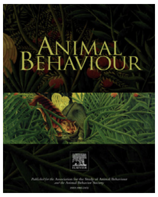
Animal Behaviour 95 (2014) 23–32

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



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

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ARTICLE INFO

Article history:
Received 4 August 2013
Initial acceptance 13 September 2013
Final acceptance 11 June 2014
Available online 16 July 2014
MS. number: 13-00644R

Keywords:
bystander
coalition
Macaca sylvanus
male–male competition
recruitment
social bonds

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.

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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http://dx.doi.org/10.1016/j.anbehav.2014.06.007
0003-3472/

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; Campennì & 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 coalitionary 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 coalitionary 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 coalitionary 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, Schülke, & Ostner, 2013; Young et al., 2014) and we predicted that males recruit supporters based solely on their dominance rank to maximize the coalition's fighting ability and that the social bond between recruiter and supporter would be less important.

METHODS

Study Site and Subjects

Data were collected from two wild groups ('Green' and 'Scarlet') of Barbary macaques living in a deciduous cedar and oak forest in the Middle Atlas Mountains of Morocco (Majolo, McFarland, Young, & Qarro, 2013). The groups consisted of seven to nine adult males and eight adult females (Green) and six males and eight females (Scarlet), respectively. Data were collected on the Green group from October 2009 to April 2011 and on the Scarlet group from July 2010 to April 2011. This study adhered to the legal requirements of Morocco, Germany and Great Britain.

Behavioural Data Collection and the Dominance Hierarchy

Behavioural data were collected by C.Y. and five field assistants from 0700 to 1900 hours. All adult males in both groups were subject to continuous focal animal observation of social and agonistic behaviour (Altmann, 1974), yielding a total of 2033 focal animal sampling hours (1676 h Green group and 358 h Scarlet group). Data were collected using handheld HP iPAQ 114 series pocket PCs loaded with Pendragon Forms Version 5.1 (Pendragon Software Corporation, Chicago, IL, U.S.A.). Focal sampling was randomized within groups and one 40 min focal session per male was recorded per observation day so as to give an even number of focal sessions per individual. Data were further split into five 3–4-month time periods for analysis. These time periods represented distinct biological periods for each group as follows: mating seasons: MS09 (October–December 2009) and MS10 (September–December 2010); postmating seasons: PostMS09 (January–April 2010) and PostMS10 (January–April 2011); and premating season: PreMS10 (May–August 2010).

Male–male affiliative behaviour recorded during focal protocols included grooming, being in social proximity (an approach to within 1.5 m of another individual without aggression) and male–infant triadic interactions ('male-agonistic buffering', Deag, 1980). The identity of males involved, the duration (to the nearest second) and the initiator were noted. Male–infant triadic interactions were defined as a behaviour whereby one male carrying an infant approached a second male. The males then sat in body contact and handled and teeth chattered with the infant in a ritualized manner (Deag, 1980; Deag & Crook, 1971).

Agonistic interactions or conflicts were defined by the occurrence of aggressive and/or submissive behaviours. The dominance hierarchy was based on a total of 1433 male–male dyadic conflicts in which a clear winner and loser could be determined with no counteraggression. Following the methods of Young, Hähndel, et al. (2013) and Young, Majolo, Heistermann, Schülke, and Ostner (2013) a separate hierarchy was constructed for each period using corrected normalized David's scores (de Vries, Stevens, & Vervaecke, 2006).

Male Social Bonds: Strength, Stability and Equability

We tested whether male affiliative relationships qualify as social bonds by assessing whether affiliative relationships were differentiated, equitable and stable, and whether the strength and stability of the relationships were positively related to grooming equitability. The strength of affiliative relationships was measured using the composite sociality index (CSI; Silk, Alberts, & Altmann, 2006; Silk, Altmann, & Alberts, 2006; Silk et al., 2010b) to examine social bond strength between male dyads in the groups. The CSI measures the extent to which affiliative behaviour of a dyad deviates from that of all other dyads in the same group and ranges from 0 to infinity with a mean score of 1 (Silk et al., 2010b). High values represent a dyad with a strong affiliative relationship and those with a low value show a weak relationship. We calculated a separate score for each dyad, time period and group giving a total of 177 dyadic scores. Following the methods of Silk et al. (2010b) we determined four affiliative behaviours to be highly correlated: these were close proximity, male–infant triadic interactions, grooming interactions and body contact. For each behaviour, we calculated two measures, the number of interactions and duration for each dyad, providing a total of eight behavioural factors with which to calculate our CSI scores (for further details of CSI calculations see Appendix).

