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Article

Infant attraction: why social bridging matters for female leadership in Tibetan macaques

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Abstract

Leadership is a key issue in the study of collective behavior in social animals. Affiliation–leadership models predict that dyadic partner preferences based on grooming relationships or alliance formation positively affect an individual’s decision to follow or support a conspecific. In the case of many primate species, females without young infants are attracted to mother–infant dyads. However, the effects of mother–infant–female associations on affiliation–leadership models remain less clear. In free-ranging Tibetan macaques *Macaca thibetana*, we used social network analysis to examine the importance of “mother–infant–adult female” social bridging events as a predictor of who leads and who follows during group movement. Social bridging is a common behavior in Tibetan macaques and occurs when 2 adults, generally females, engage in coordinated infant handling. Using eigenvector centrality coefficients of social bridging as a measure of social affiliation, we found that among lactating females, initiating bridging behavior with another female played a significant role in leadership success, with the assisting female following the mother during group movement. Among nonlactating females, this was not the case. Our results indicate that infant attraction can be a strong trigger in collective action and directing group movement in Tibetan macaques and provides benefits to mothers who require helpers and social support in order to ensure the safety of their infants. Our study provides new insights into the importance of the third-party effect in rethinking affiliation–leadership models in group-living animals.

Key words: affiliation–leadership models, collective movement, infant attraction, *Macaca thibetana*, social bridging, Tibetan macaques

Group living is argued to provide many benefits to social animals such as reducing predation threats, increasing foraging opportunities, and providing nonmaternal assistance in infant caregiving (Wrangham et al. 2007; Sussman and Garber 2011; Sperber et al. 2019). Under conditions in which the joint actions of several individuals provide advantages to all or most participating group members (i.e., by-product mutualism, reciprocity, collective action, and cooperation), selection is likely to favor the evolution of affiliative and coalitionary behavior (Sussman et al. 2011; Tokuyama and Furuichi 2016). Although kinship may increase the benefits and decrease the costs of social alliances and cooperative behavior (Lynch et al. 2019), there is evidence from long-term studies of chacma baboons *Papio ursinus* showing that the ability of mothers to establish and maintain strong friendships with groupmates, unrelated to kinship, age, or dominance status, is a critical factor in increasing offspring survivorship (Baniel et al. 2016). Similar fitness benefits accrued by females with persistent affiliative bonds with other group members have been reported in the greater ani *Crotophaga major* (Riehl and Strong 2018), feral horses *Equus caballus* (Cameron et al. 2009), and yellow baboons *P. cynocephalus* (Alberts 2019).

To take advantage of the benefits of group cohesion, social animals have evolved behavioral mechanisms to coordinate activities during feeding, foraging, and traveling (Petit and Bon 2010; Wang et al. 2015, 2016; Rowe et al. 2018; Ravignani 2019). Coordinated group movement, requires leadership, with one or more individuals initiating and directing travel (e.g., leaders: Stueckle and Zinner 2008; Sueur and Petit 2008). In some species, the highest-ranking individual is reported to successfully initiate the majority of group movements (e.g., mountain gorillas, *Gorilla beringei*: Watts 2000; black-capped chickadee, *Poecile atricapillus*: Evans et al. 2018). This process has been termed personal leadership (Leca et al. 2003). In contrast, in other species such as feral horses, *E. ferus* (Krueger et al. 2014) and olive baboons, *P. anubis* (Strandburg-Peshkin et al. 2015), several different individuals may initiate and lead group movement, although factors such as age, sex, or rank contribute to leadership success. This process has been termed distributed leadership (Conradt and Roper 2007). In group-living animals with distributed leadership, individuals are reported to preferentially follow initiators of group movement with whom they share a strong social affiliation (Seltmann et al. 2013; Farine et al. 2016; Fratellone et al. 2019; Sperber et al. 2019). In the case of wild chacma baboons, group members were found to follow those initiators who frequently engaged with them in grooming bouts or with whom they maintained close spatial associations (King et al. 2011). Affiliation–leadership models, which are defined in terms of social partner preferences where an individual’s decision to follow or support a conspecific is based on the strength of affiliative relationships (Wang et al. 2016), were argued to offer the strongest explanation for distributed leadership in chacma baboons. These models also have been used to explain social interactions in domestic geese *Anser domesticus* (Ramseyer et al. 2009), domestic horses *E. przewalski* (Briard et al. 2015), and brown lemurs *Eulemur fulvus* (Jacobs et al. 2011a). In other species, however, dominance-based or age-based models appear to offer a stronger explanation of success in directing group movement than social affiliation (Jolles et al. 2013; Lee and Teichroeb 2016).

