUED)

x

CHAPTER I

INTRODUCTION

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

Consensus in collective decision making emerges from individual interactions between group members (Ame et al., 2006). This is demonstrated in a variety of organisms including insects (Cronin, 2013; Passino & Seeley, 2006), birds (Farine et al., 2014), fish (Sumpter et al., 2008), non-human primates (Fernandez, Kowalewski, & Zunino, 2013; Jacobs, Watanabe, & Petit, 2011; Sueur, Deneubourg, & Petit, 2010; Sueur, Petit, & Deneubourg, 2009), and humans (Pratt & Sumpter, 2006; Sumpter & Pratt, 2009). Although the processes of collective decision making such as when groups decide on the most beneficial resources to exploit (Beckers et al., 1990; Deneuborg & Goss, 1989; Mallon et al., 2001), have been examined, there remains much that is unknown regarding the mechanisms underlying these processes.

Two hypotheses, quorum and mimetism, have been proposed for how a collective decision is made. The quorum hypothesis states that an individual's likelihood of performing a behavior increases until it exceeds a threshold, or quorum, above which a collective decision is made (Sumpter & Pratt, 2009). In collective

movement, once a certain number of individuals join a movement, a quorum is reached and entire group movement will occur. This mechanism aids in accuracy and cohesion during group decision-making (Passino & Seeley, 2006; Pratt et al., 2002) and has evolved separately in several organisms such as bees (Passino & Seeley, 2006), ants (Cronin, 2013), and primates (Wang et al., 2015). Alternatively, the mimetism hypothesis proposes that an individual's probability of joining a movement increases with the number of individuals who have already joined the movement (Wang et al., 2015). This mechanism is observed during collective movement in such macaque species as *Macaca thibetana* (Wang et al., 2015), *M. fuscata* (Jacobs, Watanabe, & Petit, 2011) and *M. tonkeana* (Sueur, Petit, & Deneubourg, 2009). Collective decision making in primates such as Tibetan macaques, however, can be driven by a combination of quorum and mimetic factors and mimetism may aid in achievement of a quorum threshold (Wang et al., 2015).

Tibetan macaques are listed as near threatened by the IUCN and the CITES. These primates live in groups with linear dominance hierarchies (Berman, Ionica, & Li, 2004). Groups are female philopatric with males dispersing at maturity, leading to strong female-female bonds (Berman, Ionica, & Li, 2004; Li, Wang, & Han, 1996). Due to these factors, Tibetan macaques display many complex social relationships which may influence collective decision making during group movement. Researchers at Anhui University in China have found that Tibetan macaques, particularly the YA1 group at Mt. Huangshan, display distributed leadership during collective movements and use a combination of quorum thresholds and mimetism (Wang et al., 2015). In addition, social affiliation has been shown to positively influence initiation success,

displaying the importance of selective mimetism in group movement for this species (Wang et al., 2016).

To understand the processes involved in successful collective decision making during group movement in Tibetan macaques, we dissected the mimetic principles that aid in quorum achievement through the evaluation of a fan structure consisting of fans and fandom. A fan is an individual who consistently follows a specific individual during movement, while fandom is the number of other group members an individual is a fan of. To investigate what factors make an individual have more fans and what makes an individual a fan of more group members, I used structural equation modeling (SEM) to test hypothesized associations of an *a priori* model against collected data. Discrimination in sex, maternal kinship, dominance, and age are known to play an important role in the formation of strong bonds in primate societies and were hypothesized to influence the degree of fans and fandom through a network of complex interactions that were uncovered through SEM.

Tibetan macaques' female philopatric society leads to strong female-female bonds and weaker male-male and male-female bonds (Fratellone, 2015; Xia et al., 2012). Male relationships are formed based on reciprocity and creation of alliances for support in the acquisition and maintenance of dominance positions, which influence access to females. Dominance in male primates is influenced by age through the acquisition of top dominance positions by younger males determined through agonistic encounters (Cheney, Seyfarth, & Smuts, 1986). The formation of a strong female-bonded society with the inclusion of weak male-male relationships based on reciprocity and weak male-female relationships based on copulation led to the hypothesis that a

3

strong association between sex and fans/fandom would exist, with female Tibetan macaques being more socially connected and having higher rates of fans and fandom.

While maternal kinship, rank, sex, and age in primate societies have all demonstrated an influence on rate, direction, and degree of reciprocity of interactions, maternal kinship often plays the strongest role in a network (Silk, Samuels, & Rodman, 1981). The 'kin biased attractiveness hypothesis' suggests degree of maternal relatedness will influence affiliative relationships (Sade, 1965; Yamada, 1963) and has support as an important organizing principle of alliance formation and affiliative interactions in female philopatric societies (Bernstein & Ehardt, 1985; Kapsalis & Berman, 1996; Silk, 1982; Widdig et al., 2001; Yamada, 1963). Maternal kinship can lead to more affiliative interactions such as grooming and support during agonistic encounters (Widdig et al., 2001). The formation of strong matrilineages influences the acquisition and maintenance of female dominance rank (Berman, 1983; Kawai, 1965; Kawamura, 1965). In female philopatric primate societies, females form dominance hierarchies based on maternal kinship (Berman et al., 2008) where entire matrilineages rank above or below other matrilineages (Kawai, 1958; Missakian, 1972; Sade, 1967). In these societies, where females typically are ranked below their mothers and adult sisters are ranked based on age (Kawamura, 1965), female linear dominance hierarchies often remain stable due to the support of these strong matrilineal kin relationships.

Dominance rank also influences social relationships through an attraction to higher rank (Seyfarth, 1976; 1977) where unrelated female cercopithecids will benefit from associating with high-ranking females through reciprocity. Low ranking individuals will try to associate with high-ranking individuals (Kapsalis & Berman,

1996; Seyfarth, 1977; Silk, 1982) and rank distance negatively correlates with affiliative behaviors among female macaques (Estrada, Estrada, & Ervin, 1977; Thierry, Gauthier, & Peignot, 1990). In female philopatric primate societies, a distinct relationship exists between maternal kinship and dominance and both maternal kinship and dominance influence social interactions. Based on these relationships, we hypothesized that there would be a positive relationship between maternal kinship and fans/fandom, a positive relationship between dominance and fans, and a negative relationship between dominance and fandom.

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

Additionally, we hypothesized that group members with more fans would lead highly efficient movements because more individuals would follow the initiator more quickly. To test this hypothesis, we determined the connection between fans and efficiency of movement. In this study, we found that dominant females had more fans, younger, dominant individuals with more familial connections were fans of more individuals and individuals with more fans led less unsuccessful movements. These findings uncovered the relationships and rules that were used during group movement to

5

aid in organization and to facilitate cohesion so individuals can reap the benefits of

sociality.

CHAPTER II

LITERATURE REVIEW

Sociality

The evolution of stable social groups in primates is thought to have developed in two steps: a shift from solitary foraging to unstable multi-male/multi-female aggregations, followed by a secondary transition to bonded mother-daughter and reproductive adult relationships. This transition to sociality evolved during an increased occurrence of diurnal behavior which likely led to elevated predation pressure (Shultz, Opie, & Atkinson, 2011). Many researchers attribute the success of *Homo sapiens* to the development of sociality which led to increased cognitive abilities. The social intelligence hypothesis argues that selective pressures such as competition and cooperation which emerged from sociality have played a crucial role in the evolution of the brain and cognition, particularly in primates (Seyfarth & Cheyney, 2015). While it is argued that sociality has led to superior cognitive abilities and success in *Homo sapiens*, many non-human primate species today display a clear link between sociality and increased fitness.

Sociality increases survival and longevity in a variety of species, indirectly influencing fitness. Allogrooming, a cooperative social behavior beneficial to the recipients, is a common form of sociality among primates. Allogrooming is linked to tick load and overall health in primates. Through allogrooming, baboons (*Papio cynocephalus*) can remove ticks from places they could not reach themselves, preventing the detrimental effects of associated ectoparasites (Akinyi et al., 2013).

Social integration causes thermal benefits as well. For example, the capacity of Barbary macaques (*Macaca sylvanus*) to establish and maintain social relationships allows for an increased ability to huddle and behaviorally thermoregulate to survive extreme conditions (McFarland & Majolo, 2013; McFarland et al., 2015). Along with this, sociality reduces predation risks (Cresswell & Quinn, 2004), buffers the short-term effects of stress and reduces adrenocortical activity (Silk et al., 2010). These benefits will lead to increased survival and longevity which in turn can lead to a higher lifetime fitness.

Along with the indirect effects of survival and longevity on fitness, sociality displays clear direct effects on fitness. Ruffed lemurs (*Varecia variegate*) who communally nest, show clear fitness differences between cooperative and non-cooperative individuals. Communally nesting females spend less time at their nests and more time feeding, which translates into improved maternal energetics. Infants belonging to single nesters suffer greater mortality than those belonging to communal nesters (Baden et al., 2013). In Assamese macaques (*M. assamensis*) sociality decreases stress levels, which is detected through lower fecal glucocorticoid levels, and is predicted to lead to higher lifetime fitness (Fürtbauer et al., 2014). Assamese macaques also display a link between social bonds, social status, and fitness in males (Schülke et al., 2010).

Sociality facilitates information transfer between individuals, increasing both survival and fitness (Couzin & Krause, 2003). Sociality allows for conspecific information transmission regarding the environment that increases survival through the expansion of available resources (diversification in diet and use of bioactive materials),

the avoidance of harmful materials and foods (Hardus et al., 2015; Masi et al., 2012), and improved decision making (Ward, Krause, & Sumpter, 2012). While sociality is clearly beneficial in many aspects, to reap such benefits, successful decision making by consensus must occur to promote cohesion of the group and prevent fission (Conradt & Roper, 2003; Couzin et al., 2005; King & Sueur, 2011; Ruckstuhl, 1999). To achieve this goal, social species must undergo collective decision making processes when making choices regarding the most beneficial action for the highest number of members in the group. This is particularly important in collective movement when group members coordinate their activities. Collective decision making can be complex and differs greatly among animal taxa. Studying these processes can allow us to understand complex group movement and decision making that allowed for the evolutionary success and radiation of *Homo sapiens* (King & Sueur, 2011).

Collective Decision Making

Collective decision making occurs when groups of social organisms can choose from one of two (or more) mutually exclusive behaviors. When applying collective decision making to group movement, processes can be studied prior to and during movement in an effort to investigate the choice between two or more mutually exclusive target destinations (King & Sueur, 2011). Collective decision making has been studied in a variety of organisms including insects (Cronin, 2013; Mallon, Pratt, & Franks, 2001; Passino & Seeley, 2006; Pratt et al., 2002; Seeley, Camazine, & Sneyd, 1991), birds (Ballerinie et al., 2008; Daruka, 2009; Davis, 1980; Farine et al., 2014; Major & Dill, 1978; Nagy et al., 2010; Pomeroy & Heppner, 1992), fish (Partridge et al., 1980; Radakov, 1973; Sumpter et al., 2008; Ward et al., 2008;), buffalo (Prins,

1996), sheep (Crofton, 1958), non-human primates (Jacobs, Watanabe, & Petit, 2011; Fernandez, Kowalewsi, & Zunion, 2013; Pyritz et al., 2011; Sueur, Deneubourg, & Petit, 2010; Sueur, Petit, & Deneubourg 2009), and humans (Dyer et al., 2008; Faria et al., 2009; Moussaid et al., 2010; Pratt & Sumpter, 2006; Sumpter & Pratt, 2009).

Across taxa, collective decision making manifests as the influence of individuals on the actions of other group members, resulting in collective behavior (Couzin & Krause, 2003). Consensus in collective decision making emerges from these simple interaction rules used in communication (Ame et al., 2006). In other words, large scale biological phenomenon occurs due to simple individual interactions. Collective behavior does not have to be coordinated by a leader, but instead can be due to the transfer of local information about decisions of neighbors or closely affiliated individuals (Radakov, 1973). Although the processes of collective decision-making have been examined, such as when groups decide on the most beneficial resource to exploit (Beckers et al., 1990; Deneubourg & Goss, 1989; Mallon et al., 2001), much remains unknown regarding the mechanisms underlying how collective decisions are made. This study was designed to further the understanding of these mechanisms.

Two hypotheses, quorum and mimetism, have been proposed to account for how a collective decision is made. A quorum is the number of group members required to exhibit a behavior for the entire group to exhibit the behavior. In this mechanism, the probability of members exhibiting a behavior increases with the number of group members already performing the behavior (Wang et al., 2015). An individual's likelihood of performing a behavior increases until it is above a threshold, or quorum, above which a collective decision is made (Sumpter & Pratt, 2009). In group movement

for example, once a certain number of individuals join a movement, a quorum has been reached and entire group movement will occur. This mechanism can aid in accuracy and cohesion during group decision making (Passino & Seeley, 2006; Pratt et al., 2002) and is seen in a variety of organisms such as bees (Passino & Seeley, 2006), ants (Cronin, 2013; Franks et al., 2003; Pratt et al., 2002; Pratt & Sumpter, 2006), fish (Ward, Krause, & Sumpter, 2012), non-human primates (Sueur, Deneubourg, & Petit, 2010; Wang et al., 2015), and humans (Sumpter & Pratt, 2009).

Quorum thresholds can be fixed (Wang et al., 2015) or can vary depending on environmental context (Cronin, 2013). An example of a fixed quorum is found in Tibetan macaques (*M. thibetana*), which reach a quorum threshold at seven out of 12 adult individuals (Wang et al., 2015). In contrast, to maintain group cohesion and maximize speed during group movement, some ants (*Myrmecina nipponica*) adapt their quorum thresholds to environmental context (Cronin, 2013). Honey bees also adapt their quorum thresholds to balance speed and accuracy to reach the most beneficial collective movement for the highest number of members (Passino & Seeley, 2006). In Tonkean macaques (*M. tonkeana*), speed and accuracy are balanced using multiple quorum thresholds, one for each choice made regarding direction and departure (Sueur, Deneubourg, & Petit 2010).

Recruitment of individuals is necessary to reach a quorum threshold. Many different strategies are used when individuals attempt to recruit members to move in a preferred direction. In many cases, a form of voting is used in which predeparture behavior is performed to initiate group movement (King & Sueur, 2011; Pyritz et al., 2011; Sueur, Deneubourg, & Petit, 2010; Ward et al., 2008). This voting behavior can

be visual such as backward glances (Meunier, Deneubourg, & Petit 2008; Sueur & Petit, 2008; Sueur et al., 2011) and physically moving in the desired direction (Prins, 1996), or vocal such as grunts (Pyritz et al., 2011). Although quorum responses are often found to be the only mechanism underlying collective decision making (Ward, Krause, & Sumpter, 2012), a combination of quorum thresholds and mimetism often occurs to reach consensus during collective decisions (Wang et al., 2015). Mimetism can allow for a quorum response to be achieved during collective decision making to promote consensus (Bousquet et al., 2011; Leca et al., 2003; Petit et al., 2009).

The mimetism hypothesis for collective decision making during group movement proposes an individual's probability of joining a movement depends on the number of conspecifics who have already joined (Wang et al., 2015). This mechanism is used by white faced capuchin monkeys during group movement (*Cebus capucinus*, Petit et al., 2009) and in many macaque species such as *M. thibetana* (Wang et al., 2015), *M. fuscata* (Jacobs, Watanabe, & Petit, 2011), and *M. tonkeana* (Sueur, Petit, & Deneubourg, 2009).

Mimetism can further be divided into anonymous mimetism and selective mimetism. Anonymous mimetism occurs when the probability of an individual displaying a behavior increases with how many conspecifics are already performing the behavior, independent of their identity (King & Sueur, 2011; Meunier et al., 2006). Anonymous mimetism is a common mechanism described in many social species (Couzin & Krause, 2003; Gautrais et al., 2007; Sumpter, 2006). However, due to complex social structures, primates more commonly use selective mimetism when making decisions.

Selective mimetism occurs when the probability of an individual performing a behavior is influenced by both the number of individuals already performing the behavior and the identities and relationships an individual has with group members already performing the action (King & Sueur, 2011; Sueur, Deneubourg, & Petit, 2010; Sueur, Petit, & Deneubourg, 2009). In this mechanism, the influence an individual has on the collective decision making process is weighted based on identity and social affiliation (King & Sueur, 2011; Pyrtiz et al., 2011). In many cases, individuals and their influence on the decision process are not equivalent (DeBlois & Rose, 1996; Krause, Goding, & Brown, 1996; Parrish, 1989). Selective mimetism can lead to differences in initiation success, joining order, joining speed, number of followers, and overall movement efficiency (Hockings et al., 2006; Rhine, 1975; Rhine & Tilson, 1987). Collective decision making in primates such as Tibetan macaques, however, can be driven by a combination of quorum and mimetic factors (Wang et al., 2015).

<center>Tibetan Macaques</center>

Tibetan macaques are listed as Near Threatened by the IUCN and the CITES. They are the largest species in the genus *Macaca* and are native to east-central China, ranging from Guangxi to Yangtse Gorge and Sichuan (Jiang, Wang, & Wang, 1996). Groups are found in small disjunct populations (Berman & Li, 2002) in mountainous ecosystems of the subtropical/temperate boundary (Berman et al., 2006) and are currently only studied at Mt. Huangshan (Berman et al., 2006; Berman et al., 2008; Berman & Li, 2002; Berman, Ionica, & Li, 2004; Berman, Ionica, & Li, 2007; Wang et al., 2015; Xia et al., 2012; Zhang et al., 2014), Mt. Emei (Deng & Zhao, 1987; Zhao, 1994; Zhao, 1997; Zhao & Deng, 1988) and Mt Jiuhuashan (Berman & Li, 2002). These

<center>13</center>

diurnal primates are mostly terrestrial, spending their time foraging on the forest floor (Thierry, 2011) and undergoing daily movements of 1,000-3,000 m (Thierry, Iwaniuk, & Pellis, 2000). The diet of Tibetan macaques consists primarily of leaves (Zhao, 1996), but also contains fruits, other plant parts, invertebrates, snakes and birds (Thierry, 2011; Thierry, Iwaniuk, & Pellis, 2000; Sheeran, 2013).

Tibetan macaques are highly gregarious and display complex social networks (Wang et al., 2015). A group of Tibetan macaques generally consists of 15-50 individuals (Berman, Ionica, & Li, 2004; Thierry, Iwaniuk, & Pellis, 2000). These primates live in groups with linear and despotic dominance hierarchies. Despotic species are thought to show intense, asymmetric aggression, have little tolerance around important resources, and have low rates of reconciliation (Berman, Ionica, & Li, 2004). However, male Tibetan macaques display tolerance and cooperation toward each other, presumably to prevent revolution within a group (Berman, Ionica, & Li, 2007).