The equability of social exchanges is a characteristic of strong social bonds (Mitani, 2009; Silk et al., 2010a). Male–infant triadic interactions are always bidirectional and thus always considered to be an equitable behaviour (Deag & Crook, 1971; Hesler & Fischer, 2007; Paul, Kuester, & Arnemann, 1996). We also examined the grooming equitability (grooming reciprocity) between male dyads throughout each period, as an indicator of social bond equability (Mitani, 2009; Silk et al., 2010a; see Appendix for further methodology). Furthermore, social bond stability was examined between male dyads. The consistency of a male's top three bonded partners was compared across time periods (see Appendix for further methodology). By examining social bond stability and equability between dyads we were able to determine those dyads with strong social bonds within the groups.

Coalitionary Recruitment Behaviour

A coalition was defined using the description of Bercovitch (1988) as simultaneous aggression by two or more males against a common target. Here we examined coalitions of two allies against one target only. Barbary macaque males frequently form coalitions (Berghänel, Ostner, Schröder, et al., 2011; Berghänel, Ostner, & Schülke, 2011; Berghänel, Schülke, & Ostner, 2010; Bissonnette et al., 2011; Bissonnette et al., 2009; Kuester & Paul, 1992; Widdig et al., 2000; Young, Hähndel, et al., 2013; Young et al., 2014) serving both levelling (e.g. Bissonnette et al., 2011; Young, Hähndel, et al., 2013) and rank-changing functions (Young et al., 2014). Handheld Kodak Zx1 HD video cameras were used to record coalitionary aggression with the observer of the aggression providing a spoken commentary of the aggression as soon as it began (for details see Young, Händel, et al., 2013, Young et al., 2014). Videos and spoken records together were analysed post hoc. Barbary macaque males use two behaviours to recruit an ally to a coalition: (1) 'check-look', where the male faces his opponent and turns his head in the direction of another male in a ritualized manner ('show-look', Hesler & Fischer, 2007) and (2) 'silent scream-face', where the mouth is wide open, the lips are completely retracted to show the teeth and no vocalization is produced (Deag, 1974; Hesler & Fischer, 2007). Following the methods of Perry et al. (2004; also see Range and Noë, 2005), we were cautious only to include recruitment events in our data set where we clearly observed one or more of these recruitment behaviours directed at one specific bystander. If no recruitment behaviour was observed or the directionality of the behaviour to a specific male could not be determined the recruitment event was not included in the analysis. The identity of all males present within a 15 m radius of the aggression was recorded, and termed as follows: the male performing recruitment behaviour was the 'recruiter', the recipient of coalitionary aggression was the ‘target’, the male who was recruited was the ‘supporter’ and all bystanders and the supporter were termed ‘potential supporters’. Additionally, the ID of the potential supporter closest to the recruiter when the recruitment event occurred was also recorded. Male Barbary macaques are highly terrestrial and any male within 15 m would be able to join a fight within seconds (Seltmann, Majolo, Schülke, & Ostner, 2013). Because of the high vegetation density and hilly terrain, males beyond 15 m were considered outside the visual range of the recruiting male. Coalitions were categorized into three configurations based on the rank positions of the males involved as follows: (1) all-up, where both allies were lower ranking than the target, (2) all-down, where both allies were higher ranking than the target, and (3) bridging, where the target ranked between the allies (Chapais, 1995; Pandit & van Schaik, 2003; van Schaik et al., 2004).

Additionally, unsuccessful recruitment of males by the recruiter was also recorded where the recruiter used one or more of the recruitment behaviours described above directly at another male during a dyadic contest but the male rejected the invitation to support.

Statistical Analysis

We investigated whether CSI scores predicted the frequency with which males formed coalitions during the mating season using row-wise Kendall's matrix correlations of symmetric matrices. The analysis was conducted with MATMAN 1.1.4 (Noldus Information Technology, Wageningen, The Netherlands; de Vries, Netto, & Hanegraaf, 1993; test for significance based on 10 000 permutations; Hemelrijk, 1990; Hemelrijk & Ek, 1991) controlling for repeated measurements from the same individual. For this analysis we included all coalitions observed for each dyad during the mating season irrespective of whether bystander data were available. Furthermore, social bond stability and equability were analysed as follows: grooming frequencies for each dyad (grooming given versus received) were compared for each group separately using row-wise matrix correlations to examine grooming equitability. We also investigated whether the stability of a male's social bonds was predicted by their grooming equitability and if grooming equitability was predicted by mean CSI score for each dyad across the entire study (using row-wise matrix correlations). To investigate the stability of social bonds between males we compared the CSI scores of all dyads between observation periods within groups (see Appendix for further methodology).

