



Male social bonds and rank predict supporter selection in cooperative aggression in wild Barbary macaques



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Cooperation in coalitions against coresident males has been shown to increase male reproductive success directly via increased mating success (levelling coalitions) or indirectly via increased dominance success (rank-changing coalitions). Two mechanisms guiding coalitionary supporter selection have been proposed. First, supporter selection may depend on the supporters available, whereby an animal chooses the highest ranking supporter present to maximize their chance of winning. Second, males may also select supporters based on the strength of the social bond they share with them. Different studies on male Barbary macaques, *Macaca sylvanus*, have produced support for both mechanisms but crucial assumptions and predictions remained untested. The aim of this study was to test predictions derived for both mechanisms after establishing whether Barbary macaque males formed social bonds. We observed two wild groups of macaques in Morocco (>2000 h focal animal data) and recorded the identity of males recruited to join a coalition, of all bystanders, and of the coalitionary target. We demonstrate for the first time that male Barbary macaques formed strong, equitable social bonds that were stable for 2 years. Corroborating earlier studies we found that males selected supporters by more than one criterion, namely by the strength of their social bonds to the potential ally and by their dominance rank position among potential supporters. The animals who received recruitment signals were more likely to reject the recruitment invitation the weaker their social bond to the recruiter was and if the target was higher ranking than the recruiter. In a subset in which we examined only levelling coalitions that would flatten the mating skew, males only used the mechanism that would maximize the feasibility of the coalition by more frequently selecting the highest ranked bystander. These results suggest that males flexibly apply different criteria for supporter selection depending on the context of the conflict.

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Social relationships among animals living in stable social groups are competitive as well as affiliative, since group members compete for access to resources while establishing social bonds with both kin and nonkin (Cords, 1997; Hinde, 1976, 1983; Massen, Sterck, & de Vos, 2010; Silk, 2005, 2007). If dyadic affiliative relationships are differentiated within a social group, those relationships that are characterized by high frequencies of affiliative interactions, a relatively balanced directionality of exchange and temporal stability can be construed as social bonds (Silk, 2002). Strong female–female social bonds have been shown to carry fitness benefits for the individuals involved (Armitage & Schwartz, 2000; Cameron,

Setsaas, & Linklater, 2009; Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008; Engh et al., 2006; Frère et al., 2010; Silk, 2003; Silk et al., 2009, 2010b; Wey & Blumstein, 2012; Wittig et al., 2008). Recent evidence suggests that social bonds between males may be more widespread than originally thought (Berghänel, Ostner, Schröder, & Schülke, 2011; Connor, Heithaus, & Barre, 2001; Fraser & Bugnyar, 2010; Mitani, 2009; Ostner & Schülke, 2014; Perry, 1998; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Silk, 1994; Teichroeb, Wikberg, Ting, & Sicotte, 2013), which is surprising owing to males' competition for an indivisible resource, i.e. fertilizations (van Hooff & van Schaik, 1994).

Mammalian males can cooperate with coresident males through aggressive coalition formation (Bercovitch, 1988; de Waal & Harcourt, 1992; reviewed by Bissonnette, Franz, Schülke, & Ostner, 2014; Smith et al., 2010). Coalitions generally occur in two main contexts. First, levelling coalitions (Pandit & van Schaik, 2003) can be observed in which males attempt to level the mating skew

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by breaking up consorts and gain the immediate benefit of direct access to females (Bercovitch, 1988; Bissonnette, Bischofberger, & van Schaik, 2011; Noë & Sluijter, 1990). Second, males can utilize rank-changing coalitions (van Schaik, Pandit, & Vogel, 2004, 2006) either to increase or to maintain the rank of one or both partners (Riss & Goodall, 1977; Schülke et al., 2010; Widdig, Streich, & Tembrock, 2000; Young, Schülke, & Ostner, 2014). Rank-changing coalitions can be part of a long-term reproductive strategy, requiring a stable, reliable partner, the choice of which may be mediated by strong social bonds (Ostner & Schülke, 2014; Schülke et al., 2010; Young et al., 2014). Two mechanisms have been proposed to govern the selection of a supporter for coalition formation: (1) maximizing feasibility of the coalition and (2) basing the selection of a supporter on past experiences and thus on social bond strength (Berghänel, Ostner, Schröder, et al., 2011; Campenni & Schino, 2014; Connor et al., 2001; Gilby et al., 2013; Mitani, Watts, Pepper, & Merriwether, 2002; Perry, Barrett, & Manson, 2004; Silk, 1994; Watts, 2002).

The maximizing feasibility hypothesis posits that males recruit coalition partners to optimize their probability of winning (Bissonnette, de Vries, & van Schaik, 2009; Noë, 1994; Noë & Sluijter, 1995; van Schaik et al., 2004, 2006). Accordingly, Bissonnette et al. (2009) found the success of Barbary macaque, *Macaca sylvanus*, coalitions depended on the asymmetry in strength of the coalition versus the target, with stronger coalitions being more successful. They suggested recruitment was based on simple rules of thumb to maximize success (such as selecting the highest ranked individual available) rather than more complex, cognitively taxing criteria requiring knowledge of third-party rank or social relationships (Perry et al., 2004; Range & Noë, 2005; Schino, Tiddi, & Polizzi Di Sorrentino, 2006; Silk, 1999; reviewed by Cheney, 2011).