Tibetan macaques are female philopatric with male dispersal at sexual maturity (Berman, Ionica, & Li, 2004; Li, Wang, & Han, 1996), generally delaying this dispersal until early adulthood (Zhao, 1996). This promotes formation of strong and well differentiated female-female bonds, which are critical to the group's stability (Xia et al., 2012). Females form linear dominance hierarchies that are matrilineal and use information regarding rank and maternal kinship during social interactions (Berman et al., 2008). Maintenance of these relationships is often completed through grooming, which takes up about 20% of their activity budget (Wang et al., 2007), and non-reproductive copulation. These behaviors are thought to promote cohesion and reduce conflict to maintain the social structure (Xia et al., 2012).

There are high levels of mating contest competition within Tibetan macaque groups, where alphas account for on average 64% of matings, betas 21% and gammas 8% (Berman, Ionica, & Li, 2007). There are distinct birthing and mating seasons with the birth season occurring between January and August (Yin et al., 2004) and the mating season between July and January (Li, Yin, & Wang, 2005).

These factors show that Tibetan macaques display complex social relationships, which influence collective decision making during group movements. As demonstrated in other macaques, tight social networks of group members can lead to more successful movements, which in turn benefit each member (Ramseyer et al., 2009). Affiliative relationships (Sueur, Petit, & Deneubourg, 2009) and maternal kinship (Jacobs, Watanabe, & Petit, 2011) can also influence collective decision making.

Collective decision making in Tibetan macaques involves a combination of quorum and mimetic factors to reach a consensus during group movement. Once a threshold of seven out of 12 members is reached, entire group movement occurs (Wang et al., 2015; 2016). Members of the group display distributed leadership (Wang et al., 2015) during group movement with little effect of sex, age or rank on leadership frequency (Fratellone, 2015). Successful movement time is influenced by how heavily weighted the movement is by female presence. This is likely due to the matrilineal structured society and the presence of strong F-F bonds (Fratellone, 2015). However, social affiliation measured through eigenvector centrality coefficient was shown to positively influence initiation success (Wang et al., 2016). Tibetan macaques make an ideal study system for collective decision making in primates due to their large bodied, terrestrial nature and the accessibility of the YA1 group at Mt. Huangshan. These

factors, along with the rarity of these organisms in the wild provides an opportunity to study a little known behavioral phenomenon in a primate species. Investigation of these questions can lead to simplified yet realistic models that can be applied to similar primate species along with non-primate organisms.

The complex social structure in Tibetan macaques leads to an intricate social network which means individuals will have varying levels of influence on collective decisions. While the role of leadership has been investigated within this species (Fratellone, 2015; Wang et al., 2015; 2016), the influence that followers have within a group on collective decision-making has not been studied. We investigated the mechanisms which drive collective movement in Tibetan macaques by hypothesizing and testing a fan structure, made up of fans and fandom. A fan is an individual who consistently follows another individual during group movement while fandom is the number of individuals an individual is a fan of. We dissected the processes of selective mimetism which aid in achievement of a quorum threshold through examination of this fan structure.

In this study, we addressed the following three questions and tested the three associated hypotheses. First, what is the relationship between the number of fans a leader has and the efficiency of group movement? To answer this question, we hypothesized that if the leader has many fans, collective movement efficiency will increase because more individuals will follow the leader more quickly. Second, what makes an individual a fan? We hypothesized that fans tend to be those in the core of social networks. Third, what factors make an individual have more fans? We hypothesized that, based on existing data in my study system (Fratellone, 2015);

dominant females with substantial maternal kinship networks will have more fans than other individuals. We answered the latter two hypotheses using structural equation modeling (SEM) which compared the hypothesized network of associations of an *a priori* model to the collected data.

Structural Equation Modeling

Methods for univariate analyses of data where one response variable is considered at a time can be useful in many situations, but are weak in describing systems made up of complex networks of interactions (Grace, 2006; Grace & Keeley, 2006). Therefore, evaluation of complex networks is best completed through use of multivariate techniques such as structural equation modeling (SEM).

SEM is a form of path analysis that models multivariate relationships. It allows researchers to test their data against hypothesized causal inferences formed based on previous research (Bollen, 1989). Path analysis is originally credited to Sewall Wright (1918; 1921; 1934; 1960) who investigated the topic to examine direct and indirect relationships among variables. Path analysis has since evolved into SEM, which is the more general approach used today (Grace & Pugesek, 1998).

Where traditional statistics emphasizes the importance of a null hypothesis, SEM places the priority on an *a priori* model consisting of a network of hypothesized causal relationships (Grace, 2006). SEM allows for the investigation of both direct and indirect effects of a system on a response variable through the comparison of the covariances of observed variables in a dataset to hypothesized covariances (Bowker et al., 2005; Grace & Jutila, 1999; Grace & Keeley, 2006).

One method to evaluate a SEM is through a goodness of fit test, which produces a chi-square value. The chi-square value will return a p-value with $p < 0.05$ displaying a poor fit and $p > 0.05$ being generally considered good fitting models (Bowker et al., 2005). Evaluation of multiple models to determine the best fit can be completed using indexes such as AIC (Eldridge et al., 2010). However, the finding of a good fitting model does not necessarily demonstrate a causation, but shows that hypothesized assumptions are likely valid. Other assumptions and models may also fit the data (Bollen, 1989).

While traditionally SEM is used in social sciences such as psychology and sociology, recently it has branched out to fields of ecology and animal behavior. Comprehensive reviews of the use of SEM in psychology include a review of 72 articles published between 1977 and 1987 (Breckler, 1990) and a review of 500 articles published between 1993 and 1997 (MacCallum & Austin, 2000). SEM has widely been used in psychology to investigate topics such as how race and sex can predict emotional well-being in adolescents (Rice, Cunningham, & Young, 1997), how negative thought processes affect overall well-being and job satisfaction (Judge & Locke, 1993), and in twin studies (Finkel, Pederson, & McGue, 1995; Prescott & Kendler, 1996; Suadino et al., 1995). The use of SEM in psychology is still highly prevalent today, displayed through the numerous publications produced in the last decade (Anafarta, 2010; Deng et al., 2016; Diseth et al., 2010; Marsh et al., 2010; Preacher, Zyphur, & Zhang, 2010; Topa & Moriano, 2010).

The use of SEM in sociology is historically prominent with studies including research on travel behavior (Golob, 2003), crowding effects (Regoeczi, 2002), and

sociosexuality (Christensen & Leck, 1999). Reviews involving the application of SEM to questions of marketing have been completed for research done between 1980 and 1994 (Hulland, Chow, & Lam, 1996) and 1997 to 1994 (Baumgartner & Homburg, 1996). These reviews identify 186 and 149 applications of SEM to marketing questions, respectively. Additionally, the use of SEM to answer marketing questions is prominent in recent research (Lee & Hsieh, 2010; Arslan, Yilmaz, & Aksoy, 2012; Pokhrel et al., 2015).

The use of SEM in ecology and animal behavior is a newer phenomenon than seen in psychology and sociology, but has been on the rise. Many authors in these fields have recently seen the power of this statistical method in evaluating networks and applied it to their research. In ecology, SEM has been used in more recent years to investigate complex systems (Bokony et al., 2012; Bowker et al., 2005; Eldridge et al., 2010; Gough & Grace, 1999; Grace & Jutila, 1999; Grace & Keeley, 2006; Grace & Pugesesk, 1998; Johnson, Huggins, & deNoyelles, 1991; Langen & Vehrencamp, 1998). Examples of applications of SEM in ecology include the investigation of plant diversity following wildfires (Grace & Keeley, 2006), how animals influence the infiltration process of soils (Eldridge et al., 2010), and variation of reproductive success in birds (Langen & Vehrencamp, 1998).

Although rare, examples of SEM used in animal behavioral research do exist (Coudrain, Herzog, & Entling, 2013; Dochtermann & Jenkins, 2007; Edelaar et al., 2012; Gosden & Svensson, 2009; Krams et al., 2013; Royaute, Buddle, & Vincent, 2013; Wall & Messier, 2000; Yang & Wilcyzyski, 2002). SEM has been used in animal behavior studies to answer a variety of questions including: the connection between

female mating rates and male harassment in damselflies (Gosden & Svensson, 2009), the association between behavior and immunity in birds (Krams et al., 2013), the effects of anthropogenic disturbance on behavior syndromes of spiders (Royaute, Buddle, & Vincent, 2013), and the connection between aggression and androgens in lizards (Yang & Wilcyzynski, 2002). SEM is used in a variety of contexts and has been proven to be an extremely powerful tool for analyzing complex systems with networks of connections.

While the use of structural equation modeling to analyze complex data is widespread in many fields, it is a novel approach in the analysis of social systems in non-human primates. Although novel, this method shows great promise in uncovering the complexities of these social systems. In this study, we displayed the strength of structural equation modeling by applying this method to decipher what makes an individual a fan and what makes an individual have more fans.

CHAPTER III

JOURNAL ARTICLE

COLLECTIVE DECISION MAKING IN TIBETAN MACAQUES: HOW

FOLLOWERS AFFECT THE RULES AND EFFICIENCY OF

GROUP MOVEMENT

AMANDA KATHRYN ROWE

CO-AUTHORS:

LIXING SUN

LORI SHEERAN

STEVEN WAGNER

DEREK UHEY

JIN-HUA LI

ABSTRACT

Primate societies must undergo successful collective decision making during group movement to stay cohesive and provide the ecological and evolutionary benefits of sociality. This study investigates how a fan structure facilitates successful group movement in the YA1 group of Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan National Reserve in Anhui, China. We used structural equation modeling (SEM) to determine the relative influences of sex, age, maternal kinship, dominance, and social network centrality on the number of fans (consistent followers) an individual had, and the number of group members an individual was a fan of (fandom). SEM revealed that dominant females had more fans, while younger, dominant individuals with more familial connections were fans of more individuals. Fans and fandom were most strongly influenced by dominance, displaying a strong network of females occupying top positions in the hierarchy who consistently followed each other. Rules used in affiliative interactions were maintained during movement to aid in successful collective decision making. In addition, we examined the relationship between the fan structure and movement efficiency. We found a positive regression between fans and efficiency ($R^2=0.402$), and a negative correlation between fans and number of unsuccessful movements ($Rs=-0.367$), suggesting a link between the social connections maintained in a movement and the efficiency of the movement. Dominant females with more fans initiated less efficient movements because the complex fan structure slowed the joining process. However, individuals with more fans led fewer unsuccessful movements, suggesting a relationship between fans and initiation success. These findings displayed a complex network of social relationships within Tibetan macaque

societies that were used during group movement organization to maintain cohesion and

mediate the benefits of sociality.

RESEARCH HIGHLIGHTS

- Dominant females had more fans while dominant, younger individuals with more familial connections were fans of more individuals.

- Individuals with more fans led less efficient movements, but displayed a lower rate of unsuccessful initiations.

- Social relationships observed in affiliative social interactions were maintained to aid in the structure of collective movements and promote group cohesion.

TEXT

INTRODUCTION

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

Consensus in collective decision making emerges from simple interaction rules used in communication (Ame et al., 2006). This is demonstrated in a variety of organisms including insects (Cronin, 2013; Passino & Seeley, 2006), birds (Farine et al., 2014), fish (Sumpter et al., 2008), non-human primates (Fernandez, Kowalewski, & Zunino, 2013; Jacobs, Watanabe, & Petit, 2011; Sueur, Deneubourg, & Petit, 2010; Sueur, Petit, & Deneubourg, 2009) and humans (Pratt & Sumpter, 2006; Sumpter & Pratt, 2009). Although the processes of collective decision making such as when animals decide on the best resource to exploit (Beckers et al., 1990; Deneubourg & Goss, 1989; Mallon et al., 2001), have been examined, there remains much that is unknown regarding the mechanisms underlying these processes.

Two hypotheses, quorum and mimetism, have been proposed for how collective decisions are made. The quorum hypothesis states that an individual's likelihood of performing a behavior increases until it exceeds a threshold, or quorum, above which a collective decision is made (Sumpter & Pratt, 2009). In collective movement, once a

certain number of individuals join a movement, a quorum is reached, and entire group movement will occur. This mechanism can help promote accuracy and cohesion during group decision making (Passino & Seeley, 2006; Pratt et al., 2002) and has evolved separately in many organisms such as bees (Passino & Seeley, 2006), ants (Cronin, 2013) and primates (Wang et al., 2015). Alternatively, the mimetism hypothesis proposes that an individual's probability of joining a movement increases with the number of individuals who have already joined the movement (Wang et al., 2015). This mechanism is observed during collective movement in such macaque species as *Macaca thibetana* (Wang et al., 2015), *M. fuscata* (Jacobs, Watanabe, & Petit, 2011) and *M. tonkeana* (Sueur, Petit, & Deneubourg, 2009). Collective decision making in primates such as Tibetan macaques, however, can be driven by a combination of quorum and mimetic factors, and mimetism may aid in achievement of a quorum threshold (Wang et al., 2015).

Tibetan macaques are listed as Near Threatened by the IUCN and the CITES. These primates live in groups with linear dominance hierarchies (Berman, Ionica, & Li, 2004). Groups are female philopatric with males dispersing at maturity, leading to a strong female bonded society (Berman, Ionica, & Li, 2004; Li, Wang, & Han, 1996). Due to these factors, Tibetan macaques display many complex social relationships which may influence collective decision making during group movements. Researchers have found that Tibetan macaques, particularly the YA1 group at Mt. Huangshan, China display distributed leadership during collective movements and use a combination of quorum thresholds and mimetism. Once a threshold of seven out of 12 members is reached, entire group movement occurs (Wang et al., 2015; 2016). However, initiation

success is positively correlated to the degree of social affiliation, displaying that rules

used during affiliative interactions may aid in selective mimetism to achieve successful

group movement (Wang et al., 2016).

To further the development of these findings and address the gap in knowledge

regarding how followers influence the decision-making process in Tibetan macaques,

we dissected the mimetic principles that have been shown to aid in quorum achievement

through evaluation of a fan structure consisting of fans and fandom. A fan is an

individual who consistently follows a specific individual during movement while

fandom is the number of other group members an individual is a fan of. To investigate

what factors make an individual have more fans and what makes an individual a fan of

more individuals, we used structural equation modeling (SEM) to test hypothesized

associations of an *a priori* model against collected data. Discrimination in sex, maternal

kinship, dominance, and age is known to play an important role in the formation of

strong bonds in primate societies. As such, we hypothesized that they would influence

the degree of fans and fandom through a network of complex interactions uncovered

through SEM.

Tibetan macaques' female philopatric societies lead to strong female-female

bonds and weaker male-male and male-female bonds (Fratellone, 2015; Xia et al.,

2012). Male relationships are formed based on reciprocity and creation of alliances for

support in the acquisition and maintenance of dominance positions, which influence

access to females. Dominance in male primates is influenced by age through the

acquisition of top dominance positions by younger males determined through agonistic

encounters (Cheney, Seyfarth, & Smuts, 1986). The formation of a strong female

bonded society with the inclusion of weak male-male relationships based on reciprocity and weak male-female relationships based on copulation leads to our hypothesis that a strong association between sex and fans/fandom will exist, with female Tibetan macaques being more socially connected and having higher rates of fans and fandom.

While maternal kinship, rank, sex and age in primate societies have all demonstrated an influence on rate, direction, and degree of reciprocity of interactions, maternal kinship often plays the strongest role in a network (Silk, Samuels, & Rodman, 1981). The 'kin biased attractiveness hypothesis' suggests degree of maternal relatedness will influence affiliative relationships (Sade, 1965; Yamada, 1963) and has support as an important organizing principle of alliance formation and affiliative interactions in female philopatric societies (Bernstein & Ehardt, 1985; Kapsalis & Berman, 1996; Silk, 1982; Widdig et al., 2001; Yamada, 1963). Maternal kinship can lead to more affiliative interactions such as grooming and support during agonistic encounters (Widdig et al., 2001). The formation of strong matrilines influences the acquisition and maintenance of female dominance rank (Berman, 1983; Kawai, 1965; Kawamura, 1965). In female philopatric primate societies, females form dominance hierarchies based on maternal kinship (Berman et al., 2008) where entire matrilines rank above or below other matrilineages (Kawai, 1958; Missakian, 1972; Sade, 1967). In these societies, where females typically are ranked below their mothers and adult sisters are ranked based on age (Kawamura, 1965), female linear dominance hierarchies often remain stable due to the support of these strong matrilineal kin relationships.

Dominance rank also influences social relationships through an attraction to higher rank (Seyfarth, 1976; 1977) where unrelated female cercopithecids will benefit

from associating with high-ranking females through reciprocity. Low ranking individuals will try to associate with high-ranking individuals (Kapsalis & Berman, 1996; Seyfarth, 1977; Silk, 1982), and rank distance negatively correlates with affiliative behaviors among female macaques (Estrada, Estrada, & Ervin, 1977; Thierry, Gauthier, & Peignot, 1990). In female philopatric primate societies, a distinct relationship exists between maternal kinship and dominance, both of which influence social interactions. Based on these relationships, we hypothesized that there would be a positive relationship between maternal kinship and fans/fandom, a positive relationship between dominance and fans, and a negative relationship between dominance and fandom.

Strong support also exists in primate societies for the similarity principle, where individuals most often affiliate with those of similar maternal and paternal kin, age, and rank (Silk, Alberts, & Altmann, 2006; de Waal, 1991; de Wall & Luttrell, 1986). Individual macaques who affiliate tend to be closely matrilineally related and close in rank (Kapsalis & Berman, 1996). Based on these findings, we hypothesized that dominant females would have more fans, and individuals at the core of the social network (highly connected to individuals of varying traits) would be fans of more individuals. Additionally, we hypothesized that monkeys with more fans would lead highly efficient movements because more individuals would follow the initiator more quickly.

In this study, we examined the relationship between sex, age, dominance, maternal kinship, social network centrality, fans and fandom by using SEM to compare hypothesized relationships of an *a priori* model against the data. Additionally, we used

regression analyses to determine the relationship between fans and movement efficiency. Our findings uncovered the relationships and rules that are used in Tibetan macaque society during group movement to aid in organization. These rules facilitate cohesion so individuals can reap the benefits of sociality.