To investigate the effect of proximity on supporter recruitment, we examined a subset of coalitions for which the identity of the closest bystander male to the recruitment event was known ($N = 92$). Of these coalitions we calculated how frequently the closest male was recruited. We also calculated how frequently the closest male should be recruited by chance. For each coalition, we calculated the probability the closest male would be recruited depending on the number of bystanders present, i.e. if two bystanders were present there was a 50% chance the closest male would be recruited and if three bystanders were present a 33% chance the closest male would be recruited by chance, etc. We summed the scores across all coalitions and divided them by the total number of coalitions observed to give the frequency a male would be selected by chance alone. We then compared this value to the empirical data using a chi-square test.

To understand what drives a male's selection of a supporter from the pool of males available when a dyadic conflict occurs we adopted the following approach. First, we compiled a data set comprising all coalitions in which a male recruited a supporter and two or more individuals were present as potential supporters (i.e. the recruiting male had a choice of at least two males to select from). For each coalition, we included data for both the recruited male and the bystander males. This gave a data set with a repeated measures structure and nonindependent data points. Following Kulik, Muniz, Mundry, and Widdig (2012), to control for this nonindependence, we used a repeated random selection of all events. We used a generalized linear mixed model (GLMM; Baayen, 2008) with binomial error structure and logit link function (‘lmer’; Bates, Maechler, & Bolker, 2012). To establish the significance of the full model we used a likelihood ratio test, comparing the deviance with that of the null model comprising only the intercept and random effects; the full and null model were compared using the R-function anova (R Development Core Team, 2012). If the full model was significantly different from the null model we ran 10 000 selections of the full model to test the significance, each containing one randomly chosen data point (i.e. only one of the potential supporters) for each recruitment event, to determine the coefficients for the fixed effects. We calculated the mean of the results for each coefficient (estimate; SE; z; *P*) as the result of the model.

Model 1: is the highest ranked male selected as a supporter and does selection depend on social bond strength? To examine supporter selection in coalition formation we ran a GLMM examining whether the rank of the potential supporter and the CSI score between the recruiter and the potential supporter influenced whether the potential supporter was recruited from the audience ($N = 174$). The response variable was whether a male from the audience was selected as a coalition partner by the recruiting male (Recruited: yes/no). The predictor variables were (1) dominance rank of the potential supporter in relation to the other members of the audience present (highest ranked male in the audience: yes/no) and (2) the CSI score of the recruiter and potential supporter. To examine the effect of the competitive nature of coalitions we first ran the model including rank difference between the recruiter and target as an interaction term with the two predictor variables above. If the interaction terms were not significant we constructed a reduced model containing only the main effects without interaction terms and reran the model to allow interpretation of the main effects (Underwood, 1997; Zar, 1999). The number of audience members available was included as a control variable. We included the identity of the potential supporter, recruiter and target and group ID as random factors.

Model 2: whom do males recruit for levelling coalitions? To further investigate whether the competitive nature of the coalition influenced supporter selection, we looked only at levelling coalitions, i.e. coalitions in a sexual context ($N = 76$). We ran a GLMM consisting of the same predictor, response, control and random variables as model 1 but using this subset of data.

Model 3: why do males refuse to join a recruiter in a coalition? To examine whether male social bond strength or rank relations influenced the potential supporter's decision to accept or reject the recruiter's recruitment attempt we ran an additional GLMM (model 3) with binomial error structure. Whether a male chose to reject the recruiter's signal for support or not was the response variable (reject recruitment: yes/no; $N = 245$). As with model 1 we ran the model including rank difference between the recruiter and target as an interaction term with the following predictor variables: (1) whether the target was higher ranking than the recruiter (binomial: target higher ranked: yes/no), (2) the CSI score between the potential supporter and the recruiter and (3) the CSI score between the potential supporter and the target. We included the identity of the potential supporter, the recruiter and group ID as random factors. If the interaction terms were not significant we constructed a reduced model without interaction terms and reran the model to allow interpretation of the main effects (Underwood, 1997; Zar, 1999).

All predictor variables were set to a mean of zero and a standard deviation of one via *z*-transformation. Assumptions about the lack of overdispersion were respected for the analyses and collinearity was not a problem as variance inflation factors (Field, 2005) were less than 10 (range 1.01–1.73) indicating that covariation between predictors was not a problem (Bowerman & O'Connell, 1990; Mayers, 1990).