Building on traditional models of dyadic relationships, polyadic associations highlight the impact that a third party can have on social relationships between 2 initial interactants (Fruteau et al. 2011; Kubenova et al. 2017). This has been reported in carrion crows *Corvus corone* (Sima et al. 2018), rooks *C. frugilegus* (Seed et al.

2007), orangutans *Pongo abelii* (Gruber 2013), and Japanese macaques *Macaca fuscata* (Sekizawa and Kutsukake 2019). In several macaque species (e.g., stump-tailed macaques *M. arctoides*: Estrada and Sandoval 1977; Barbary macaques *M. sylvanus*: Kubenova et al. 2017; Tibetan macaques *M. thibetana*: Zhang et al. 2018), 2 group members use an infant as a third party and engage in coordinated infant handling, a behavior called social bridging. As a role of a third party, infants attract the attention of female members in the group (Bădescu et al. 2015). In general, social bridging involves an infant’s mother, her infant, and another adult female, and is hypothesized to play an important role in regulating and reaffirming social relationships among participants (Ogawa 1995a, 1995b).

In this study, we examine the role of third-party associations (mother–infant–adult female) in affiliation–leadership models in a group of free-ranging and provisioned Tibetan macaques. This was accomplished by recording adult female social relationships in the forest (where social bridging occurs, Figure 1), and using these interactions to examine leadership success and consensus building among females when individuals depart from a provisioning area to return to the forest (Figure 2). In a previous study of the same Tibetan macaque group, Berman et al. (2007) reported that rates of aggression among adult females in the provisioning area were higher than that in the forest, and rates of infant mortality were positively correlated with rates of aggression in the provisioning area but not in the forest. Thus, the forest represents a safer area for a mother and her infant compared with the provisioning area. Based on a 5-month study in a group of Tibetan macaques, Wang et al. (2016) reported evidence of distributed leadership in which all adult group members were successful in leading group movements, although adult females led group movements 73% of the time. These authors suggested that individuals who formed strong dyadic affiliative bonds were more successful in soliciting close associates to join them in directing group movement than were less closely affiliated group members.

Given that the use of an infant (third party) as a social bridge to strengthen affiliative relationships between 2 adult females is a common behavior in Tibetan macaques, within the framework of an affiliation–leadership model, we tested the following hypotheses: an adult female who was more central in a social network (based on bridging events), irrespective of whether she was the infant’s mother, would be more successful in leading group movement than females who were less well connected in a social network (H1). Further, a female who more frequently initiated social bridging with another



Figure 1. Social bridging behavior in female Tibetan macaques.

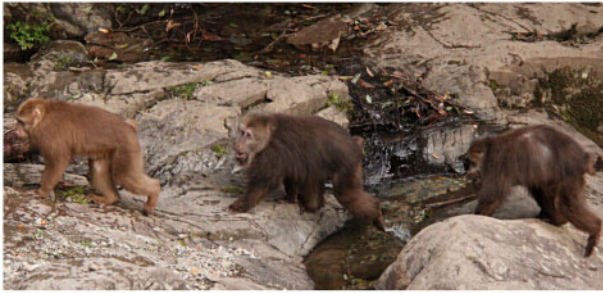


Figure 2. Initiation of group movement in Tibetan macaques.

female and an infant (irrespective of whether she was the infant's mother or her position within a social network) would lead more successful group movements than females who less frequently initiated social bridging interactions (H2). It is important to note that H1 differs from H2 in assuming a relationship between social affiliation and leadership of group movement, whereas H2 examines the relationship between the frequency of initiating a social bridging event and successful leadership of group movement. Moreover, given that females without infants are attracted to females with infants (recent mothers), we analyzed the relationship between initiation of group movement and social bridging behavior among lactating and nonlactating females. Accordingly, we hypothesized (H3) that females who initiated social bridging using their own infants (i.e., lactating females) would be more successful in leading group movements than females who initiated social bridging using another female's infant (i.e., nonlactating females).

Materials and Methods

Study site and subjects

We studied a habituated group of Tibetan macaques (group Yulinkeng 1 or YA1) inhabiting the “Valley of the Wild Monkeys” (30°04'25.1"N/118°08'59.3"E) at Huangshan, China. For more details of the study site, see Xia et al. (2010, 2012). Each group member was individually and unambiguously recognized based on the presence of distinctive physical features such as scars, hair color patterns, and/or facial/body appearance (Li 1999; Xia et al. 2012).