METHODS

Study Subjects and Site

This study was conducted at the Valley of the Wild Monkeys, Mt. Huangshan National Reserve in Anhui, China (N 30°04'25.1"/E 118°08'59.3"). This location is a UNESCO world culture site and a popular tourist destination. The terrain is made up of a mountainous ecosystem ranging from scarce vegetation to dense deciduous and evergreen forests. There are several groups of protected Tibetan macaques at this site. At present, no known predators threaten these groups (Berman et al., 2006).

Researchers from Anhui University have monitored the Tibetan macaques at Mt. Huangshan since 1986. In February 1992, wildlife wardens supervised by the local government drove the macaques one km from their natural range to an unoccupied area, for tourist viewing. Since 1986, wardens provisioned the group four times daily and restricted its movement, causing a reduction in range from 7.75 km² to < 3 km² (Li, Wang, & Han, 1996). This range restriction and provisioning led to strong intragroup competition for food, subsequently leading to group fission one year after relocation (Berman & Li, 2002). This fission consisted of ten individuals forming a group (YB) which succeeded in returning to their original range (Li, Wang, & Han, 1996). A second fission occurred in 1996 when nine members of the original group (YA1) also broke off and returned to their original range (YA2) (Berman & Li, 2002).

This study was conducted through the observation of the Yulinkeng 1 (YA1) group of wild, but habituated Tibetan macaques. The YA1 group engages in social activity in the forest during the day with no range restriction, but are provisioned with a total of three to four kg of corn daily at a viewing platform (Berman & Li, 2002; Berman et al., 2008; Xia et al., 2012). Movement from the platform to the forest occurs several times a day, allowing for the opportunity to observe collective decision making during group movements. The observation of these macaques since 1986 has allowed for data acquisition regarding individual identities and life histories (Berman & Li, 2002). Information regarding identities, maternal kinship, dominance, age and sex are known and kept by Anhui University researchers. During the study period, the YA1 group consisted of 47 individuals, composed of eight adult males, 13 adult females, four subadult males, six juvenile males, ten juvenile females, and six infants (Table 1).

All research protocols reported in this manuscript were reviewed and approved by Central Washington University Institutional Animal Care and Use Committee board (#A121501) and were conducted in accordance with all applicable Chinese laws. In this research, we followed the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

<center>Procedures</center>

We collected data from 2016-06-26 to 2016-08-27, six to eight hours a day, six to seven days a week. We conducted all observations from the feeding platforms (Appendix A). We collected data regarding group movement using an all occurrence sampling method (Altmann, 1974). Focal animals were all adults and subadults of the group, totaling 25 individuals (Table 1). We considered an individual an initiator of a movement when

they moved more than ten meters away from the stationary group in less than 40 s (Lusseau & Conradt, 2009; Petit et al., 2009; Sueur & Petit, 2008; Pyritz et al., 2011; Sueur et al., 2011). We considered an individual a follower when they moved more than five m within a 45° angle of the initiator's movement direction, within five min of the initiator (Jacobs et al., 2011; Sueur et al., 2011). We treated each individual who adhered to this rule in relation to the previous follower as a follower. We identified a movement as successful when more than two individuals followed an initiator, unsuccessful when less than or equal than two individuals followed an initiator within a five min (Jacobs et al., 2011; Pyritz et al., 2011), and finished when no individual joined the movement within five min (Jacobs et al., 2011; Sueur et al., 2011; Appendix B).

During group movement, we recorded the identity of the initiator along with the time of initiation. We recorded the sequence of subsequent followers and each follower was given a time stamp for when their movement began and when movement was completed. We recorded movement data throughout the day when monkeys were approaching or leaving the field site. When group movement was not occurring, we used focal animal sampling (Altmann, 1974) to record affiliative and agonistic interactions to build a social network model and calculate centrality. Focal samples were five minutes and were completed per a previously established sampling schedule.

Table 1. Yulinkeng 1 (YA1) Focal Animals (Adults and Subadults).

INDIVIDUAL	FULL NAME	SEX	AGE	RANK	KINSHIP
YRB	YeRongBing	M	7-10	1	2
TG	TouGui	M	11-15	2	5
YH	YeHong	F	11-15	3	4
GS	GaoShan	M	21+	4	0
YXX	YeXiaXue	F	1-6	5	4
BT	BaiTou	M	16-20	6	0
YCY	YeChenYu	F	7-10	7	4
YM	YeMai	F	21+	8	4
TXH	TouXiaHua	F	7-10	9	2
HH	HuaHong	F	11-15	10	1
ZB	ZouBa	M	11-15	11	0
TH	TouHong	F	11-15	12	2
HT	HeiTou	M	16-20	13	0
DS	DuanShou	M	11-15	14	0
YCL	YeChunLong	M	1-6	15	4
TXX	TouXiaXue	F	7-10	16	2
TT	TouTai	F	21+	17	5
HM	HuangMa	M	16-20	18	0
TR	TouRui	F	11-15	19	3
HXM	HuaXiaMing	M	1-6	20	1
TRG	TouRouGong	M	1-6	21	4
YRQ	YeRongQiang	M	1-6	22	2
TRY	TouRongYu	F	7-10	23	4
THY	TouHuaYu	F	7-10	24	5
YZ	YeZhen	F	21+	25	2

*Age was either known or estimated by long-term researchers. Dominance was calculated using the Brown (1975) index. Maternal kinship was calculated through the number of familial connections within a group.

Table 2. Ethogram of Affiliative Behaviors Recorded During Focal Animal Samples.

AFFILIATIVE BEHAVIOR	DEFINITION
AGONISTIC SUPPORT	An individual joins an ongoing aggressive interaction on the side of one of the opponents. The receiver of support may be either the original attacker or target of the attack. We excluded cases in which the target was human.
CO-FEEDING	A bout in which a focal subject and another individual begin to eat within 1m of each other.
GROOMING	One individual orally or manually manipulates the fur of another.
PROXIMITY	An individual is within 1 m of another individual.
BRIDGE	A pair of individuals holds an infant between them and simultaneously lick the infant's genital or body while teeth-chattering vigorously.
PRESENT	One individual displays his or her rump to another.
COPULATE	One individual approaches from behind and mounts. Thrusting and intromission occur.
SOCIAL MOUNT	One individual approaches from behind and mounts. A full ankle clasp may be used but there is no thrusting or evidence of intromission.
EMBRACE	One individual approaches another and one or both individuals hold each other and may lightly bite each other.

*(Berman, Ionica, & Li, 2004; Ogawa, 1995)

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

During samples, we recorded affiliative behaviors (Table 2). The ethogram of behaviors was adapted from previous work on Tibetan macaques (Berman, Ionica, & Li, 2004; Ogawa, 1995; Appendix B). Between focal animal samples, we used scan sampling (Altmann, 1974) to record proximity (<1m) of all visible individuals in relation to one another (Fratellone, 2015). Any time when group movement occurred, we switched our sampling back to an all occurrence method.

Analysis

We analyzed 1,102 movements to derive a definition of fans and fandom. We recorded the number of times individual A followed individual B within 180 s during these movements. We selected 180 s because the majority of the movement data fell within this period. We grouped the totals from this analysis into percent groups (the percentage of movements individual A was involved in where individual B followed individual A) to decipher random following from deliberate following (Figure 1).

These data deviated from a normal distribution above 10%. Values below 10% fit a normal distribution (Anderson Darling test: $A = 1.0574$, $P = 0.4955$), values over 10% were not consistent with a normal distribution ($A = 0.895$, $P = 0.013$) and the overall data were not consistent with a normal distribution ($A = 1.0574$, $P < 0.01$).
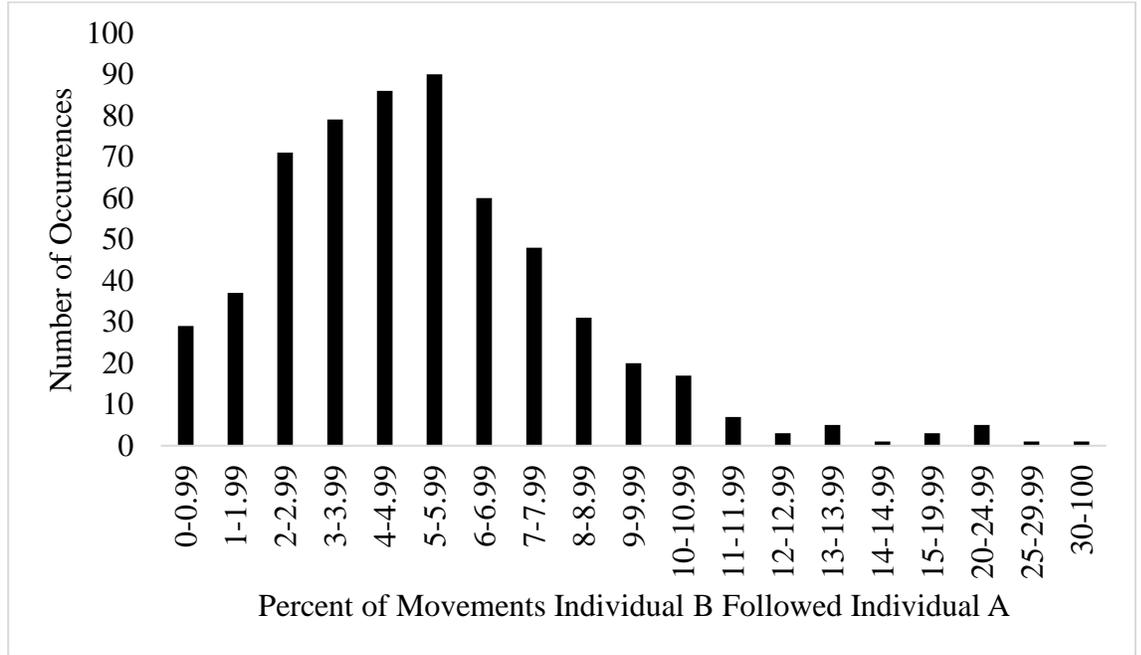
Figure 1. Distribution of occurrences of individual B following individual A within 180 s during a percentage of movements where individual A was involved. These data are right-skewed, displaying a point at which following is not random.

These results suggested that following was not random if the behavior occurred during more than 10% of the movements in which individual A was involved.

Therefore, a fan was defined as individual B, when individual B followed individual within the first 180 s of movement during at least 10% of movements in which individual A was involved. Fandom is the opposite, defined as the number of other group members individual B followed within 180 s of movement during at least 10% of movements those individuals were involved in (Appendix B).

These data showed the occurrence of "super fans", where individual B followed individual A within 180 s during greater than 20% of the movements in which individual A was involved. Due to this occurrence of these "superfans", we weighted the fan and fandom rate of each individual. We calculated the number of fans through

the addition of percentages of time above 10% in which all focal individuals followed individual A, while we calculated fandom through addition of percentages of time above 10% in which individual A followed all focal individuals. We analyzed fans and fandom data by totals and divided into July and August to account for temporal differences. No differences in the biological explanation of the data existed temporally, so we eliminated the temporal analysis and pooled all data (Appendix D).

Sociality leads to the development of bonds that can be hierarchical or affiliative. The sum of all associations between individuals of a social structure is known as a social network. Social network analysis can be used to examine social groups and determine if differences exist in terms of associations and if certain individuals are more central to the group (Sueur & Petit, 2008). We collected affiliative, agonistic, and movement data to build a social network for the YA1 group. We completed social network analysis using SOCPROG 2.7 (Whitehead, 2009).

Through SOCPROG 2.7, we used group movement data and affiliative data to calculate the Half Weight Index (HWI). We used HWI matrices to calculate an Eigenvector Centrality Coefficient (ECC) for each individual. A high ECC represents an individual who is connected to many individuals or is connected to others that are highly central (Whitehead, 2008; Appendix C).

Univariate analyses of data are weak in describing systems like the one in question made up of complex networks of interactions (Grace, 2006; Grace & Keeley, 2006). The evaluation of these complex networks is best completed using multivariate techniques such as structural equation modeling (SEM). SEM is a form of path analysis that models multivariate relationships, allowing the researcher to test their data against

37

hypothesized causal inferences based on previous research (Bollen, 1989). Where

traditional statistics emphasize the importance of a null hypothesis, SEM places the

priority on the *a priori* model consisting of a network of causal relationships

hypothesized by the researcher, usually based on previous literature (Grace, 2006).

SEM allows for the investigation of both direct and indirect effects of a system on a

response variable through the comparison of the covariances of observed variables in a

dataset to hypothesized covariances (Bowker et al., 2005; Grace & Jutila, 1999; Grace

& Keeley, 2006).

While traditionally SEM is commonly used in social sciences such as

psychology (Breckler, 1990; MaCallum & Austin, 2000) and sociology (Golob, 2003;

Regoeczi, 2002), recently it has been used in fields like ecology (Bokoney et al., 2012;

Bowker et al., 2005; Grace & Keeley, 2006;) and animal behavior (Yang & Wilczynski,

2002). Using SEM in the field of primatology is a novel approach. To determine the

relationship between the fan or fandom assignments and age, sex, dominance, maternal

kinship, and centrality, we constructed structural equation models (SEM) using SPSS

Amos (Arbuckle, 2006).

We used SEM to investigate the network of interactions influencing fans and

fandom in the YA1 group. This method of analysis allowed us to determine how

measured factors work collectively to influence fans and fandom within the YA1 group

rather than investigating each factor individually. We created an *a priori* model of

hypothesized pathways based on available literature (Figure 2, see Introduction). We

calculated the Brown (1975) dominance index for each individual through SOCPROG

2.7 using existing agonistic data collected from 2015-8-13 to 2016-05-24. This metric

showed to have the best fit in the model through preliminary analysis and has the

tendency to minimize interactions where the actor is the lower ranking individual

(Whitehead, 2008). Age was either precisely known or estimated (with an error within

1-2 years at most based on our long-term observation of the group). We assigned

individuals age groups of: 1-6, 7-10, 11-15, 16-20, and 21+. We represented maternal

kinship as the number of known familial connections within the YA1 group. We

selected variables for the structural equation model through the completion of Spearman

Rank correlation tests where the variables with the strongest regressions were included

in the model.

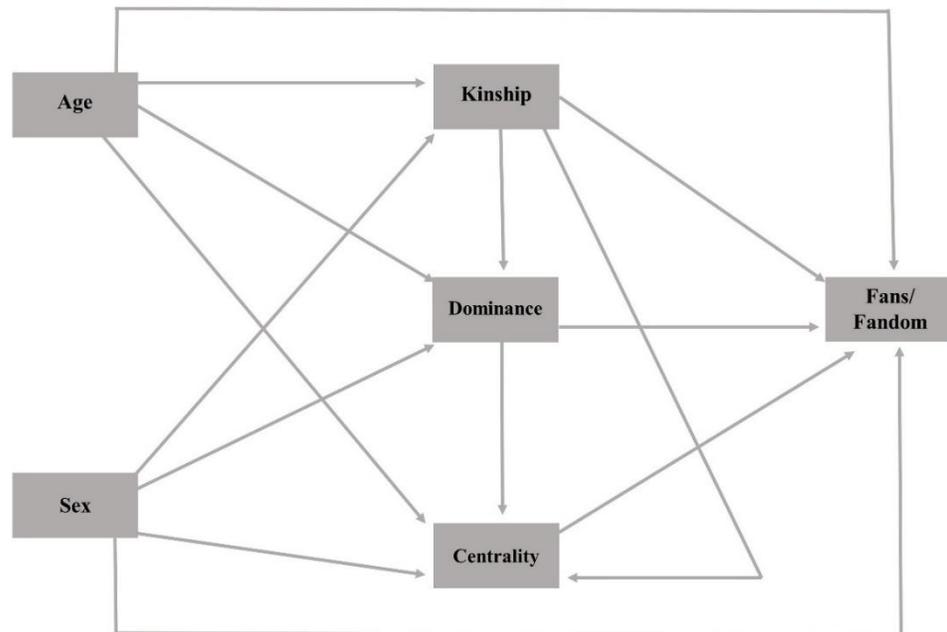**Figure 2.** *A priori* model prediction of the relationship among the number of fans/fandom and age, sex, dominance, centrality and maternal kinship. Boxes represent measured variables and arrows represent hypothesized causal relationships. Based on previous research, strong relationships exist between age, sex, maternal kinship, dominance, and centrality that are hypothesized to strongly influence fans and fandom (see Introduction).

In this model, boxes represent measured variables and arrows represent the hypothesized causal relationships. Data were placed in the model to create path coefficients based on correlation values that estimate effect sizes and direction between variables. The variation explained by the model of each endogenous variable was estimated by R^2 values, the coefficient of variance. We ran all models using a Bollen-Stine Bootstrap method with 1000 repetitions. Once the models were complete, we used chi-square goodness of fit tests and AIC values to determine the best fitting models. We tested structural equation models using both affiliative and movement data.

To determine the relationship between fan assignments for initiator and the efficiency of the movement, we performed Spearman Rank correlation analysis and regression analysis using R statistical programming (R Core Team, 2015).

RESULTS

During the study period, we completed 972 focal samples, totaling 81 hours of focal animal sampling; we completed 953 proximity scans to aid in the construction of a social network; we observed and recorded 1,102 group movements, including 410 successful movements and 692 unsuccessful movements.

The weighted fan rate varied between 0-124 percent. Individuals displaying the highest fan rates were YH and TH (Table 2). The weighted fandom rate varied between 0-119 percent. YXX and TG displayed the highest rates of fandom. Based on a combined linear dominance hierarchy utilizing the Brown's index (1975), YRB was the most dominant individual and YZ was the least dominant individual. Eigenvector centrality coefficient based on affiliative behaviors displayed YRQ and YCL as the most central (0.4, 0.36), and, BT and YM as the least central to the social network (0,

Figure 3). When calculating total ECC based on movement data, YZ and TXH were the most central (0.23, 0.22) while HXM was the least central (0).