Where appropriate, we report mean values ± SD. All statistical analyses were carried out using R 2.15.0 software (R Development Core Team, 2012). The level of significance was set at $\alpha < 0.05$.

RESULTS

Male Social Bonds: Strength, Stability and Equability

We found affiliative relationships to be highly differentiated with two-thirds of dyads showing below average CSI scores and every male forming only 2.31 ± 1.53 (mean ± SD) strong bonds (CSI > 1; Fig. 1). We found the dyadic CSI scores between time periods to be significantly correlated from one period to the next for all 4-month periods in both groups (Kendall row-wise matrix correlation: mean $\tau_{rw} = 0.699$, range 0.481–0.868; mean $P = 0.001$, range < 0.001–0.023; see Appendix Tables A1 and A2 for individual correlations). In Green group, which was observed from September 2009 to December 2011, dyadic CSI scores from the first 4-month block were highly correlated with CSI scores from the last block ($\tau_{rw} = 0.796$, $P < 0.001$) indicating that affiliative relationships were stable for 2 years (see Appendix for details). Relationship strength (mean CSI score) was positively correlated with grooming equitability (Kendall row-wise matrix correlation: Green: $\tau_{rw} = 0.491$, $P < 0.001$; Scarlet: $\tau_{rw} = 0.376$, $P = 0.066$; see Appendix for details) and grooming equitability was positively correlated with stability (Kendall row-wise matrix correlation: Green: $\tau_{rw} = 0.584$, $P < 0.001$; Scarlet: $\tau_{rw} = 0.438$, $P = 0.008$; see Appendix for details).

Coalitionary Recruitment Behaviour

We observed 476 male–male coalitions throughout the study period across both groups; of these, 100 had more than two allies against the target and, of the remaining 376, there was a total of 174 coalitions for which two or more bystanders were available and recruitment behaviour was clearly directed to only one of the bystanders (mean ± SD number of bystanders present: 2.6 ± 0.8, range 2–5). In these coalitions the mean ± SD ranks were target 3.8 ± 1.6, recruiter 2.8 ± 2.1, supporter 2.9 ± 1.7 and bystander 3.8 ± 2.0. Additionally, we observed 71 occasions on which the potential supporter rejected the invitation to support the recruiter; the mean ranks ± SD were target 3.7 ± 1.7, recruiter 2.9 ± 2.0 and potential supporter 2.8 ± 1.7.

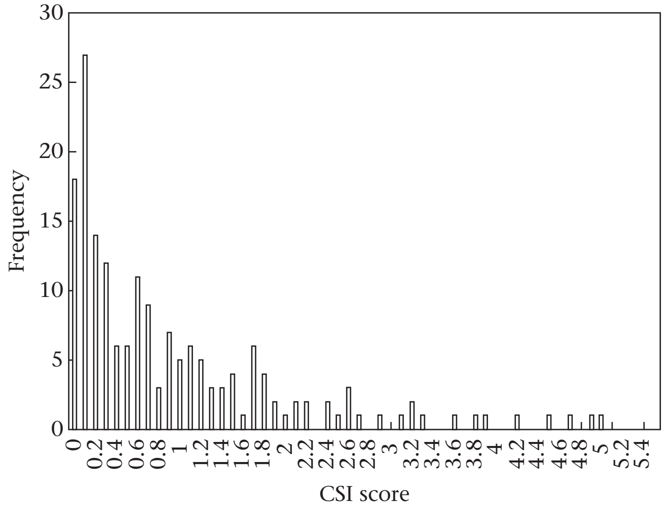

Figure 1. The distribution of male–male CSI scores between all dyads in the two study groups and all time periods. CSI scores of 1 and above are considered to show above average affiliation within a group.

Of all coalitions for which two or more bystanders were present, we observed 48.9% as all-down (see Methods for definitions), 43.4% as bridging and 9.8% as all-up. Overall, of the 174 coalitions for which bystanders were present the highest ranked male was selected 57.4% of the time and the male with the strongest social bond to the recruiter 51.2% of the time. For 60 of these coalitions observed this was the same individual (Fig. 2). For 92 coalitions, we were able to determine the closest bystander male to the aggression when the recruitment event occurred. Of these events the closest male was recruited 39.1% of the time and the closest male was also the highest ranked male 40.2% of the time. The bystander with the strongest social bond to the recruiter was also the closest male for 35.7% of the coalitions (Fig. 2; not shown are 28 coalitions for which the closest male was not recruited and was neither the strongest bonded nor highest ranked male bystander). We found that the closest male to the recruiter was not more likely to be recruited than by chance alone ($\chi^2_1 = 0.02$, $N = 92$, $P = 0.880$).