Alternatively, social bond strength may drive supporter selection based on previous experiences and recruiters may select the male with the strongest bond with them. In the same macaque population male coalition formation was found to be predicted by the strength of males' social bonds (Berghänel, Ostner, Schröder, et al., 2011). Dyadic social bond strength and the frequency of coalitional support are correlated in several mammalian species, including several macaques (Connor et al., 2001; Gilby et al., 2013; Mitani et al., 2002; Perry et al., 2004; Silk, 1994; Watts, 2002; also see Schino, 2007). In Assamese macaques, *Macaca assamensis*, frequent coalition partners were strongly bonded and not necessarily the highest ranked males, and frequent coalition formation led to an increase in dominance rank in the future (Schülke et al., 2010). Since rank predicts paternity success in Assamese macaques these rank-based coalitions came with mutual long-term benefits for both allies (Sukmak, Wajjwalku, Ostner, & Schülke, 2014). Strong social bonds may be particularly important in rank-changing coalitions as these may be long-lasting, high-risk affairs and social bonds could act to build and test the reliability of, and trust between, partners (Ostner & Schülke, 2014; van Schaik, Pandit, & Vogel, 2006; Young et al., 2014). Here we investigated whether an adaptive benefit of strong social bonds may accrue from coalitional support or whether selection of a supporter in a coalition is guided by more immediate criteria concerning the expected success of the coalition.

The two proposed mechanisms are not mutually exclusive, as an animal may select supporters on the basis of more than one criterion (Bergman, Beehner, Cheney, & Seyfarth, 2003). Therefore, here we went beyond the two previous studies on Barbary macaques (Berghänel, Ostner, Schröder, et al., 2011; Bissonnette et al., 2009) by considering both mechanisms concurrently and we added crucially to the previous broad-scale correlational approach (Berghänel, Ostner, Schröder, et al., 2011) by considering the

situational availability of supporters for each recruitment event. Previous studies on triadic awareness and agonistic support in primates have focused on other age–sex classes (i.e. females or juveniles) or one criterion only (Range & Noë, 2005; Silk, 1999) or on a different criterion (kinship instead of social bonds, Schino et al., 2006). Only one study investigated the role of both dominance and affiliative relationships in supporter selection in males (Perry et al., 2004). Here we aimed to extend this work by (1) concentrating on wild, dispersing males which may form more transient relationships than philopatric females, (2) assessing whether dominance relationships between the recruiter and target affected the choice of mechanism for supporter selection, and (3) assessing whether the context of the coalition (levelling versus other) affected the relative roles of the two mechanisms.

Following the approach of Perry et al. (2004), we aimed to control for the effect of differential supporter availability to address an alternative explanation for observed relationships between coalition formation and affiliative relationships. Results from agent-based modelling suggest that fighting behaviour forces individuals in groups into a rank-based spatial structure and that this structure affects both patterns of affiliation and coalition formation (Hemelrijk & Puga-Gonzalez, 2012; Puga-Gonzalez, Hildenbrandt, & Hemelrijk, 2009). Individuals similar in dominance rank spend more time in close proximity, affiliate more and are also close by if one individual becomes involved in an agonistic conflict. Thus, they support each other more regularly because they often have the opportunity and not because of their social relationships per se (Hemelrijk & Puga-Gonzalez, 2012; Puga-Gonzalez et al., 2009). In a similar vein, Noë and Sluijter (1995) suggested frequent coalition formation may lead to false inferences about the levels of affiliation between these males. Individuals may remain in close proximity prior to or after a coalition and thus inflate the time spent in social proximity. Previous studies on male Barbary macaques did not address this issue.

In this study, we first investigated male–male affiliative relationships to examine whether males, under natural conditions, form strong, enduring and equitable social bonds (sensu Mitani, 2009; Silk, 2002; Silk et al., 2010b) with coresidents. Second, we examined coalitional recruitment behaviour during agonistic interactions to determine which of the mechanisms are utilized by males during supporter selection and rejection of solicitation events. We predicted that if males select partners following the maximizing feasibility hypothesis they should use a simple 'rule of thumb' and select the highest ranking male as the supporter (see Bissonnette et al., 2009). Alternatively, if males based their recruitment decisions on previous experience they should solicit help from the individual with which they shared the strongest social bond. Taking the perspective of the potential supporter, we expected that the rejection of a solicitation would be predicted by the weakness of the social relationship between the two individuals and/or the feasibility of this coalition, i.e. whether the target ranks above the recruiter. Males may use different criteria for supporter selection depending on the competitive nature of the coalition (i.e. the rank relationship between the recruiter and target). Thus, we also examined an interaction between rank difference of the recruiter and target and both the main effect of social bond strength and rank of the potential supporter. We expected that when the target outranks the recruiter then the rank of the potential supporter plays a greater role in supporter selection than when the rank of the target is lower. We investigated the effect of context for the relative roles that criteria played in supporter selection by analysing a subset of only levelling coalitions. Levelling coalitions occur over direct access to mating opportunities with females; these coalitions may also be considered highly competitive in nature (for full description see Young, Hähndel, Majolo,

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