The Brown dominance index was selected based on the most number of strong relationships with fans and fandom. There was a significant negative correlation between fandom and dominance (Spearman's rank correlation, Rs=-.0595, df=24, P=0.002). Also, there were strong, non-significant correlations between total fans and dominance (Spearman's rank correlation: Rs = -0.325, df = 24, P = 0.113). We dropped all other dominance indices from the model.
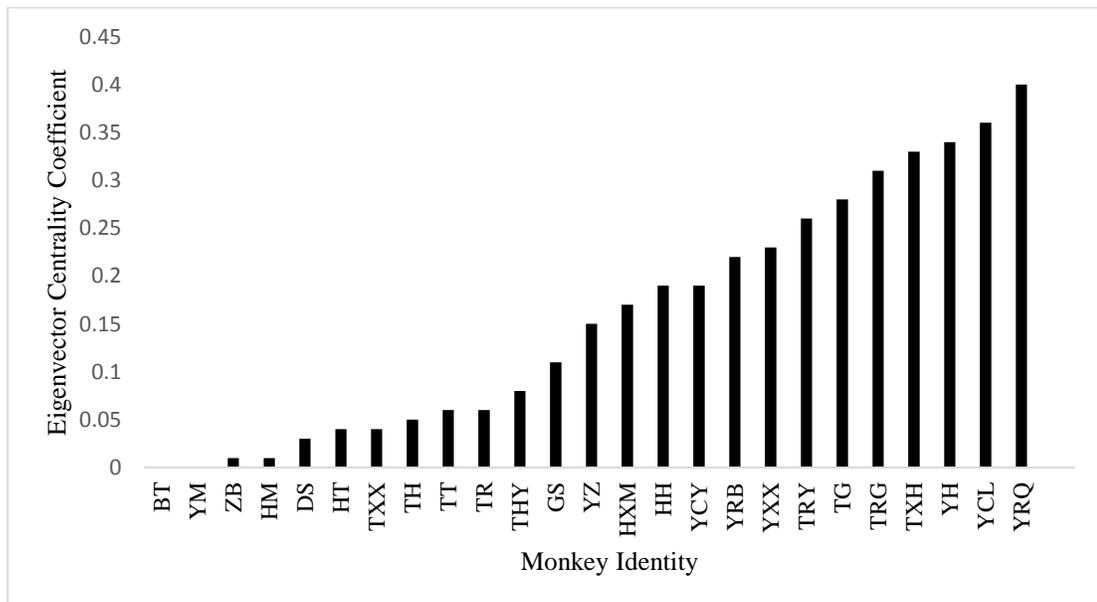
Figure 3. Eigenvector centrality coefficient calculated using affiliative behaviors for each adult or subadult of the YA1 group of Tibetan macaques.

When investigating the causation in variation of fans, the causal scenario of the *a priori* model was consistent with the data. There was no significant difference in model fit whether using movement or affiliative data in fan totals ($\chi^2 = 61$, df = 3, P = 0.892, AIC = 36.619). We dropped the movement model to incorporate affiliative and

movement interactions in the model. The affiliative model explains almost exactly 60%

of the variation in fans (R^2 = 0.598, Figure 4). Significant positive direct effects of sex

on maternal kinship (R = 0.511, P = 0.002), sex on fans (R = 0.794, P < 0.001) and

dominance on fans (R = 0.498, P < 0.001) existed. Total effects, including direct and

indirect effects display sex and dominance as having strong positive effects on fans (R =

0.558, R = 0.507), and weaker effects of maternal kinship, age and centrality on fans (R

= -0.16, R = 0.12, R = -0.02) (Figure 4).

Figure 4. Structural equation model of total life history and sociality variable effects on fans built using affiliative data (χ^2 = 0.619, df = 3, P = 0.892). Boxes represent measured variables, arrows show regressions within the model and are scaled to effect size (dashed = negative, solid = positive). Standardized correlative path coefficients show estimated effect sizes. Percent variance (R^2) is displayed above each measured variable. Starred pathways were significant (*< 0.05, **< 0.01). There were strong positive direct effects of sex on maternal kinship, sex on fans and dominance on fans. Sex and dominance best explained the variation in fans.

When investigating the variation of fandom within the system, satisfactory fit criteria existed when we used both affiliative and movement data. We found no difference in the fit criteria or AIC values between the models (χ^2=0.271, df=2, P=0.873, AIC=38.271, Figure 5). To be consistent, we dropped the movement model. There were significant positive direct effects of sex on maternal kinship (P = 0.002, R = 0.511), maternal kinship on centrality (P = 0.034, R = 0.582) and dominance on fandom (P < 0.001, R = 0.541). In addition, a significant negative effect of age on centrality occurred (P < 0.001, R = -0.526). Dominance (R = 0.543) and age (R = -0.308) had the strongest total effects on fandom. Maternal kinship (R = 0.25), sex (R = 0.078) and centrality (R = 0.02) had weaker total effects on fandom. Forty-six percent of the variation in fandom was explained by the model (R^2 = 0.457, see Figure 5).
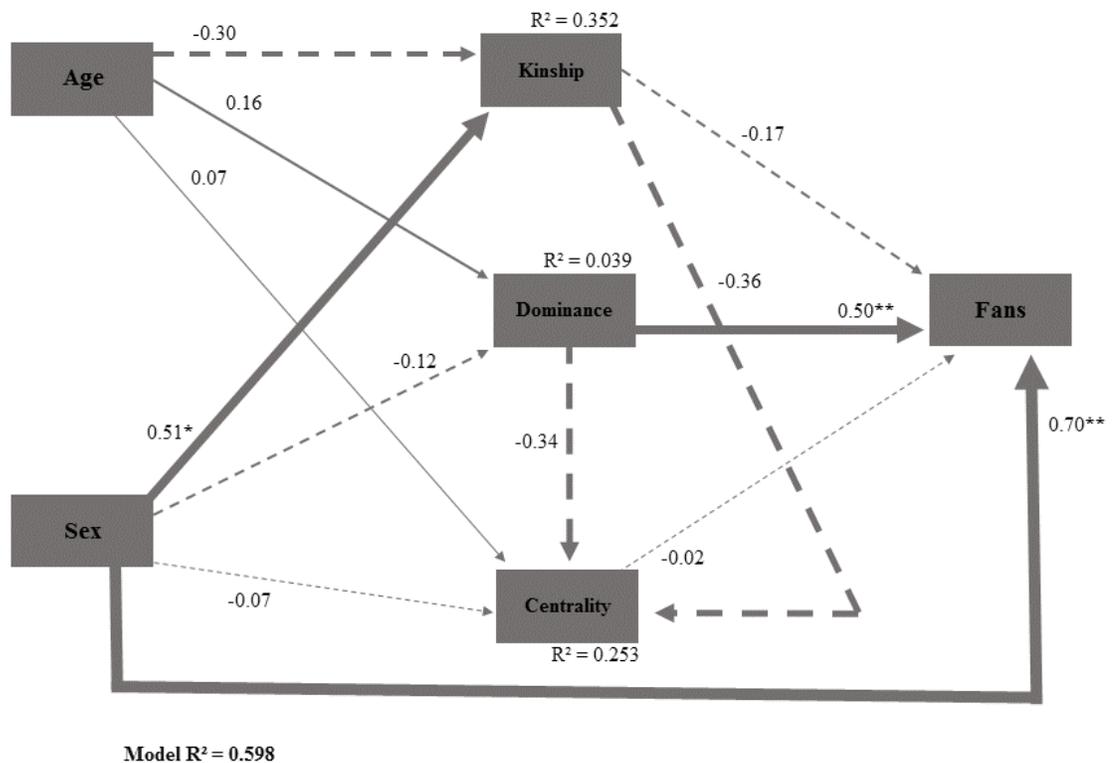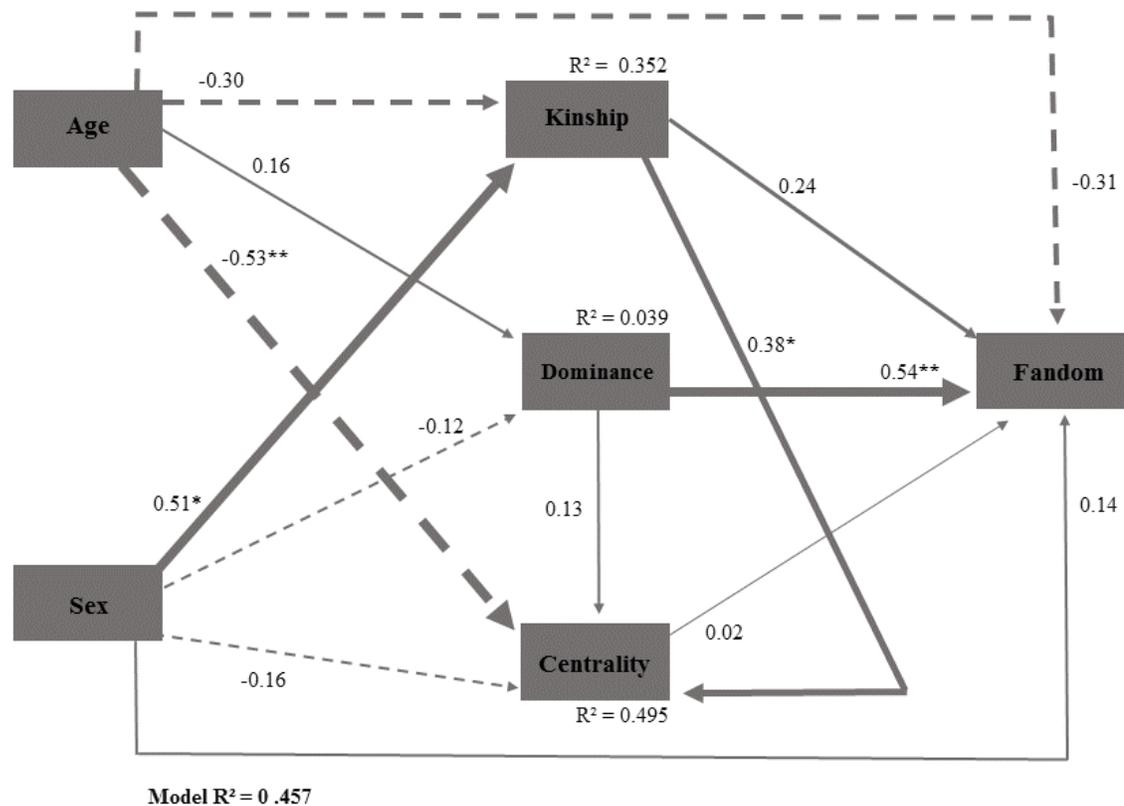

Figure 5. Structural equation model of total life history and sociality variable effects on fandom built

using affiliative data ($\chi^2 = 0.271$, df = 2, P = 0.873). Boxes represent measured variables, arrows show correlations within the model and are scaled to effect size (dashed=negative, solid=positive). Standardized correlative path coefficients show estimated effect sizes. Percent variance (R^2) is displayed above each measured variable. Starred pathways were significant (*< 0.05, **< 0.01). There were significant direct positive effects of sex on maternal kinship, maternal kinship on centrality and dominance on fandom and a significant negative effect of age on centrality. The variation in fandom is explained through strong total effects of dominance and age on fandom.

There was a significant positive relationship between fans and movement efficiency ($R^2 = 0.402$, df = 1, 23, P < 0.001), where the more fans an individual had the less efficient the movement was. No other significant relationships existed between efficiency and fans or fandom. No significant relationship existed between total fandom and efficiency ($R^2 = -0.041$, df = 1,23, P = 0.805). We found a strong, non-significant negative relationship between fans and number of unsuccessful movements was found (Spearman's rank correlation: $R_s = 0.367$, df = 24, P = 0.072).

DISCUSSION

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

Fans

In our study, we found that sex and dominance best described the variation in fans (Figure 4). Both the direct and total positive effects of sex on fans showed that

females had more fans than did males. This is consistent with the female philopatric society where females who remain in the society their whole lives tend to build strong, stable bonds with other females (Berman, Ionica, & Li, 2004; Li, Wang, & Han, 1996; Xia et al., 2012). The significant direct and total effects of dominance on fans displayed that more dominant individuals had more fans. Therefore, dominant females within the society had the most fans. In addition, the complex fan structure may have aided in the achievement of higher dominance positions, showing a network of social rules used in interactions within and outside movements. This is consistent with recent findings that within the YA1 group, a relationship exists between social affiliation and movement initiation success (Wang et al., 2016).

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

<div align="center">Fandom</div>

Variation in fandom was best described by a direct positive relationship between dominance and fandom, and total effects of dominance, age and maternal kinship on

<div align="center">45</div>

fandom. Indirect effects of maternal kinship on centrality, age on centrality, age on fandom and age on maternal kinship also existed (Figure 5). There were both significantly positive direct and total effects of dominance on fandom, suggesting that more dominant individuals were fans of more individuals. This described a highly connected society where not only do dominant individuals have more fans, but they were fans of more individuals. In female philopatric primate societies, females form dominance hierarchies based on maternal kinship (Berman et al., 2008) where entire matrilineages rank above or below other matrilineages (Kawai, 1958; Missakian, 1972; Sade, 1967). The formation of strong matrilineages influences the acquisition and maintenance of female dominance rank (Berman, 1983; Kawai, 1965; Kawamura, 1965). The result of dominance playing a strong role in both fan and fandom reflects highly connected, likely matrilineal social groups that occupy the top positions of the dominance hierarchy and travel consistently together. During the collection period, the "Ye" family occupied the top positions of the hierarchy (Table 1) and were often seen traveling together.

Individuals who occupy top positions in the hierarchy and were seen associating and moving together, often were individuals of similar age, specifically young females with similar age infants. This is consistent with the similarity principle, where individuals most often affiliate with those of similar maternal and paternal kin, age and rank (Silk, Alberts, & Altmann, 2006; de Waal, 1991; de Wall & Luttrell, 1986). Overall, individual macaques who affiliate tend to be close maternal kin and close in rank (Kapsalis & Berman, 1996) and therefore a strong connection of fans and fandom to rank was evident.

The strong negative total effects of age on fandom suggests that younger individuals were fans of more individuals. Our result that younger individuals follow a variety of individuals on a consistent basis and therefore have a higher fandom rate agrees with the attraction to higher rank hypothesis (Seyfarth, 1976; 1977) and the similarity principle (Silk, Alberts, & Altmann, 2006; de Waal, 1991; de Wall & Luttrell, 1986). Young individuals of lower rank will aim to associate with higher ranking individuals to benefit from reciprocity (Seyfarth, 1976; 1977). However, they will also be consistently interacting with individuals of their own age and rank (Silk, Alberts, & Altmann, 2006; de Waal, 1991; de Wall & Luttrell, 1986). In our study, this behavior was often seen in the subadult males (Table 1) who consistently affiliated and travelled together, but also were seen interacting and traveling with higher ranking individuals and kin. This interaction with a variety of individuals would lead them to have a higher fandom rate than do older individuals. This might also lead to them being more central to the group, because they were more connected to a variety of individuals.

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

Efficiency

The hypothesis that individuals with more fans will lead more efficient movements was not supported. A significant positive relationship between fans and efficiency suggests that the more fans an individual had, the less efficient the movement was in terms of how long it took for each individual to join the movement. The highly connected network of fans and fandom constructed through the female, dominant, matrilineal bonds hindered progress of the movement. A lag in joining occurred when individuals were waiting for their fans or individuals they are fans of to join the movement, which influenced the movement efficiency. If an individual had few or no fans, they left the group without caring who is following, while an individual with a high number of fans needed to stop consistently to wait for their network of fans, slowing the movement. This finding is consistent with previous studies that have found the more individuals involved in a movement, the more time it takes for the movement to be completed (Fratellone, 2015).

Wang et al. 2015 has found that Tibetan macaques used a combination of mimetism and quorum thresholds in collective movements. In our study, the strong network of connections that was displayed in fans may complicate the process of selective mimetism in the beginning of a movement because these top individuals were waiting for the entire network to move before they moved. However, although slow, the fan/fandom network showed selective mimetism was being used when deciding when to

join the movement. This selection process allowed the quorum threshold to be reached so entire group movement could occur.

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

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

This highly connected society may have hindered overall movement efficiency with respect to time due to needing all individuals of a fan/fandom network to join before comfortably moving, but it also may have influenced initiation success. This network aided in decisions regarding selective mimetism and allowed for the group to reach a quorum threshold stimulating entire group movement. The trade-off between movement efficiency and initiation success should be further investigated from a fitness perspective.

In conclusion, studying collective decision making during group movement through the lens of fans/fandom can help us to understand whether relationships observed in affiliative interactions are maintained in the structure of collective movements. Furthermore, our use SEM in this study proves a powerful tool to study these complex primate social networks. Applying these methods to other primate societies can allow for further insight into social relationships of a society and how these relationships are utilized during movement to promote cohesion and access the benefits of sociality.

Foundation (No. 31372215). Approval for this project was obtained from the Central

Washington University (CWU) Institutional Animal Care and Use Committee (IACUC)

board (# A121501). This project was conducted within the laws and regulations of the

People's Republic of China, and we followed the American Society of Primatologists'

(ASP) Principles for the Ethical Treatment of Non-Human Primates.

REFERENCES

Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour*, *49*, 227-267.

Ame, J. M., Halloy, J., Rivault, C., Detrain, C., & Deneubourg, J. L. (2006). Collegial decision making based on social amplification leads to optimal group formation. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 188-192.

Arbuckle, J.L. (2006). Amos (Version7.0) [Computer Program]. Chicago: SPSS.

Beckers, R., Deneubourg, J. L., Goss, S., & Pasteels, J. M. (1990). Collective decision making through food recruitment. *Insectes Sociaux*, *37*, 258–367.

Berman, C. M. (1983). Matriline differences and infant development. In Hinde, R. A. (ed.), *Primate Social Relationships: An Integrated Approach* (pp. 229-241). Sunderlands, MA: Sinauer Associates.

Berman, C. M., Ionica, C. S., Dorner, M., & Li, J. H. (2006). Postconflict affiliation between former opponents in *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology*, *27*(3): 827-854.

Berman, C., Ionica, M., & Li, C. (2004). Dominance style among *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology*, *25*, 1283-1312.

Berman, C. M. & Li, J. H. (2002) Impact of translocation, provisioning and range restriction on a group of *Macaca thibetana*. *International Journal of Primatology*, *23*, 383-397.

Berman, C., Yin, H., Ogawa, H., Li, J., & Ionica, C. (2008). Variation in kin bias over time in a group of Tibetan macaques at Huangshan, China: Contest competition, time constraints or risk response? *Behaviour*, *145*, 863-896.

Bernstein, I. S. & Ehardt, C. L. (1985). Agonistic aiding: maternal kinship, rank, age, and sex influences. *American Journal of Primatology*, *8*, 37-52.

Bokony, V., Kulcsar, A., Zoltan, T., & Liker, A. (2012). Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). *PLoS ONE*, *7*, e36639. DOI:10.1371/journal.pone.0036639.

Bollen, K. A. (1989) *Structural equations with latent variables*. New York, New York, USA: Wiley InterScience.

Bowker, M. A., Belnap, J., Davidson, D. W., & Phillips, S. L. (2005). Evidence for micronutrient limitation of biological soil crusts: Importance to arid-lands restoration. *Ecological Applications*, *16*, 1941-1951.