During our study period (1 August 2012 to 28 May 2013), the troop consisted of 38 members including 8 adult females, 4 adult males, 6 subadults, 9 juveniles, and 11 infants (4 infants were born prior at the start of the study and 7 infants were born during the study period). We defined infants as individuals younger than 12 months of age. The study group has been observed since 1986 (Berman et al. 2004). Long-term observations (for >30 years) have provided detailed information about individual identities and life histories for all group members, and therefore we have accurate information on the age of individuals in the group (age categories follow Li 1999).

The study group ranged freely in the forest during much of the day, but to facilitate tourist viewing, the group was provisioned with a total of 3–4 kg of corn 4 times each day by park rangers in an open, highly visible area (216 m²; Berman and Li 2002; Berman et al. 2008; Xia et al. 2012). Provisioning occurred at 09:00 AM, 11:00 AM, 03:00 PM, and 05:00 PM. At the provisioning area, the monkeys were provided with dried corn kernels that were scattered across the ground. The corn was widely distributed to ensure that it could not be monopolized by a single or small number of high-ranking individuals. Consequently, all group members, regardless of

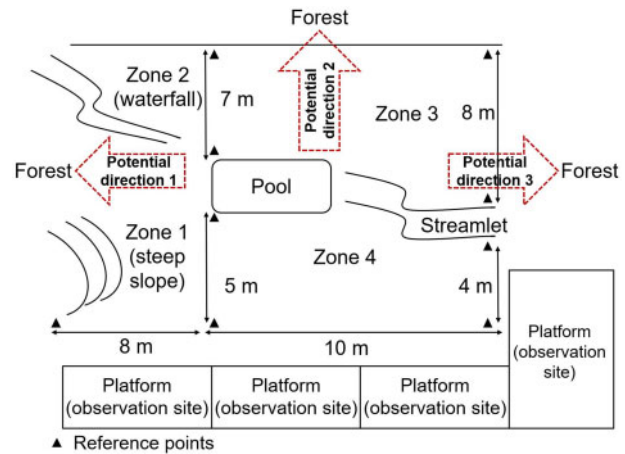


Figure 3. Diagram of the 4 zones of the provisioning area and the 3 potential directions the macaques could take to reach the forest.

rank, foraged together at the provisioning area. Feeding sessions usually lasted <30 min. When the monkeys finished consuming the corn, they moved from the feeding site to the surrounding forest (Wang et al. 2016).

Data collection

Data were collected by a single researcher (X.W.). When the monkeys were feeding at the provisioning site, the observer recorded the identities of all individuals present. Owing to excellent visibility, the observer was able to record the context and set of behaviors associated with group movement (starting from the provisioning area and moving into the forest). The observer collected data on the identity, order of departure, and initiator(s) of group movement using a video camera (Canon EOS 550D; Canon Inc., Tokyo, Japan) and an all occurrence sampling method (Altmann 1974). We used the definitions from Wang et al. (2015, 2016) for collecting data on collective movement as follows:

1. A group movement initiation attempt: when 1 individual moved >10 m in <30 s in the direction away from the provisioning area and toward the forest. We termed the first individual to move the “initiator.”
2. A “follower”: any individual that walked >5 m and within 45° of the direction taken by the initiator within a period of 5 min after the initiator first moved or after the previous follower moved.
3. A successful group movement: at least two-thirds of all group members followed an initiator's movement.

To accurately record the positions and movement distances of each monkey, we divided the provisioning area (216 m²) into 4 zones (total area of each zone = 40 m², 56 m², 70 m², and 50 m²) by imposing a systematic grid of reference points (Figure 3). To reduce biases in the data, we did not record initiation attempts during periods of intragroup conflict or copulations that resulted in fighting, sexual chases, or the chaotic movements of individuals within the group (Sueur and Petit 2008).