We found that the CSI scores between dyads during the mating season were significantly correlated with the frequency with which dyads formed coalitions for the Green group (Kendall row-wise matrix correlation: MS09: $\tau_{rw} = 0.502$, $P < 0.001$; MS10: $\tau_{rw} = 0.463$, $P < 0.001$), as well as the Scarlet group (Kendall row-wise matrix correlation: MS10: $\tau_{rw} = 0.429$, $P < 0.001$).

Model 1: Who is recruited from the audience?

We found that the interaction terms between the rank difference between the target and recruiter and (1) the CSI score of the potential supporter and the recruiter (estimate ± SE = −0.063 ± 0.121, $z = -1.214$, $P = 0.225$) and (2) the highest ranking male available

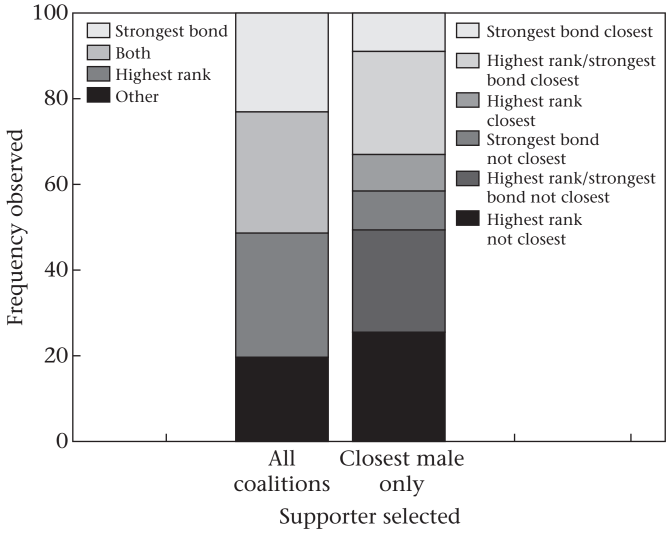

Figure 2. The frequency of partner recruitment selection for all coalitions observed ($N = 174$) and a subset of coalitions in which the closest male to the aggression could be identified and was either the strongest bonded male or the highest ranked male present ($N = 64$). To simplify the illustration of the 'closest male only' bar, we do not show coalitions for which the closest male was neither the strongest bonded nor the highest ranked male and additionally not recruited for the coalition ($N = 28$).

Table 1
GLMM binomial regression results for model 1: is the highest ranked male selected as a supporter and does selection depend on social bond strength?

Independent variable	GLMM estimate	SE	Z	P (>|Z|)
Intercept	−0.589	0.226	−2.630	0.009
Highest ranked audience member recruited (Yes)	0.608	0.133	2.886	0.004
CSI score between recruiter and potential supporter	0.301	0.130	2.328	0.020
Number of bystanders	−0.401	0.120	−0.263	0.792

GLMM results (mean estimates of 10 000 random selections) for the relationship between potential supporter recruited (yes/no) and their rank in comparison to the other audience members (was highest ranked audience member selected) and the CSI score between the recruiter and the potential supporter (N = 174). We controlled for the identity of the potential supporter, the identity of the recruiter and target, the number of audience members present and group.

(estimate ± SE = 0.111 ± 0.127, $z = 0.112$, $P = 0.911$) were not significant. Thus, we ran a reduced model excluding the interaction terms in order to interpret the main effects. We found that both predictors had independent effects on which male was recruited from the audience. The highest ranked potential supporter was significantly more likely to be recruited to form a coalition than another male from the audience. Additionally, the stronger the social bond was between the recruiter and the potential supporter the more likely the potential supporter was to be recruited from the audience (Table 1; full versus null model: $\chi^2_3 = 45.561$, $N = 174$, $P < 0.001$).

Model 2: Who is recruited for levelling coalitions?

We found that for coalitions in a levelling context the rank of the potential supporters but not the strength of social bonds influenced which male was recruited from the audience. The recruiter male was more likely to select the highest ranked potential supporter (Table 2; full versus null model: $\chi^2_3 = 11.461$, $N = 76$, $P < 0.001$).

Model 3: Why refuse to join a coalition?