Breckler, S. J. (1990). Applications of covariance structure modeling in psychology: Cause for concern? *Psychological Bulletin*, *107*, 260-273.

Brown, J.L. 1975. *The evolution of behavior*. Norton, New York.

Cheney, D., Seyfarth, R., & Smuts, B. (1986). Social relationships and social cognition in nonhuman primates. *Science*, *234*, 1361-1366.

Cronin, A. (2013). Synergy between pheromone trails and quorum thresholds underlies consensus decisions in the ant *Myrmecina nipponica*. *Behavioral Ecology and Sociobiology*, *67*, 1643-1651.

Deneubourg J. L. & Goss, S. (1989) Collective patterns and decision making. *Ethology, Ecology & Evolution*, *1*, 295-311.

Estrada, A., Estrada, R., & Ervin, F. (1977). Establishment of a free-ranging colony of stumptail macaques (*Macaca arctoides*): Social relations I. *Primates*, *18*,647-676.

Farine, D. R., Aplin, L. M., Garroway, C. J., Mann, R. P., & Sheldon, B. C. (2014). Collective decision making and social interaction rules in mixed-species flocks of songbirds. *Animal Behaviour*, *95*, 173-182.

Fernández, V., Kowalewski, A. & Zunino, M. (2013). Who is coordinating collective movements in black and gold howler monkeys? *Primates*, *54*, 191-199.

Fratellone, P. G. (2015) *Female social connectivity through the leadership and movement progression of Tibetan macaques at Mt. Huangshan, China.* (unpublished master's thesis). Central Washington University, Washington.

Golob, T. F. (2003). Structural equation modeling for travel behavior research. *Transportation Research Part B: Methodological*, *37*, 1-25.

Grace, J. B. (2006). *Structural equation modeling and natural systems*. Cambridge

University Press.

Grace, J. B. & Jutila, H. (1999). The relationship between species density and community biomass in grazed and ungrazed coastal meadows. *Oikos*, *85*, 398-408.

Grace, J.B. & Keeley, J. E. (2006). A structural equation model analysis of postfire plant diversity in California shrublands. *Ecological Applications*, *16*, 503-514.

Grace, J. B. & Pugesek, B. H. (1998). On the use of path analysis and related procedures for the investigation of ecological problems. *The American Naturalist*, *152*, 151-159.

Hamilton, W. D. (1964). The genetical evolution of social beahviour. II. *Journal of Theoretical Biology*, *7*, 17-52

Jacobs, A., Watanabe, K., & Petit, O. (2011). Social structure affects initiations of group movements but not recruitment success in Japanese macaques (*Macaca fuscata*). *International Journal of Primatology*, *32*, 1311-1324.

Kapsalis, E. & Berman, C. M. (1996). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) II. Testing predictions for three hypothesized organizing principles. *Behaviour*, *133*, 1235-1263.

Kawai, M. (1958). On the system of social ranks in a natural troop of Japanese monkeys. Basic and dependent rank. *Primates*, *1*,206-258.

Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates*, *6*, 1-30.

Kawamura, S. (1965). Matriarchal social ranks in the Minoo-B troop: A study of the rank system of Japanese monkeys. *Japanese monkeys*, 105-112.

Li, J. H., Wang, Q. S., & Han, D. M. (1996) Fission in a free-ranging Tibetan macaque troop at Huangshan Mountain, China. *Chinese Science Bulletin*, *41,* 1377-1381.

Li, J.H., Yin, H.B., & Zhou, L.Z. (2007). Non-reproductive copulation behavior among Tibetan macaques (*Macaca thibetana*) at Huangshan, China. *Primates*, *48*, 64-72. DOI:10.1007/s10329-006-0002-5.

Lusseau, D. & Conradt, L. (2009). The emergence of unshared consensus decisions in bottlenose dolphins. *Behavioral Ecology and Sociobiology*, *63*, 1067-1077.

MacCallum, R. C. & Austin, J. T. (2000). Applications of structural equation modeling in psychological research. *Annual Review of Psychology*, *51*, 201-226.

Mallon, E. B., Pratt, S. C., & Franks, N. R. (2001) Individual and collective decision-making during nest site selection by the ant *Leptothorax albipennis*. *Behavioral Ecology and Sociobiology*, *50*, 352-359.

Missakian, E. A. (1972). Genealogical and cross genealogical dominance relationships in a group of free ranging rhesus monkeys on Cayo Santiago. *Primates*, *13*,169-180.

Ogawa, H. (1995). Bridging behavior and other affiliative interactions among male Tibetan macaques (*Macaca thibetana*). *International Journal of Primatology*, *16*, 707–729.

Passino, K. & Seeley, M. (2006). Modeling and analysis of nest-site selection by honeybee swarms: the speed and accuracy trade-off. *Behavioral Ecology and Sociobiology*, *59*, 427-442.

Petit, O., Gautrais, J., Leca, J. B., Theraulaz, G. & Deneubourg, J. L. (2009). Collective decision-making in white-faced capuchin monkeys. *Proceedings of the Royal Society B*, *276*, 3495-3503.

Pratt, S. C., Mallon, E. B., Sumpter, D. J. T. & Franks, N. R. (2002). Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis. Behavioral Ecology and Sociobiology*, *52*, 117–127.

Pratt, S. C. & Sumpter, D. J. T. (2006) A tunable algorithm for collective decision-making. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 15906-15910.

Pyritz, L. W., King, A. J., Sueur, C. & Fichtel, C. (2011). Reaching a consensus: Terminology and concepts used in coordination and decision-making research. *International Journal of Primatology*, *32*, 1268-1278.

R Core Team (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Ramseyer, A., Boissy, A., Dumont, B., & Thierry, B. (2009). Decision making in group departures of sheep is a continuous process. *Animal Behaviour*, *78*, 71-78.

Regoeczi, W. C. (2002). The impact of density: The importance of nonlinearity and selection on flight and fight responses. *Social Forces*, *81*, 505-530.

Sade, D. S. (1965). Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. *American Journal of Physical Anthropology*, *23*, 1-17.

Sade, D. S. (1967). Determinants of dominance in a group of free-ranging rhesus monkeys. In Altmann S. A. (ed.), *Social Communication in Primates.* Chicago: University of Chicago Press.

Seyfarth, R. M. (1976). Social relationships among adult female baboons. *Animal Behaviour*, *24*, 917-938.

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, *65*, 671-698.

Silk, J. B. (1982). Altruism among female *Macaca radiate*: Explanations and analysis of patterns of grooming and coalition formation. *Behaviour*, *79*,162-188.

Silk, J. B., Alberts, A. C., & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, *61*,197-204.

Silk, J. B., Samuels, A., & Rodman, P. S. (1981). The influence of maternal kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiate*). *Behaviour*, *78*, 111-137.

Sueur, C., Deneubourg, J., & Petit, O. (2010). Sequence of quorums during collective decision making in macaques. *Behavioral Ecology and Sociobiology*, *64*, 1875-1885.

Sueur, C. & Petit, O. (2008). Organization of group members at departure is driven by social structure in *Macaca*. *International Journal of Primatology*, *29*, 1085-1098.

Sueur, C., Petit, O., & Deneubourg, J.L. (2009). Selective mimetism at departure in collective movements of *Macaca tonkeana*: An experimental and theoretical approach. *Animal Behaviour*, *78*, 1087-1095.

Sueur, C., Petit, O., De Marco, A., Jacobs, A.T., Watanabe, K., & Thierry, B. (2011). A comparative network analysis of social style in macaques. *Animal Behaviour*, *82*, 845-852.

Sumpter, D. J. T., Krause, J., James, R., Couzin, I. D., & Ward, A. J. W. (2008). Consensus decision making by fish. *Current Biology*, *18*, 1773-1777.

Sumpter, D. J. T. & Pratt, S. C. (2009). Quorum responses and consensus decision making. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *364*, 743-753.

Thierry, B., Gauthier, C., & Peignot, P. (1990) Social grooming in Tonkean macaques. *International Journal of Primatology*, *11*, 357-375.

de Waal, F. B. M. (1991) Rank distance as a central feature of rhesus monkey organization: a sociometric analysis. *Animal Behavior*, *41*, 393-395.

de Waal, F. B. M. & Luttrell, L. M. (1986). The similarity principle underlying social bonding among female rhesus macaques. *Folia Primatoligica*, *46*, 215-234.

Wang, G., Yin, H., Yu, G., & Wu, M. (2007). Time budget of adult Tibetan macaques in a day in spring. *Chinese Journal of Wildlife*, *29*, 6–10 (In Chinese).

Wang, X., Sun, L., Li, J., Xia, D. P., Sun, B. A., & Zhang, D. (2015). Collective movement in the Tibetan macaques (*Macaca thibetana*): Early joiners write the rule of the game. *PloS One*, *10*, E0127459.

Wang, X., Sun, L., Sheeran, L.K., Sun, B.H., Zhang, Q.X., Zhang, D., Xia, D.P., & Li, J.H. (2016). Social rank versus affiliation: Which is more closely related to leadership of group movements in Tibetan macaques (*Macaca thibetana*)? *American Journal of Primatology*, *78*, 816-824. DOI: 10.1002/ajp.22546.

Whitehead, H. (2008). *Analyzing animal societies: Quantitative methods for vertebrate social analysis*. University of Chicago Press.

Whitehead, H. (2009). SOCPROG programs: Analyzing animal social structures. *Behavioral Ecology and Sociobiology*, *63*, 765-778.

Widdig, A., Nurnberg, P., Krawczak, M., Streich, W. J., & Bercovitch, F. B. (2001). Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proceedings of the National Academy of Sciences*, *98*, 13769-13773.

Xia, D. P., Li, J., Garber, P. A., Sun, L., Zhu, Y., & Sun, B. A. (2012). Grooming reciprocity in female Tibetan macaques *Macaca Thibetana*. *American Journal of Primatology*, *74*, 569-579.

Yamada, M. (1963). A study of blood-relationship in the natural society of the Japanese macaque. *Primates*, *4*, 43-65.

Yang, E. J. & Wilczynski, W. (2002). Relationships between hormones and aggressive behavior in green anole lizards: An analysis using structural equation modeling. *Hormones and Behavior*, *42*, 192-205.

Ziegler, L., Arim, M., & Narins, P.M. (2011). Linking amphibian call structure to the environment: The interplay between phenotypic flexibility and individual attributes. *Behavioral Ecology*, *22*, 520-52.

CHAPTER IV

CONCLUSION

We examined the mechanisms driving collective decision making during group
movement in the YA1 group of Tibetan macaques at Huangshan National Park, China.
Specifically, we uncovered the network of affiliations utilized during selective
mimetism to aid in reaching a quorum threshold through the lens of fans and fandom.
We used structural equation modeling (SEM) to investigate what factors make an
individual have more fans and what makes an individual a fan of more individuals
(fandom). SEM supported the hypotheses that dominant females tend to have more fans
and those in the core of social networks are fans of more individuals. Specifically,
dominant, younger individuals with a greater number of familial connections in the
group had a higher rate of fandom due to their tendency to interact with a variety of
individuals in the group. Dominance had the strongest effects on the variation in both
fans and fandom, displaying a highly connected network of females occupying top
positions in the dominance hierarchy who consistently followed one another. These data
show relationships that are maintained in affiliative encounters, such as grooming, are
utilized in movement to aid in selective mimitism to achieve quorum thresholds.

Regression analysis showed that the highly connected network of individuals
with high fan and fandom rates may hinder movement efficiency. While undergoing
selective mimitism, individuals who are highly connected may be concerned that all
their strong connections are joining the movement before they are willing to move,
leading to a decreased movement efficiency. However, while individuals with more
fans led less efficient movements, they were less likely to initiate unsuccessful

movements, displaying a connection between number of fans and movement initiation

success. This connection should be pursued in future studies. Particularly the trade-off

between movement efficiency and initiation success should be pursued through a fitness

perspective. Is it more beneficial to lead more efficient movements, or initiate more

successful movements? If a monkey leads more movements that are successful, they

may be more often displacing the group to a desirable resource that would benefit the

initiator, increasing overall fitness.

This study introduced novel methods of analyzing social structures during

movement through the utilization of fan/fandom structures, social network analysis, and

SEM. The investigation of fans and fandom allows us to understand how affiliative

social relationships that are studied using traditional methods such as focal animal

sampling are maintained in other aspects of the group's life, such as movement. These

methods can branch out from primatology and be applied to a variety of social

organisms. SEM has been utilized in ecology and animal behavior studies, but has never

been used in primatology to study a network of social relationships. This method allows

for the investigation of a network of causal relationships and for the understanding of

both direct and indirect effects of various factors on a response variable. SEM allows us

to gain a better picture of what is happening within a complex system than univariate

methods would and should be considered for use in future primatological studies of

complex social systems.

This study has allowed for a greater understanding of the social systems, which

exist in Tibetan macaques that allow them to stay cohesive as a group to reap the

benefits of sociality. A better understanding of these social systems and movement in

the group can aid in increased success in conservation and maintenance of their

population, including efforts to maintain a non-invasive tourist location. Understanding

group movement, mechanisms and social systems in our primate ancestors can increase

our understanding of these systems in humans, which have allowed us to expand and

spread to a variety of habitats.

REFERENCES

Akinyi, Tung, Jeneby, Patel, Altmann, & Alberts. (2013). Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*). *Animal Behaviour*, 85(3), 559-568.

Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour*, *49*, 227-267.

Ame, J. M., Halloy, J., Rivault, C., Detrain, C., & Deneubourg, J. L. (2006). Collegial decision making based on social amplification leads to optimal group formation. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 188-192.

Anafarta, N. (2011). The relationship between work-family conflict and job satisfaction: A structural equation modeling (SEM) approach. *International Journal of Business and Management, 6*(4), 168-177.

Arbuckle, J.L. (2006). Amos (Version7.0) [Computer Program]. Chicago: SPSS.

Arslan, T., Yilmaz, V., & Aksoy, H.K. Structural equation model for environmentally conscious purchasing behavior. (2012). *International Journal of Environmental Research, 6*(1), 323-334.

Baden, A., Wright, L., Louis, P., & Bradley, C. (2013). Communal nesting, maternal kinship, and
maternal success in a social primate. *Behavioral Ecology and Sociobiology, 67*(12), 1939-1950.

Ballerinie, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Lecomte, V., Orlandi, E., Parisi, G., Procaccini, A., Viale, M., & Zdravkovic, V. (2008). Interactions ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *Proceedings of the National Academy of Sciences*, 105(4), 1232-1237.

Baumgartner, H. & Homburg, C. (1996). Applications of structural equation modeling in marketing and consumer research: A review. *International Journal of Research in Marketing, 13*(2), 139-161.

Beckers, R., Deneubourg, J. L., Goss, S., & Pasteels, J. M. (1990). Collective decision making through food recruitment. *Insectes Sociaux*, *37*, 258–367.

Berman, C. M. (1983). Matriline differences and infant development. In Hinde, R. A. (ed.), *Primate Social Relationships: An Integrated Approach* (pp. 229-241). Sunderlands, MA: Sinauer Associates.

Berman, C. M., Ionica, C. S., Dorner, M., & Li, J. H. (2006). Post conflict affiliation

between former opponents in *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology, 27*(3), 827-854.

Berman, C., Ionica, M., & Li, C. (2004). Dominance style among *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology, 25*(6), 1283-1312.

Berman, C., Ionica, C., & Li, J. (2007). Supportive and tolerant relationships among male Tibetan macaques at Huangshan, China. *Behaviour, 144*, 631-661.

Berman, C. M. & Li, J. H. (2002). Impact of translocation, provisioning and range restriction on a group of *Macaca thibetana*. *International Journal of Primatology, 23*(2), 383-397.

Berman, C., Yin, H., Ogawa, H., Li, J., & Ionica, C. (2008). Variation in kin bias over time in a group of Tibetan macaques at Huangshan, China: Contest competition, time constraints or risk response? *Behaviour, 145*(7), 863-896.

Bernstein, I. S. & Ehardt, C. L. (1985). Agonistic aiding: Maternal kinship, rank, age, and sex influences. *American Journal of Primatology, 8*(1), 37-52.

Bokony, V., Kulcsar, A., Zoltan, T., & Liker, A. (2012). Personality traits and behavioral syndromes in differently urbanized populations of house sparrows (*Passer domesticus*). *PLoS ONE, 7*(5), e36639. DOI:10.1371/journal.pone.0036639.

Bollen, K. A. (1989) *Structural equations with latent variables*. New York, New York, USA: Wiley InterScience.

Bousquet, C. A. H., Sumpter, D. J. T., & Manser, M. B. (2011). Moving calls: A vocal mechanism underlying quorum decisions in cohesive groups. *Proceedings of the Royal Society B*. DOI:10.1098/ rspb.2010.1739.

Bowker, M. A., Belnap, J., Davidson, D. W., & Phillips, S. L. (2005). Evidence for micronutrient limitation of biological soil crusts: Importance to arid-lands restoration. *Ecological Applications, 16*(6), 1941-1951.

Breckler, S. J. (1990). Applications of covariance structure modeling in psychology: Cause for concern? *Psychological Bulletin, 107*(2), 260-273.

Brown, J.L. 1975. *The evolution of behavior*. Norton, New York.

Cheney, D., Seyfarth, R., & Smuts, B. (1986). Social relationships and social cognition in nonhuman primates. *Science, 234*(4782), 1361-1366.

Christensen, P. N. & Leck, K. (1999). Fluctuating asymmetry, sociosexuality, and

intrasexual competitive tactics. *Journal of Personality and Social Psychology, 76*(1), 159-172.

Conradt, L. & Roper, T. J. (2003) Group decision-making in animals. *Nature, 421*, 1555-158.

Coudrain, V., Herzog, F., & Entling, M. H. (2013). Effects of habitat fragmentation on abundance, larval food and parasitism of a spider-hunting wasp. *PLos ONE, 8*(3), e59286. DOI:10.1371/journal.pone.0059286.

Couzin, I.D. & Franks, N.R. (2003). Self-organized lane formation and optimized traffic flow in army ants. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 270*, 139-146.

Couzin, I. D. & Krause, J. (2003). Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior, 32*, 1-75.

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, *433*, 513–516.

Cresswell, W. & Quinn, J. I. (2004). Faced with a choice, sparrowhawks more often attack the more vulnerable prey group. *Oikos, 104*, 71-76.

Crofton, H. D. (1958). Nematode parasite populations in sheep on lowland pasture. V1. Sheep behavior and nematode infections. *Parasitology, 48*, 251-260.