To document the use of infants as a social bridge by adult females, we conducted 10-min focal animal sampling (Altmann 1974) when the group was in the forest, away from the viewing platforms frequented by tourists. This was done to avoid the potential influence of the presence of tourists on the monkeys' behavior (Xia

Table 1. Reproductive state, social rank, age, social bridging initiations, and initiations of group movement in female Tibetan macaques

ID	Reproductive state	Social rank	Age (year)	Number of successful bridging initiations	Number of successful movement initiations
YH	Lactating, nonlactating	1	9	48	44
Hhui	Lactating, nonlactating	2	7	31	39
YM	Lactating	3	22	16	33
TH	Lactating	4	9	12	38
HH	Lactating, nonlactating	5	9	25	20
TR	Lactating	6	8	8	7
TT	Lactating, nonlactating	7	21	8	20
YZ	Lactating, nonlactating	8	20	10	14

et al. 2012). Our focal animals were the 8 adult female group members (Table 1). We selected focal animals randomly and completed 1 round of follows for each of the 8 adult females before beginning a new round of observations. If we temporarily could not find a focal subject, we chose the next female on the list and returned to the previous female when she reappeared (Xia et al. 2012). In our study, focal observations of the 8 adult females totaled 199.9 h (per individual: 25.0 ± 0.05 h, mean \pm SE). During each sampling period, we recorded the number of times a focal female used an infant as a social bridge to interact with another adult female (Table 1). Following Ogawa (1995a) and Bauer et al. (2014), we defined the initiator of a social bridging event as a female who held the infant as she turned to solicit an interaction with another adult female (Figure 1). We termed this a social bridging initiation (Li 1999). For each female, we determined the rate of social bridging initiations as the number of times she successfully used an infant to initiate an interaction with another female divided by her observation time (i.e., episodes/hour).

Data analysis

To assess the potential effect of social rank on female leadership, we calculated a David's Score (DS) to identify the dominance rank of each of the 8 adult females (Gammell et al. 2003). Dominance was based on intrasexual dyadic agonistic (aggressive/submissive) interactions (Li 1999; Zhang et al. 2014). A larger DS value corresponds to a higher social rank.

To measure female affiliation during social bridging, we used SOCPROG 2.4 (Whitehead 2009; Funkhouser et al. 2018) to calculate each individual's eigenvector centrality coefficients in a social network based on matrices of social bridging rates (bridging initiation). The eigenvector centrality quantifies the ability of adult females to use infants as a social bridge to build affiliative bonds. A higher centrality coefficient means that based on social bridging, the target adult female has a stronger social relationship with other group members than does an adult female with a lower value (Newman 2004).

Leadership success was measured as the standardized number of successful movement initiations (when at least two-thirds of group members followed). We calculated the standardized number using the following formula: $X'_i = X_i/T_i \times 1,000$, where X'_i is the standardized number of successful initiations for individual i calculated from T : the number of times that individual i was identified by the observer and X : the number of successful initiations recorded for

individual i (Jacobs et al. 2011b). Multiplying the rate by 1,000 facilitated a clearer presentation of standardized values on all figures (Wang et al. 2016).

The effect of eigenvector centrality (H1), social bridging (H2), and infant attraction (H3) on leadership success was tested using a generalized linear mixed model (GLMM) with a binomial distribution (GLMMb). In the model, eigenvector centrality, bridging initiations, reproductive state (lactating or nonlactating), social rank, and age were included as fixed factors, whereas month and the identities of adult females were treated as random factors. The data used in the GLMMs included 80 rows for 8 females \times 10 months. In Tibetan macaques, the mating season ranges from July to December, and the birth season is from January to May (Li 1999). As each season is divided by months, eigenvector centrality, bridging initiations, social rank, and age were calculated on a monthly basis. To check whether the results obtained from the GLMMs were robust, we also modeled the data using a resampling method. A 95% confidence interval (CI) was constructed for each parameter based on bootstrapping (1,000 bootstrap datasets). GLMMs were performed in R version 3.6.1.

In addition, we used a Wilcoxon signed-rank test to compare variation in the rate of social bridging/leadership success for a given female when she was lactating and when nonlactating. Following Li (1999), we defined lactating females as individuals with nursing infants who were ≤ 12 months of age. Wild Tibetan macaques are generally weaned by 12 months of age (see Li 1999). We report the data as a mean (\pm SE) for leadership success and the rate of social bridging (episodes/hour). These statistical analyses and calculations were performed in SPSS 22.0 software (SPSS Inc., Chicago, IL, USA).

Results

We scored a total of 215 successful group movement initiations and 158 successful bridging initiations among the 8 adult females (Table 1). The average hourly rate a female successfully used an infant as a social bridge was 0.75 ($N = 8$, SE = 0.21), and ranged from 0.08 to 1.90.