Cronin, A. (2013). Synergy between pheromone trails and quorum thresholds underlies consensus decisions in the ant *Myrmecina nipponica*. *Behavioral Ecology and Sociobiology, 67*(10), 1643-1651.

Daruka, I. (2009). A phenomenological model for the collective landing of bird flocks. *Proceedings of the Royal Society B, 276*, 911-917.

Davis, J. M. (1980). The coordinated aerobatics of dunlin flocks. *Animal Behavior, 28*, 668-673.

DeBlois, E. M. & Rose, G. A. (1996). Cross-shoal variability in the feeding habits of migrating Atlantic cod (*Gadus morhua*). *Oecologia, 108*, 192-196.

Deneubourg J. L. & Goss, S. (1989) Collective patterns and decision-making. *Ethology, Ecology & Evolution*, *1*, 295-311.

Deng, J., Sun, P.S., Zhao, F.Z., Han, X.H., Yang, G.H., & Feng, Y.Z. (2016). Analysis of the ecological conservation behavior of farmers in payment for ecosystem service programs in eco-environmentally fragile areas using social psychology models. *Science of the Total Environment, 550*, 382-390.

Deng, Z. Y. & Zhao, Q. K. (1987). Social structure in a wild group of *Macaca thibetana* at Mount Emei, China. *Folia Primatologica, 49*, 1-10.

Detrain, C. & Deneubourg, J. (2006). Self-organized structures in a superorganism: Do ants "behave" like molecules? *Physics of Life Reviews*, *3*, 162–187.

Diseth, A., Pallesen, S., Brunborg, G.S., & Larsen, S. (2010). Academic achievement among first semester undergraduate psychology students: The role of course experience, effort, motives and learning strategies. *Higher Education, 59*, 335-352.

Dochtermann, N. A & Jenkins, S. H. (2007). Behavioural syndromes in Merriam's kangaroo rats (*Dipodomys merriami*): A test of competing hypotheses. *Proceedings of Royal Society B, 274*, 2343-2349.

Dyer, J.R.G., Ioannou, C.C., Morrel, L.J., Croft, D.P., Couzin, I.D., Waters, D.A., & Krause, J. (2008). Consensus decision making in human crowds. *Animal Behaviour, 75*, 461-470.

Edelaar, P, Serrano, D., Carrete, M., Blas, J., Potti, J., & Luis Tella, J. (2012). Tonic immobility is a measure of boldness toward predators: An application of Bayesian structural equation modeling. *Behavioral Ecology*. DOI:10.1093/beheco/ars006.

Eldridge, D. J., Bowker, M. A., Maestre, F. T., Alonso, P., Mau, R. L., Papadopoulos, J., & Escudero, A. (2010). Interactive effects of three ecosystem engineers on infiltration in semi-arid Mediterranean grassland. *Ecosystems, 13*(4), 499-510.

Estrada, A., Estrada, R., & Ervin, F. (1977). Establishment of a free-ranging colony of stumptail macaques (*Macaca arctoides*): Social relations I. *Primates, 18*(3), 647-676.

Faria, J.J., Codling, E.A., Dyer, J.R.G., Trillmich, F., & Krause, J. (2009). Navigation in human crowds: Testing the many-wrongs principle. *Animal Behaviour, 78*, 587-591.

Farine, D. R., Aplin, L. M., Garroway, C. J., Mann, R. P., & Sheldon, B. C. (2014). Collective decision making and social interaction rules in mixed-species flocks of songbirds. *Animal Behaviour, 95*, 173-182.

Fernández, V., Kowalewski, A., & Zunino, M. (2013). Who is coordinating collective movements in black and gold howler monkeys? *Primates, 54*(2), 191-199.

Finkel, D., Pederson, N., & McGue, M. (1995). Genetic influences on memory performance in adulthood: comparison of Minnesota and Swedish twin data. *Psychology and Aging, 10*, 437-446.

Franks, N.R., Dornhaus, A., Fitzsimmons, J.P., & Stevens, M. (2003). Speed versus accuracy in collective decision making. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 270*, 2457-2463.

Frattelone, P. G. (2015) *Female social connectivity through the leadership and movement progression of Tibetan macaques at Mt. Huangshan, China*. (Master's thesis). Central Washington University, Washington.

Fürtbauer, I., Heistermann, M., Schülke, O., & Ostner, J. (2014). Low female stress hormone levels are predicted by same or opposite sex sociality depending on season in wild Assamese macaques. *Psychoneuroendocrinology, 48*, 19-28.

Gautrais, J., Michelena, P., Sibbald, A., Bon, R., & Deneubourg, J. (2007). Allelomimetic synchronization in Merino sheep. *Animal Behaviour, 74*, 1443–1454.

Golob, T. F. (2003). Structural equation modeling for travel behavior research. *Transportation Research Part B: Methodological, 37*, 1-25.

Gosden, T. P. & Svensson, E. I. (2009). Density-dependent male mating harassment, female resistance, and male mimicry. *The American Naturalist, 173*(6), 709-721.

Gough, L. & Grace, J. B. (1999). Predicting effects of environmental change on plant species density: experimental evaluations in a coastal wetland. *Ecology, 80*, 882-890.

Grace, J. B. (2006). *Structural equation modeling and natural systems*. Cambridge University Press.

Grace, J. B. & Jutila, H. (1999). The relationship between species density and community biomass in grazed and ungrazed coastal meadows. *Oikos*, *85*, 398-408.

Grace, J.B. & Keeley, J. E. (2006). A structural equation model analysis of postfire plant diversity in California shrublands. *Ecological Applications, 16*(2), 503-514.

Grace, J. B. & Pugesek, B. H. (1998). On the use of path analysis and related procedures for the investigation of ecological problems. *The American Naturalist, 152*(1), 151-159.

Hamilton, W. D. (1964). The genetical evolution of social beahviour. II. *Journal of Theoretical Biology, 7*, 17-52.

Hardus, M., Lameira, E., Wich, A., Vries, R., Wahyudi, S., Shumaker, A., & Menken, H. (2015). Effect of repeated exposures and sociality on novel food acceptance and consumption by orangutans. *Primates, 56*(1), 21-27.

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2006). Road crossing in chimpanzees: A risky business. *Current Biology, 16*, R668–670.

Hulland, J., Chow, Y. H., & Lam, S. (1996). Use of causal models in marketing research: A review. *International Journal of Research in Marketing, 13*, 181-197.

Jacobs, A., Watanabe, K., & Petit, O. (2011). Social structure affects initiations of group movements but not recruitment success in Japanese macaques (*Macaca fuscata*). *International Journal of Primatology, 32*(6), 1311-1324.

Jiang, X., Wang, Y., & Wang, Q. (1996) Taxonomy and distribution of Tibetan macaque (*Macaca thibetana*). *Zoological Research, 17*(4), 361-369.

Johnson, M. L., Huggins, D. G., & deNoyelles, F. Jr. (1991) Ecosystem modeling with LISREL: A new approach for measuring direct and indirect effects. *Ecological Applications*, *4*, 383-398.

Judge, T. A. & Locke, E. A. (1993). Effect of dysfunctional thought processes on subjective well-being and job satisfaction. *Journal of Applied Psychology, 78*, 475-490.

Kapsalis, E. & Berman, C. M. (1996). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) II. Testing predictions for three hypothesized organizing principles. *Behaviour, 133*(15/16), 1235-1263.

Kawai, M. (1958). On the system of social ranks in a natural troop of Japanese monkeys. Basic and dependent rank. *Primates, 1*, 206-258.

Kawai, M. (1965). Newly acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates, 6*(1), 1-30.

Kawamura, S. (1965). Matriarchal social ranks in the Minoo-B troop: A study of the rank system of Japanese monkeys. *Japanese monkeys*, 105-112.

King, A. J. & Sueur, C. (2011) Where next? Group coordination and collective decision making by primates. *International Journal of Primatology, 32*(6), 1245-1267.

Krams, I., Vrublevska, J., Cirule, D., Kivleniece, I., Krama, T., Rantala, M. J., Kaasik, A., Horak, P., & Sepp, T. Stress. (2013). Behaviour and immunity in wild-caught wintering great tits (*Parus major*). *Ethology, 119*, 387-406.

Krause, J., Goding, J. J., & Brown, D. (1996) Phenotypic variability within and between fish shoals. *Ecology, 77*, 1586-1591.

Langen, T. A. & Vehrencamp, S. L. (1998). Ecological factors affecting group and territory size in white-throated magpies. *The Auk, 2*, 327-339.

Leca, J., Gunst, N., Thierry, B., & Petit, O. (2003). Distributed leadership in semifree-ranging white-faced capuchin monkeys. *Animal Behaviour, 66*, 1045–1052.

Lee, J.S. & Hsieh, C.J. (2010). A research in relating entrepreneurship, marketing capability, innovative capability and sustained competitive advantage. *Journal of Business & Economic Research, 8*(9), 109-120.

Li, J. H., Wang, Q. S., & Han, D. M. (1996) Fission in a free-ranging Tibetan macaque troop at Huangshan Mountain, China. *Chinese Science Bulletin, 41*, 1377-1381.

Li, J. H., Yin, H., & Wang, Q. (2005). Seasonality of reproduction and sexual activity in female Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan, China. *Acta Zoologica Sinica, 51*, 365-375.

Lusseau, D. & Conradt, L. (2009). The emergence of unshared consensus decisions in bottlenose dolphins. *Behavioral Ecology and Sociobiology, 63*, 1067-1077.

MacCallum, R. C. & Austin, J. T. (2000). Applications of structural equation modeling in psychological research. *Annual Review of Psychology, 51*, 201-226.

Major, P. F. & Dill, L. M. (1978). The three-dimensional structure of airborne bird flocks. *Behavioral Ecology and Sociobiology, 4*, 111-122.

Mallon, E. B., Pratt, S. C., & Franks, N. R. (2001) Individual and collective decision-making during nest site selection by the ant *Leptothorax albipennis*. *Behavioral Ecology and Sociobiology*, *50*, 352-359.

Marsh, M., Lüdkte, O., Muthén, B., Asparouhov, T., Morin, A., Trautwin, U., & Nagengast, B. (2010). A new look at the big five factor structure through exploratory structural equation modeling. *Psychological Assessment, 22*(3), 471-491.

Masi, S., Gustafsson, E., Saint Jalme, M., Narat, V., Todd, A., Bomsel, M. C., & Krief, S. (2012). Unusual feeding behavior in wild great apes, a window to understand origins of self-medication in humans: Role of sociality and physiology on learning process. *Physiology & Behavior*, *105*(2), 337-349.

McFarland, R., Fuller, A., Hetem, R., Mitchell, D., Maloney, S., Henzi, S., & Barrett, L. (2015). Social integration confers thermal benefits in a gregarious primate. *Journal of Animal Ecology, 84*(3), 871-878.

Mcfarland, R. & Majolo, B. (2013). Coping with the cold: Predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biology Letters*, *9*(4).

Meunier, H., Deneubourg, J., & Petit, O. (2008). How many for dinner? Recruitment and monitoring by glances in capuchins. *Primates, 49*(1), 26-31.

Meunier, H., Leca, J. B., Deneubourg, J. L., & Petit, O. (2006). Group movement decisions in capuchin monkeys: The utility of an experimental study and a mathematical model to

explore the relationship between individual and collective behaviours. *Behaviour*, *143*, 1511–1527.

Missakian, E. A. (1972). Genealogical and cross genealogical dominance relationships in a group of free ranging rhesus monkeys on Cayo Santiago. *Primates*, *13*, 169-180.

Moussaid, M., Perozo, N., Garnier, S., Helbing, D., & Theraulaz, G. (2010). The walking behaviour of pedestrian social groups and its impact on crowd dynamics. *PLos ONE, 5*(4), e10047.

Nagy, M., Akos, Z., Biro, D., & Vicsek, T. (2010). Hierarchical group dynamics in pigeon flocks. *Nature, 464*(7290), 890-893.

Ogawa, H. (1995). Bridging behavior and other affiliative interactions among male Tibetan macaques (*Macaca thibetana*). *International Journal of Primatology*, *16*, 707–729.

Parrish, J. K. (1989). Layering with depth in a heterospecific fish aggregation. *Environmental Biology Fishes*, *26*, 79-85.

Partridge, B. L. (1980) The effect of school size on the structure and dynamics of minnow schools. *Animal Behavior*, *28*, 68-77.

Passino, K. & Seeley, M. (2006). Modeling and analysis of nest-site selection by honeybee swarms: the speed and accuracy trade-off. *Behavioral Ecology and Sociobiology, 59*(3), 427-442.

Petit, O., Gautrais, J., Leca, J. B., Theraulaz, G., & Deneubourg, J. L. (2009). Collective decision-making in white-faced capuchin monkeys. *Proceedings of the Royal Society B, 276*, 3495-3503.

Pokhrel, P., Fagan, P., Kehl, L., & Herzog, T.A. (2015). Receptivity to e-cigarette marketing, harm perceptions, and e-cigarette use. *American journal of health behavior, 39*(1), 121-131.

Pomeroy, H. & Heppner, F. (1992). Structure of turning in airborne rock dove (*Columba livia*) flocks. *Auk, 109*, 256-261.

Pratt, S. C., Mallon, E. B., Sumpter, D. J. T., & Franks, N. R. (2002) Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis. Behavioral Ecology and Sociobiology, 52*, 117–127.

Pratt, S. C. & Sumpter, D. J. T. (2006) A tunable algorithm for collective decision-making. *Proceedings of the National Academy of Sciences of the United States of America, 103,* 15906-15910.

Preacher, K.J., Zyphur, M.J., & Zhang, Z. A general multilevel SEM framework for assessing multilevel mediation. (2010). *Psychological Methods, 15*(3), 209-233.

Prescott, C. A. & Kendler, K. S. (1996). Longitudinal stability and change in alcohol consumption among female twins: contributions of genetics. *Developmental Psychopathology, 8*, 849-866.

Prins, H. H. T. (1996). *Social inequality and decision-making. Ecology and behavior of the African Buffalo*. London: Chapman & Hall.

Pyritz, L. W., King, A. J., Sueur, C., & Fichtel, C. (2011). Reaching a consensus: Terminology and concepts used in coordination and decision-making research. *International Journal of Primatology, 32*(6), 1268-1278.

R Core Team (2015*). R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

Radakov, D. (1973). *Schooling in the Ecology of Fish.* New York: John Wiley & Sons.

Ramseyer, A., Boissy, A., Dumont, B., & Thierry, B. (2009). Decision making in group departures of sheep is a continuous process. *Animal Behaviour*, *78*(1), 71-78.

Regoeczi, W. C. (2002). The impact of density: The importance of nonlinearity and selection on flight and fight responses. *Social Forces, 81*(2), 505-530.

Rhine, R. J. (1975). The order of movement of yellow baboons (*Papio cynocephalus*). *Folia Primatologica, 23*, 72-104.

Rhine, R. J. & Tilson, R. (1987). Reactions to fear as a proximate factor in the sociospatial organization of baboon progressions. *American Journal of Primatology, 13*, 119 –128.

Rice, K. G., Cunningham, T. J., & Young, M. B. (1997). Attachment to parents, social competence, and emotional well-being: a comparison of black and white late adolescents. *Journal of Counseling Psychology, 44*, 89-101.

Royaute, R., Buddle, C.M., & Vincent, C. (2013). Interpopulation variations in behavioral syndromes of a jumping spider from insecticide-treated and insecticide-free orchards. *Ethology, 119*, 1-13.

Ruckstuhl, K.E. (1999) To synchronise or not to synchronise: A dilemma for young bighorn males? *Behaviour, 136* (6), 805-818.

Sade, D. S. (1965). Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. *American Journal of Physical Anthropology, 23(*1), 1-17.

Sade, D. S. (1967). Determinants of dominance in a group of free-ranging rhesus monkeys. In Altmann S. A. (ed.), *Social Communication in Primates*. Chicago: University of Chicago Press.

Schülke, Bhagavatula, Vigilant, & Ostner. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology, 20*(24), 2207-2210.

Seeley, T.D., Camazine, S., & Sneyd, J. (1991). Collective decision-making in honeybees: How colonies choose among nectar sources. *Behavioral Ecology and Sociobiology, 28*, 277-290.

Seyfarth, R. M. (1976). Social relationships among adult female baboons. *Animal Behaviour, 24*(4), 917-938.

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology, 65*, 671-698.

Seyfarth, R.M. & Cheney, D.L. (2015) Social Cognition. *Animal Behaviour*, *103*, 191-202.

Sheeran, L.K. (2013). Tibetan Macaque. In R. A. Mittermeier, A. B. Rylands, D. E. Wilson & S. D. Nash (Eds.), *Handbook of the Mammals of the World, Volume 3: Primates* (pp. 642-643). Barcelona: Lynx Edicions.

Shultz, S., Opie, C., & Atkinson, Q. (2011). Stepwise evolution of stable sociality in primates. *Nature, 479*(7372), 219-22.

Silk, J. B. (1982). Altruism among female *Macaca radiate*: Explanations and analysis of patterns of grooming and coalition formation. *Behaviour, 79*(2/4), 162-188.

Silk, J. B., Alberts, A. C. & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology, 61*:197-204.

Silk, J. B., Beehner, Bergman, Crockford, Engh, Moscovice, & Cheney. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology, 20*(15), 1359-1361.

Silk, J. B., Samuels, A., & Rodman, P. S. (1981). The influence of maternal kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiate*). *Behaviour, 78*(1/2), 111-137.

Suadino, K. F., McGuire, S., Reiss, D., Hetherington, E. M., & Plomin, R. (1995). Parent ratings of EAS temperaments in twins, full siblings, half siblings, and step siblings. *Journal of Personality and Social Psychology, 68*, 723-733.

Sueur, C., Deneubourg, J., & Petit, O. (2010). Sequence of quorums during collective decision making in macaques. *Behavioral Ecology and Sociobiology, 64*(11), 1875-1885.

Sueur, C. & Petit, O. (2008). Organization of group members at departure is driven by social structure in *Macaca*. *International Journal of Primatology, 29*, 1085-1098.

Sueur, C., Petit, O., De Marco, A., Jacobs, A.T., Watanabe, K., & Thierry, B. (2011). A comparative network analysis of social style in macaques. *Animal Behaviour, 82*, 845 852.

Sueur, C., Petit, O., & Deneubourg, J.L. (2009). Selective mimetism at departure in collective movements of *Macaca tonkeana*: An experimental and theoretical approach. *Animal Behaviour, 78*(5), 1087-1095.

Sumpter, D. (2006). The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences, 361*, 5-22.

Sumpter, D. J. T., Krause, J., James, R., Couzin, I. D., & Ward, A. J. W. (2008).Consensus decision making by fish. *Current Biology, 18*, 1773-1777.

Sumpter, D. J. T. & Pratt, S. C. (2009). Quorum responses and consensus decision-making. *Philosophical Transactions of the Royal Society B-Biological Sciences, 364*, 743-753.

Thierry, B. (2011). The Macaques: A Double-Layered Social Organization. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder & R. M. Stumpf (Eds.), *Primates in Perspective* (pp. 229-241). New York: Oxford University Press.

Thierry, B., Gauthier, C., & Peignot, P. (1990) Social grooming in Tonkean macaques. *International Journal of Primatology, 11*, 357-375.

Thierry, B., Iwaniuk, A.N., & Pellis, S.M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology, 106*, 713-728.

Topa, G. & Moriano, J.A. (2010). Theory of planned behavior and smoking: meta-analysis and SEM model. *Substance abuse and rehabilitation, 1*, 23-33.

de Wall, F. B. M. (1991) Rank distance as a central feature of rhesus monkey organization: a sociometric analysis. *Animal Behavior, 41, 393*-395.

de Waal, F. B. M. & Luttrell, L. M. (1986). The similarity principle underlying social bonding among female rhesus macaques. *Folia Primatoligica, 46*, 215-234.

Wall, P. M. & Messier, C. (2000). Ethological confirmatory factor analysis of anxiety-like behaviour in the murine elevated plus-maze. *Behavioural Brain Research, 114*(1-2), 199-212.

Wang, G., Yin, H., Yu, G., & Wu, M. (2007). Time budget of adult Tibetan macaques in a day in spring. *Chinese Journal of Wildlife, 29*, 6-10 (In Chinese).

Wang, X., Sun, L., Li, J., Xia, D. P., Sun, B. A., & Zhang, D. (2015). Collective movement in the Tibetan macaques (*Macaca thibetana*): Early joiners write the rule of the game. *PloS One, 10*(5), E0127459.

Wang, X., Sun, L., Sheeran, L.K., Sun, B.H., Zhang, Q.X., Zhang, D., Xia, D.P., & Li, J.H. (2016). Social Rank versus Affiliation: Which is more closely related to leadership of group movements in Tibetan macaques (*Macaca thibetana*)? *American Journal of Primatology*. DOI: 10.1002/ajp.22546.

Ward, A. J. W., Krause, J., & Sumpter, D. J. T. (2012). Quorum decision-making in foraging fish shoals. *PLoS One, 7*, e32411.

Ward, A. J. W., Sumpter, D. J. T., Couzin, I. D., Hart, P. J. B., & Krause, J. (2008). Quorum decision-making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences, 105*(19), 6948–6953.

Whitehead, H. (2008). *Analyzing animal societies: quantitative methods for vertebrate social analysis*. University of Chicago Press.

Whitehead, H. (2009). SOCPROG programs: analyzing animal social structures. *Behavioral Ecology and Sociobiology, 63*, 765-778.

Widdig, A., Nurnberg, P., Krawczak, M., Streich, W. J., & Bercovitch, F. B. (2001). Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proceedings of the National Academy of Sciences, 98*, 13769-13773.

Wright, S. (1918). On the nature of size factors. *Genetics, 3*, 367-374.

Wright, S. (1921). Correlation and causation. *Journal of Agricultural Research, 20*, 557-585.

Wright, S. (1934). The method of path coefficients. *Annals of Mathematical Statistics, 5*, 161-215.

Wright, S. (1960). Path coefficients and path regressions: Alternative or complementary concepts? *Biometrics, 16*, 189-202.

Xia, D. P., Li, J., Garber, P. A., Sun, L., Zhu, Y., & Sun, B. A. (2012). Grooming reciprocity in female Tibetan macaques *Macaca thibetana*. *American Journal of Primatology, 74*(6), 569-579.

Yamada, M. (1963). A study of blood-relationship in the natural society of the Japanese macaque. *Primates, 4*(3), 43-65.

Yang, E. J. & Wilczynski, W. (2002). Relationships between hormones and aggressive behavior in green anole lizards: An analysis using structural equation modeling. *Hormones and Behavior, 42*, 192-205.

Yin, H., Li, J., Zhou, L., Ge, J., Ionica, C., & Berman, C. (2004). Birth of Tibetan monkey (*Macaca thibetana*) in winter. *Acta Theriologica, 24*, 19-22.

Zhang, Q. X., Li, J. H., Xia, D. P., Zhu, Y., Wang, X., & Zhang, D. (2014) Influence of dominance rank and affiliation relationships on self-directed behavior in female Tibetan macaques (*Macaca thibetana*). *Zoological Research, 35* (3), 214-221.

Zhao, Q. K. (1994). Mating competition and intergroup transfer for males in Tibetan macaques (*Macaca thibetana*) at Mt. Emei, China. *Primates, 35*, 57–68.

Zhao, Q. K. (1996). Male-infant-male interactions in Tibetan macaques. *Primates, 37*(2), 135-143.

Zhao, Q. K. (1997). Intergroup interaction in Tibetan macaques at Mt. Emei, China. American *Journal of Physical Anthropology, 104*, 459-470.

Zhao, Q. K. & Deng, Z. Y. (1988). Ranging behavior of *Macaca thibetana* at Mt. Emei, China. *International Journal of Primatology, 9*, 8–47.

APPENDIX A
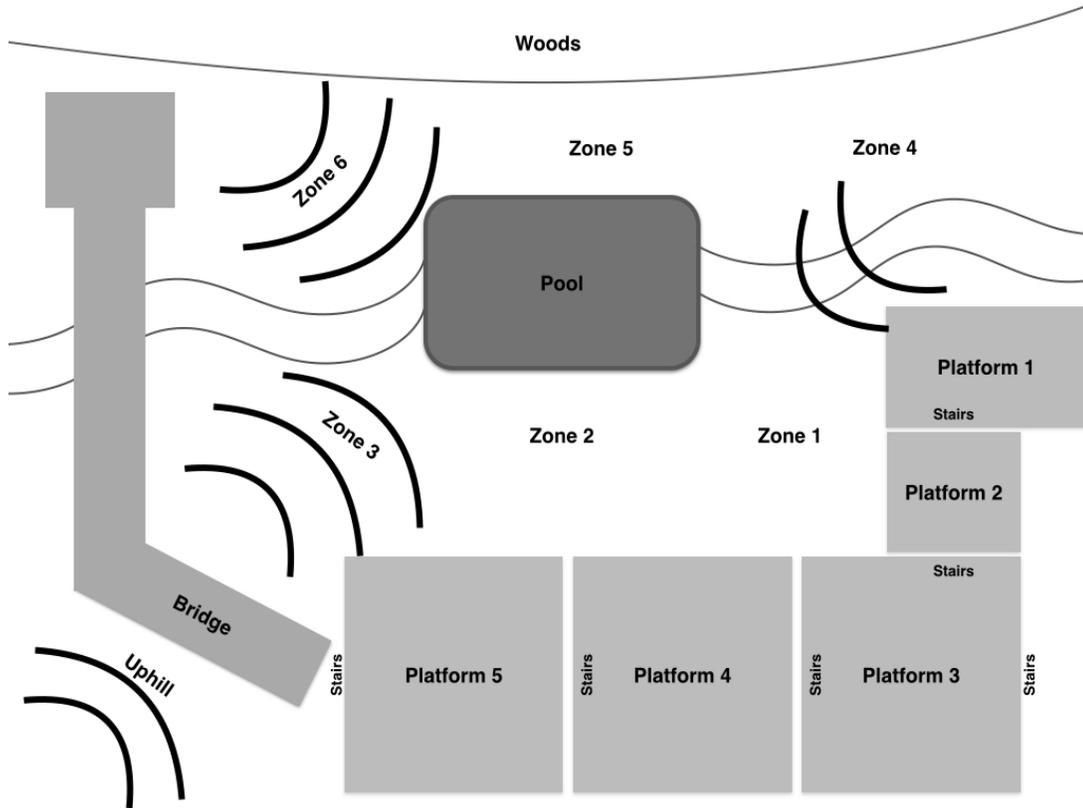
Explanatory Graphics – Study Site Map

Figure 6. Map of the study site including platforms from where all observations occurred (Fratellone, 2015).

APPENDIX B

Explanatory Graphics - Definitions

Table 3. Agonistic and Other Behavior Recorded During Focal Animal Samples of Adults and Subadults of the YA1 Group to Aid in Completion of a Dominance Hierarchy.

AGONISTIC BEHAVIOR	DEFINITION
THREAT	An individual directs an open mouth agonistic gesture or any of its components (e.g., stare, raised eyebrows, lowered jaw, ground slap) to another individual.
SHORT LUNGE	An individual directs agonistic movement of less than two body lengths toward another individual.
LONG LUNGE	An individual directs agonistic movement of two or more body lengths bud does not go into a full chase.
CHASE	An individual runs after another individual at great speed.
SLOW GRAB	An individual seizes another individual slowly and holds while staring.
GRAB	An individual roughly and quickly seizes another individual and holds for at least a few seconds.
BITE	An individual bites hard, either releasing the victim quickly or hanging on for several seconds. Soft bites (seen during embracing or play not included).
SLAP	An individual hits another individual.
OTHER	An individual is engaged in behavior not included in ethogram.
OUT OF SITE	The researcher cannot see an individual.

*(Berman, Ionica, & Li 2004; Ogawa, 1995)

Table 4. Definitions Used in Collection and Analysis of Data. See Methods for Movement Definition References.

BEHAVIOR	DEFINITION
INITIATOR	An individual moves more than 10 m away from a stationary group in less than 40 s.
FOLLOWER	An individual moves more than 5 m within a 45° angle of the initiator's movement direction within 5 min of the initiator.
MOVEMENT SUCCESSFUL	2 or more individuals followed the initiator within 5 min.
MOVEMENT UNSUCCESSFUL	Less than 2 individuals followed the initiator within 5 min.
MOVEMENT COMPLETED	No individuals joined the movement within 5 min.
FAN	Individual B, when individual B follows individual A within the first 180 s of movement during at least 10% of movements individual A is involved in. Calculated through the addition of percentages of time above 10% in which all focal individuals followed individual A.
FANDOM	Calculated through addition of percentages of time above 10% in which individual A followed all focal individuals.

APPENDIX C

Half Weight Index and Eigenvector Centrality Coefficient

Through SOCPROG 2.7 (Whitehead, 2009), we used group movement data and

affiliative data to calculate the Half Weight Index (HWI) as below:

$$HWI_{AB} = X/(X+Y_{AB}+0.5(Y_A+Y_B))$$

where X is the association strength or the number of times individual A and B both

participated in the movement. Y_{AB} is the number of times one individual participated in

the movement or interaction while the other did not. Y_A is the number of times

individual A participated in a movement or interaction and Y_B is the number of times

individual B participated in a movement or interaction (Cairns & Schwager, 1987). The

result of the HWI is a continuum of zero to one where zero shows the individuals were

never associated during movement or interactions and one shows the individuals always

associated during movement or interactions (Sueur & Petit, 2008).

HWI matrices were used to calculate an Eigenvector Centrality Coefficient

(ECC) for each individual. ECC measures how closely associated an individual is to

other individuals in the network. A high ECC represents an individual who is connected

to many individuals or is connected to others that are highly central (Newman, 2004;

Whitehead, 2008).

APPENDIX D

Temporal Analysis – July and August

Fan (W = 477, P = .001) and fandom (W = 467.5, P = .003) values differed temporally between July and August. All questions were therefore analyzed and addressed for totals, July and August data. Temporal analysis was eliminated from the journal article due to no differences in interpretation of data.

Fans and Fandom

The weighted fan rate varied greatly with values as high as 185% in July and 159% in August and as low as 0% in all periods. Individuals displaying the highest fan rates varied temporally, with YH and TH having the highest rate overall, YCY and YH in July and YCY in August (Table 2, Figure 7). The weighted fandom rate varied with rates as high as 119% overall, 143% in July and 199% in August and a rate of 0% for many individuals in all time periods. YXX and TG displayed the highest rates of fandom in all periods (Table 2, Figure 8).

Fans/Fandom and Efficiency

There was no significant relationship between July fans and efficiency (R^2 = -0.041, df = 1,23, P = 0.8135) or July fandom and efficiency (R^2 = 0.002, df = 1,23, P = 0.32). No significant relationship was found between August fans and efficiency (Spearman's rank correlation: R_s = -0.034, df = 24, P = 0.85). A slight positive correlation between efficiency and August fandom existed, although not significant (R_s = 0.357, df = 24, P = 0.078).
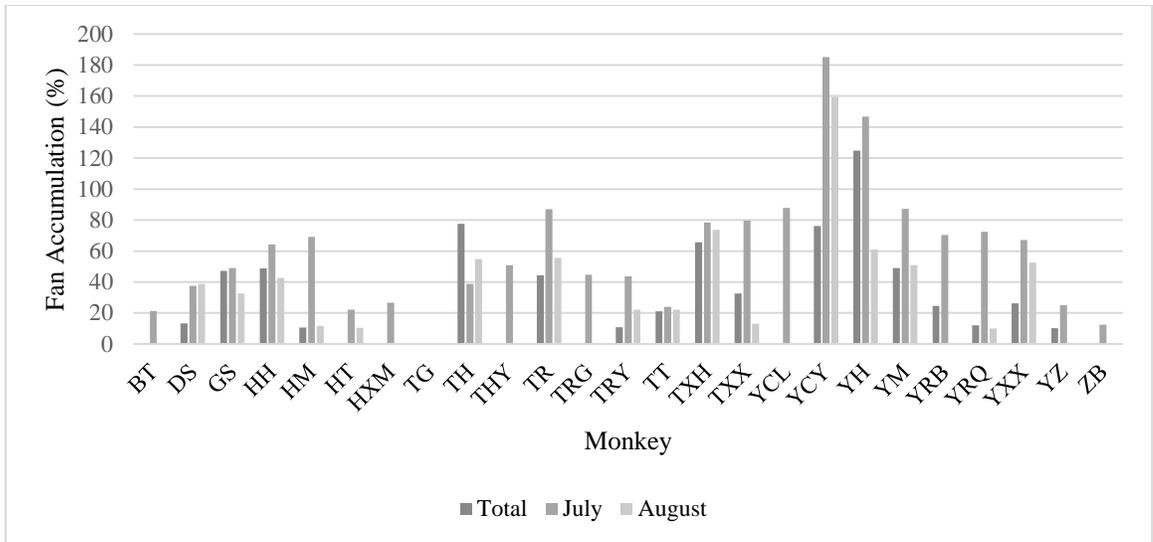
Figure 7. Distribution of fans for adult and subadult Tibetan macaques of the YA1 group. Fans were weighted and calculated through the addition of percentages of time above 10% in which all focal individuals followed individual A.
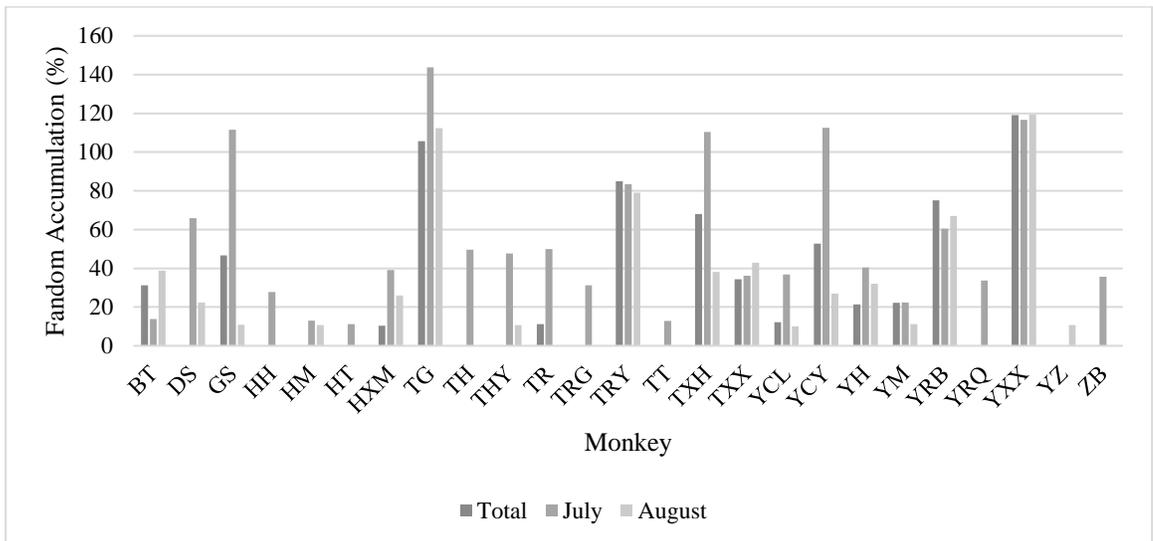

Figure 8. Distribution of fandom for each adult and subadult Tibetan macaque of the YA1 group. Fandom was weighted and calculated through the addition of percentages of time above 10% in which individual A followed all focal individuals.

Structural Equation Modeling

In July, YH, YRQ and TXH were the most central (0.4, 0.36, 0.36) and DS and BT were the least central (0.01, 0.02). In August, TXH and HH were the most central (0.39, 0.37) and HT and YZ were the least central (0, 0.01) (Figure 9).
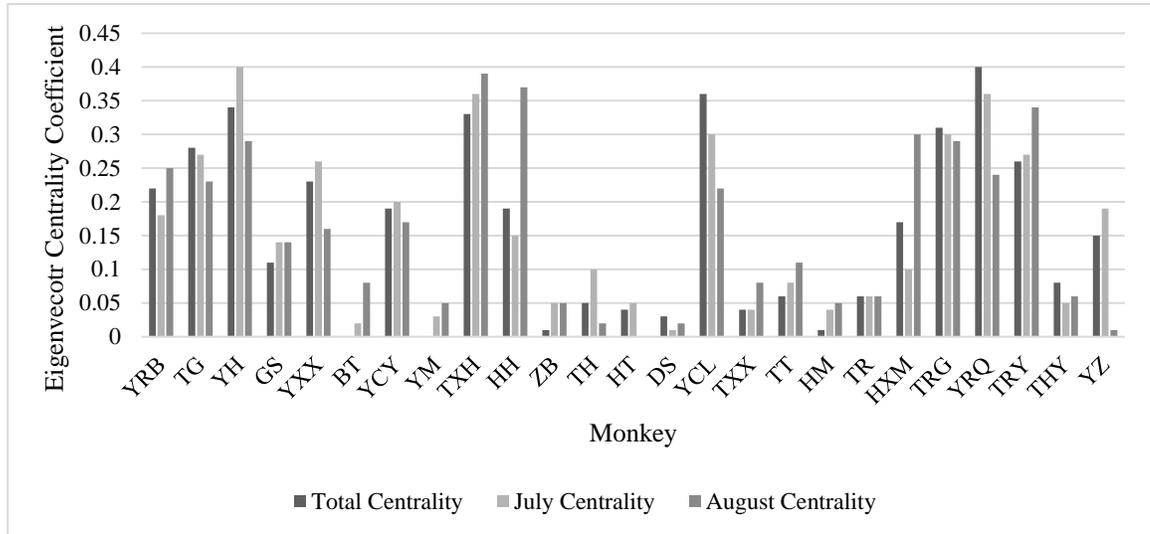
Figure 9. Eigenvector centrality coefficient calculated through use of affiliative behaviors for each adult and subadult of the YA1 group of Tibetan macaques. These data are arranged by dominance from left to right.