Hypothesis 1 tested the effect of adult female centrality on success in leading group movement. The results (Table 2) indicated a significant positive effect of eigenvector centrality (calculated by social bridging matrices) on leadership success. Thus, based on bridging matrices, an adult female's social centrality played a determining role in her ability to lead group movement. However, neither individual social rank nor age was correlated with leadership success. This suggests that regardless of a female's position in the group's hierarchy or age, the higher her value of eigenvector centrality was, the more successful she was in initiating group movement.

Hypothesis 2 examined the relationship between the frequency an adult female initiated a social bridging event and her success in leading group movement. The results (Table 2) indicated that the more frequently a female initiated social bridging, the more likely that the female was successful in leading group movement. In contrast, neither social rank nor age was correlated with the successful initiation of group movement. The data demonstrated that unrelated to a female's position in the group's hierarchy or age, the more frequently she initiated the use of an infant as a social bridge, the more successful she was in leading group movement.

To examine the potential effect of infant attraction on female leadership in determining group movement (Hypothesis 3), we first analyzed the differences of movement initiations for females when

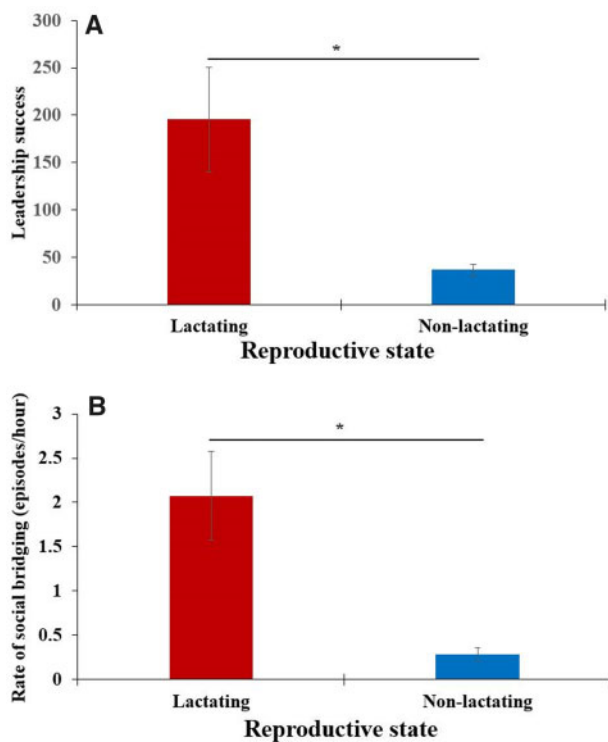


Figure 4. Differences in the success of lactating and nonlactating adult female Tibetan macaques as (A) leaders in initiating group movement (leadership success measured by the standardized number) and (B) using an infant as a social bridge (successful initiations of social bridging). Error bars indicate SE.

lactating versus when nonlactating, controlling for the number of infants in the group. We then tested the role of reproductive state (lactating vs. nonlactating) on success in the initiation of group movement.

Overall, 5 of our 8 females were both lactating and nonlactating during the study period. Even with only 5 females, we found that when they were lactating, they had greater leadership success than when they were not lactating (lactating vs. nonlactating: 195.4 ± 55.3 vs. 36.8 ± 6.0 , $Z = -2.023$, $P = 0.043$, Figure 4A). Females also were characterized by greater success in bridging initiations when they used their own infants than when they initiated social bridging using another female's infant (lactating vs. nonlactating: 2.076 ± 0.5 vs. 0.3 ± 0.1 episodes/hour, $Z = -2.023$, $P = 0.043$, Figure 4B).

The results using GLMM models (Table 2) showed a significant positive effect of reproductive state on leadership success. The ability of lactating females to use their own infants as a social bridge had a significant and positive effect on their ability to lead group movements compared with nonlactating females.

Finally, the GLMM models were bootstrapped using a resampling approach to evaluate stability of the model and estimate CIs for all parameters. The 95% CI values were consistent with the parameter estimates (Table 3). The 95% CIs for the effect of parameters on leadership success, providing support that eigenvector centrality, social bridging, and reproductive state had effect on success in leading group movement.

Discussion

In this study, we examined the importance of affiliative polyadic associations on affiliation–leadership models in a group of free-

Table 2. Results of generalized linear mixed models testing whether the successful initiation of group movement was related to eigenvector centrality, social bridging, reproductive state, social rank, or age

Term	Estimate	SE	Z	P
Intercept	-1.91425	0.48272	-3.966	<0.001
Eigenvector centrality coefficients	0.61923	0.17296	3.580	<0.001
Initiations of social bridging	0.33233	0.03153	10.540	<0.001
Reproductive state	-0.77402	0.09838	-7.867	<0.01
Social rank	-0.07757	0.08165	-0.950	0.342114
Age	0.06676	0.03031	2.203	0.276232

ranging and provisioned Tibetan macaques. We tested whether social centrality, social bridging, and/or infant attraction affected female leadership using a GLMM. We answered why social bridging relationships among a mother, her infant, and a female without a young infant can be a strong predictor of that mother's ability to lead group movement.