When calculating ECC through use of movement data, in July, BT and YCL were the most central (0.41, 0.38) and DS was the least central (0). In August, TR and TRY were also the most central (0.41, 0.38) and TH was the least central (0) (Figure 10).

When investigating the variation of fans within the system in July, satisfactory fit criteria existed using both affiliative and movement data. The movement data model was a better fitting model ($\chi^2 = 0.271$, df = 3, P = 0.965, AIC = 36.372, Figure 9). The affiliative model was dropped. There was significant positive direct effects of sex on maternal kinship (R = 0.51, P = 0.002) and sex on fans (R = 0.45, P = 0.009).
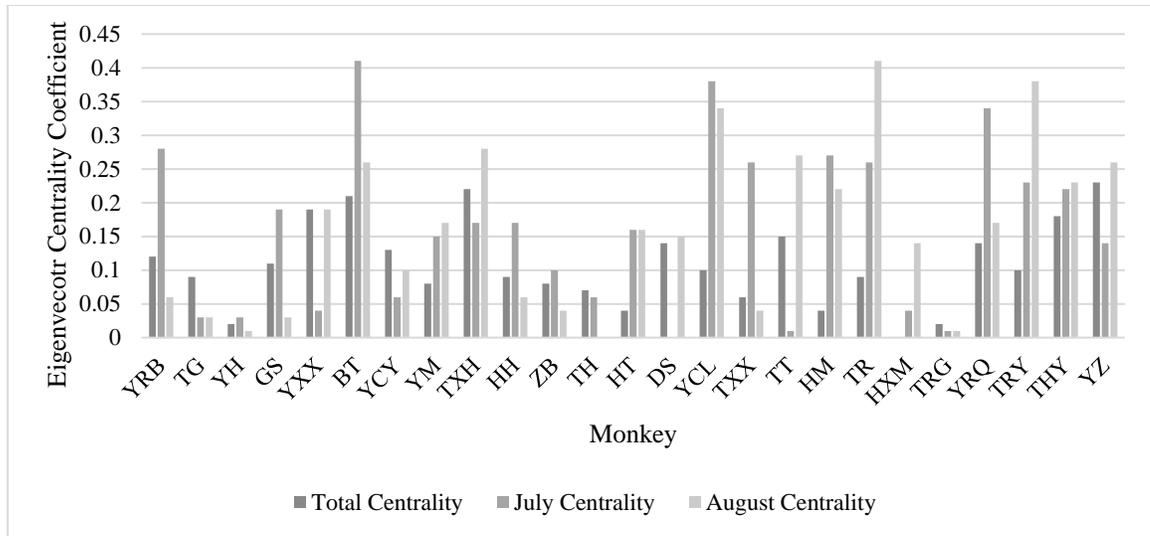
Figure 10. Eigenvector centrality coefficient calculated through use of movement data for each adult and subadult of the YA1 group of Tibetan macaques. These data are arranged by dominance from left to right.

We found a strong, but non-significant positive effect of dominance on fans (R = 0.312, P = 0.071) and a strong, non-significant negative effect of age on fans (R = -0.327, P = 0.051). Sex (R = 0.423, dominance (R = 0.32) and age (R = -0.284) had strong total effects on fans, while centrality(R = 0.04) and maternal kinship (R = 0.001) had weaker total effects. 46% of the variation in July fans was explained by the model (R = 0.358) (Figure 11). When investigating the variation of fandom within the system using July data, satisfactory fit criteria existed using both affiliative and movement data. There was no difference in the fit criteria or AIC values between the models (χ^2 = 0.271, df = 2, P = 0.873, AIC = 38.271, Figure 12). To be consistent, the affiliative model was dropped. We found significant positive direct effects of sex on maternal kinship (R = 0.511, P = 0.002), and dominance on fandom (R = 0.563, P < 0.001). Additionally, a significant negative effect of age on fandom existed (R = -0.339, P = 0.045). There was a strong, non-significant negative effect of age on maternal kinship (R = -0.302, P =

0.066). Dominance (R = 0.545) and age (R = -0.305) had the strongest total effects on
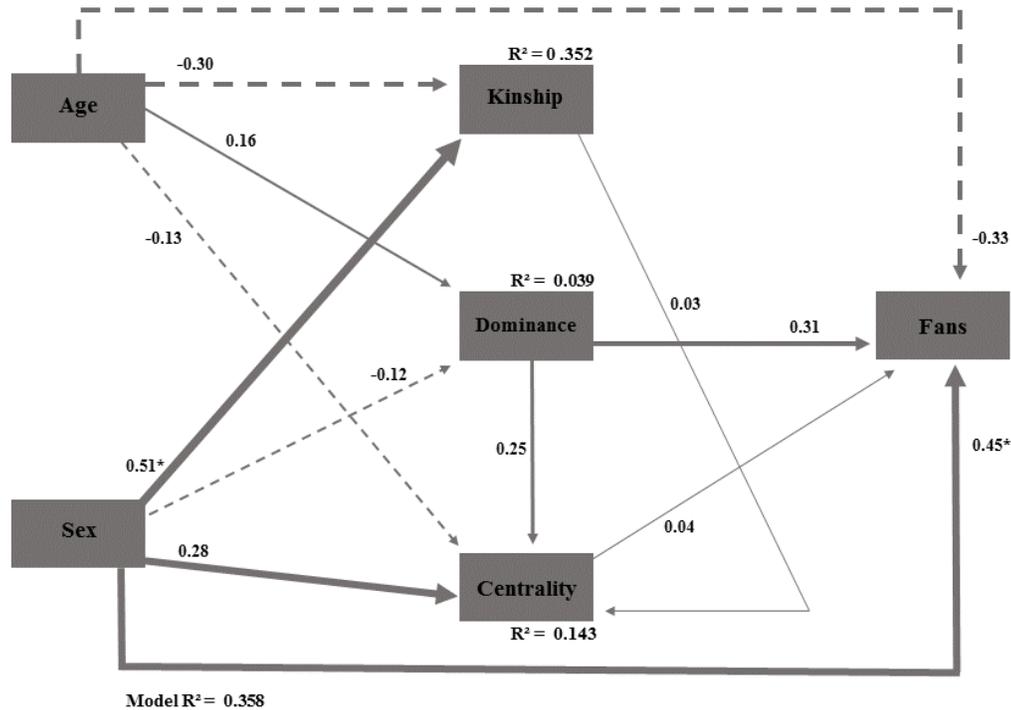
fandom.

Figure 11. Structural equation model of July life history and sociality variable effects on fans built using movement data (χ^2 = 0.271, df = 3, P = 0.965). Boxes represent measured variables, arrows show correlations within the model and are scaled to effect size (dashed=negative, solid=positive). Standardized correlative path coefficients show estimated effect sizes. Percent variance (R^2) is displayed above each measured variable. Starred pathways were significant (*< 0.05, **< 0.01). There were significant positive effects of sex on maternal kinship and sex on fans. Sex, dominance and age best explained the variation in fans in July.

Maternal kinship (R=0.199), sex(R=0.091) and centrality (R=-0.05) had weaker

total effects on fandom. 42% of the variation in fandom in July was explained by the

model (R^2=0.419) (Figure 12). When investigating the variation of fans within the

system using August data, satisfactory fit criteria existed using both affiliative (χ^2 =

4.497, df = 7, P = 0.721) and movement data (χ^2 = 0.271, df = 2, P = 0.873). The

movement data model was a better fitting model (AIC = 38.271) than the affiliative data

model (AIC = 46.497), the affiliative model was dropped. There were significant

positive direct effects of sex on maternal kinship (R = 0.511, P = 0.002), sex on fans (R

= 0.648, P < 0.001) and dominance on fans (R = 0.399, P = 0.01). We found a strong,

non-significant negative effect of age on maternal kinship (R = -0.302, P = 0.066). Sex

(R = 0.54) and dominance (R = 0.42) had the strongest total effects on fans in August

while maternal kinship(R = -0.16), centrality (R = 0.07) and age (R = -0.065) had

weaker total effects on fandom in August. Forty-eight percent of the variation in

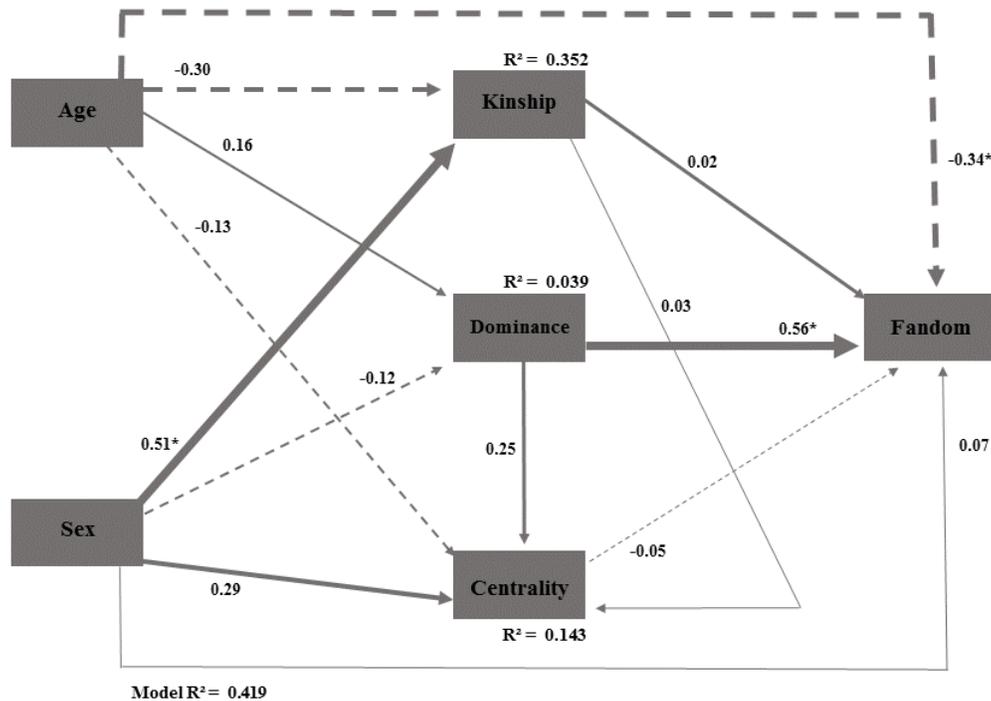fandom in July was explained by the model (R^2 = 0.483) (Figure 13).

Figure 12. Structural equation model of July life history and sociality variable effects on fandom built using movement data (χ^2 = 0.271, df = 2, P = 0.873). Boxes represent measured variables, arrows show correlations within the model and are scaled to effect size (dashed=negative, solid=positive). Standardized correlative path coefficients show estimated effect sizes. Percent variance (R^2) is displayed above each measured variable. Starred pathways were significant (*< 0.05, **< 0.01). There were significant positive direct effects of sex on maternal kinship and dominance on fandom and a significant negative effect of age on maternal kinship. Dominance and age best explained the variation in fandom in July.
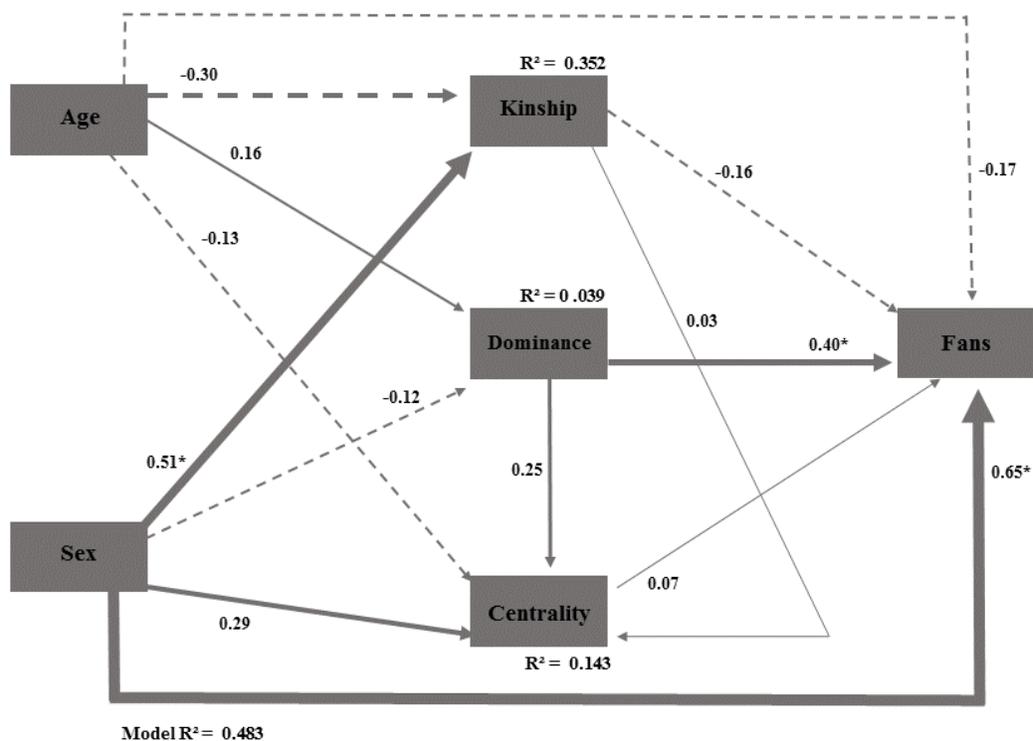
Figure 13. Structural equation model of August life history and sociality variable effects on fans built using movement data ($\chi^2 = 0.271$, df = 2, P = 0.873). Boxes represent measured variables, arrows show correlations within the model and are scaled to effect size (dashed=negative, solid=positive). Standardized correlative path coefficients show estimated effect sizes. Percent variance (R^2) is displayed above each measured variable. Starred pathways were significant (*< 0.05, **< 0.01). There were significant positive direct effects of sex on maternal kinship, sex on fans and dominance on fans. Sex and dominance best described the variation in fans in August.

When investigating the variation of fandom within the system using August data, satisfactory fit criteria existed using both affiliative and movement data. No difference was found in model fit between affiliative and movement data ($\chi^2 = 0.271$, df = 2, P = 0.873, AIC = 38.271). To be consistent, the affiliative model was dropped. There were significant positive direct effects of sex on maternal kinship (R = 0.511, P = 0.002) and dominance on fandom (R=0.49, P=0.004). We found a negative relationship between age and maternal kinship (R = -0.302, P = 0.033) and a strong non-significant relationship between age and fandom (R = -0.297, P = 0.089). Dominance (R = 0.498),

age (R = -0.306) and maternal kinship (R = 0.271) display strong total effects on

fandom while sex (R = 0.077) and centrality (R = 0.03) display weaker effects on

fandom in August. 39% of the variation in fandom in July was explained by the model
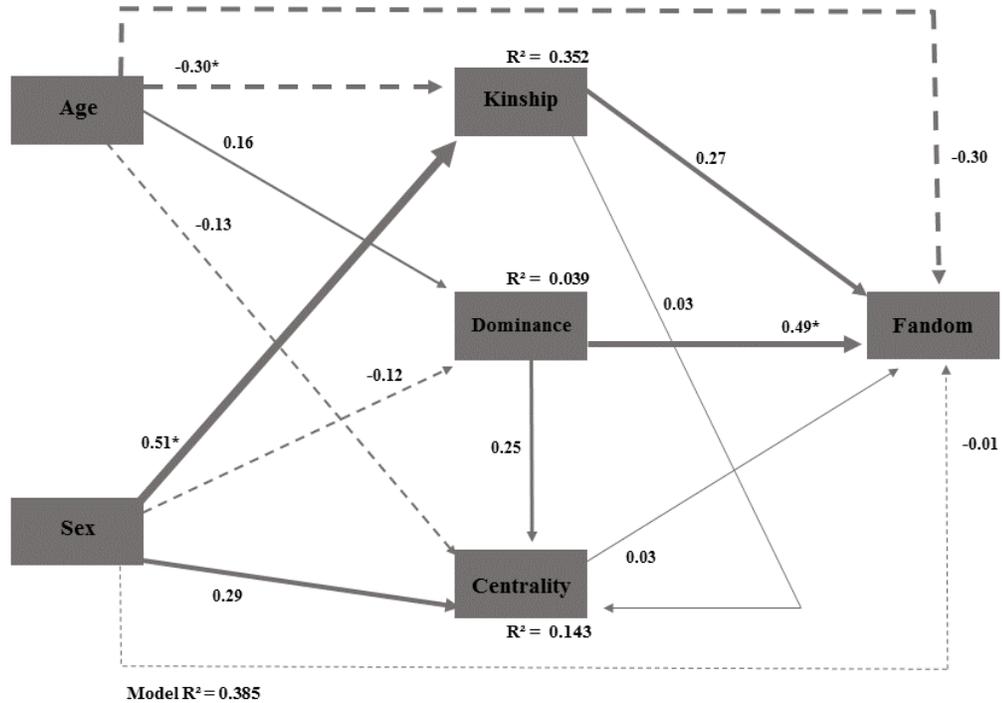
(R^2 = 0.385) (Figure 14).

Figure 14. Structural equation model of August life history and sociality variable effects on fandom built using movement data (χ^2 = 0.271, df = 2, P = 0.873). Boxes represent measured variables, arrows show correlation within the model and are scaled to effect size (dashed=negative, solid=positive). Standardized correlative path coefficients show estimated effect sizes. Percent variance (R^2) is displayed above each measured. Starred pathways were significant (*< 0.05, **< 0.01). There were significant positive direct effects of sex on maternal kinship and dominance on fandom. Dominance, age and maternal kinship best described the variation in fandom in August.