Female Tibetan macaques that were more central in a social network based on bridging matrices (i.e., higher values of eigenvector centrality) were found to initiate more successful group movements than did females who were less central, unrelated to age and social rank. Our results are consistent with observations in other studies and support a model of distributed leadership. For example, in wild black howler monkeys *Alouatta pigra*, females positioned at the leading edge of the group, and therefore possibly directing group movement, were characterized by the highest eigenvector centrality values in their spatial association matrices compared with other adult group members (Van Belle et al. 2013). Further, Fratellone et al. (2019) found that in Tibetan macaques, clusters of more affiliated females reached a consensus on group movement faster than clusters with fewer affiliated females. Thus, we suggest that female Tibetan macaques that develop strong intrasexual affiliative bonds are more likely to engage in coordinated behavior and support each other across a range of social and ecological contexts.

We also found that when females were lactating, they led more successful group movements than when they were not lactating. Assuming that the forest represents a less competitive and less aggressive social arena compared with the provisioned area (Berman et al. 2007), 1 potential advantage for lactating females who successfully lead group movement away from the provisioning area and into the forest is increased safety for themselves and their infants. Across many animal species, lactating females have been found to initial and lead group movement, including herds and harems of plains zebra *E. burchellii* (Fischhoff et al. 2007) and in multimale, multifemale groups of blue-eyed black lemurs *E. flavifrons* (Volampeno et al. 2011). Maternal nutritional and energetic requirements may increase by at least 50% for lactating females (Portman 1970; Furrer et al. 2012), and females with young infants are also at increased risk of predation. Therefore, we consider that Tibetan macaque mothers are under strong selective pressure to develop social relationships that increase their ability to direct conspecifics to parts of their range that provide refuge and safety for the infants.

A female's use of her own infant as a social tool played a significant role in her success in leading group movement compared with periods when she was not lactating and engaged in social bridging using other females' infants. It appears that lactating females take advantage of the attraction that females without infants have

Table 3. Parameter estimates for covariate effects on leadership success

Parameter	χ^2	P	95% CI	
			Lower	Upper
Eigenvector centrality coefficients	12.8179	<0.001	0.217602825	0.99200199
Initiations of social bridging	111.0860	<0.001	0.270038562	0.40466478
Reproductive state	61.8949	<0.01	-0.967249342	-0.56306252
Social rank	0.9025	0.3421142	-0.238009051	0.08575602
Age	4.8515	0.2762321	-0.005994908	0.13030542

toward their young infants to build strong social alliances. Newborn infants attract the attention of other group members in several primate taxa (e.g., tufted capuchin monkeys *Sapajus apella*: Tiddi et al. 2010; sooty mangabeys and vervet monkeys *Cercocebus atys* and *Chlorocebus aethiops*: Fruteau et al. 2011; golden snub-nosed monkeys *Rhinopithecus roxellana*: Yu et al. 2013; white-headed langurs *Trachypithecus leucocephalus*: Jin et al. 2015). In these species, females without young offspring are reported to approach new mothers and attempt to greet, sniff, nuzzle, and inspect their newborn infants (Silk 1999; Zhang et al. 2018). Although infants were not necessarily an active third party in selecting or avoiding which adult females their mother engaged with, the ability of lactating Tibetan macaques to use infants as a third party in social manipulation highlights the important role that infants play in macaque group dynamics.

Our results support the hypothesis that female social affiliation based on triadic associations is consistent with a model of affiliation–leadership. In the case of Tibetan macaques, infants are used as a tool to develop and reinforce social bonds that enhance her ability to direct group movement. Although this study did not quantify the benefits individual Tibetan macaques obtain by leading group movement or identify age, sex, or rank-based differences in leadership in the context of predator avoidance or traveling to feeding sites, we plan to explore these issues of decision-making and consensus building in our future research.

Ethical Statement

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

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Authors' Contribution

All authors contributed to the planning of the experiments, the data analysis, and interpretation as well as the preparation of the manuscript. X.W. and D.-P.X. equally contributed to this work.

Conflict of Interest

The authors declare that they have no conflict of interest.

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