We found that the interaction terms between the rank difference between the target and recruiter and (1) the CSI score of the potential supporter and the recruiter (estimate ± SE = −0.068 ± 0.154, $z = -0.444$, $P = 0.657$), (2) the CSI score of the potential supporter and the target (estimate ± SE = 0.096 ± 0.149, $z = 0.648$, $P = 0.517$) and (3) whether the target was higher ranked than the recruiter (estimate ± SE = −0.269 ± 0.306, $z = -0.881$, $P = 0.378$) were not significant. Thus, we ran a reduced model excluding the interaction terms in order to interpret the main effects. We found that both social bonds and rank relationships influenced the likelihood that a potential supporter joined the conflict after being solicited. First, the potential supporter was more likely to refuse the recruiter's invitation to support if the target was higher ranking than the recruiter. We found that the CSI score between the target and the potential supporter did not influence the potential supporter's decision to reject the recruitment invitation or not; however, the potential supporter was more likely to reject the invitation to support the lower the social bond strength was between him and the recruiter (Table 3; full versus null model: $\chi^2_3 = 12.048$, $N = 245$, $P = 0.007$).

Table 2
GLMM binomial regression results for model 2: whom do males recruit for levelling coalitions?

Independent variable	GLMM estimate	SE	Z	P (>|Z|)
Intercept	−0.535	0.346	−0.398	0.691
Highest ranked audience member recruited (Yes)	0.394	0.206	2.140	0.032
CSI score between recruiter and potential supporter	0.393	0.222	1.543	0.123
Number of bystanders	−0.471	0.205	−0.970	0.332

GLMM results (mean estimates of 10 000 random selections) for the relationship between potential supporter recruited (yes/no) and their rank in comparison to the other audience members (was highest ranked audience member selected) and the CSI score between the recruiter and the potential supporter ($N = 76$). We used a subset of data only examining coalitions in a levelling context. We controlled for the identity of the potential supporter, the identity of the recruiter and target, the number of audience members present and group.

Table 3
GLMM binomial regression results for model 3: why do males refuse to join a recruiter in a coalition?

Independent variable	GLMM estimate	SE	Z	P (>|Z|)
Intercept	−0.963	0.149	−6.445	<0.001
Target higher ranked than recruiter (Yes)	0.536	0.141	3.750	<0.001
CSI score between recruiter and potential supporter	−0.322	0.150	−2.156	0.031
CSI score between target and potential supporter	−0.060	0.150	−0.394	0.694

GLMM regression results for the relationship between a potential supporter rejecting an invitation to support (yes/no) and the target being higher ranked than the recruiter, the CSI score between the potential supporter and the recruiter and the CSI score between the potential supporter and the target ($N = 245$).

DISCUSSION

Wild Barbary macaque males of our study formed strong, stable, equitable social bonds, similar to those of female baboons, *Papio* sp. (Silk, Alberts, et al., 2006; Silk, Altmann, et al., 2006; Silk et al., 2010b), male chimpanzees, *Pan troglodytes* (Mitani, 2009) and male Assamese macaques (Schülke et al., 2010). In seasonally breeding species, male affiliative relationships may break down during the highly competitive mating season (Berghänel, Ostner, Schröder, et al., 2011; Berghänel, Ostner, & Schülke, 2011). However, affiliative relationships were stable for 2 years including three consecutive mating seasons in our study. Highly differentiated grooming relationships, as well as correlations between grooming equitability and relationship strength and stability of dyads, suggest that males formed social bonds or ‘friendships’ (Silk, 2002). The formation and maintenance of strong social bonds can be temporally demanding (Dunbar, 1992; Dunbar, Korstjens, & Lehmann, 2009). In Barbary macaques, male–infant triadic interactions, used by males as a social mediator, can also be physiologically costly (Henkel, Heistermann, & Fischer, 2010; Paul et al., 1996) and should thus provide benefits, such as support in coalitions. By examining recruitment behaviour from the perspective of the recruiting male across all coalition contexts, we found independent effects for the highest ranked male in the audience to be more likely to be recruited and the strength of the social bond between the recruiter male and the potential supporter to increase the likelihood of recruitment. These results are in agreement with the idea that males can classify bystanders simultaneously by different criteria. But we also found that in the highly competitive context of levelling coalitions males were more likely to maximize the chance of success of the coalition by selecting a supporter based solely on his dominance rank relative to other bystanders. Additionally, social bond strength also predicted the likelihood that a male rejected an invitation to join a coalition. The probability of rejection increased as the social relationship strength decreased and rejection was also more likely if the target was higher ranked than the recruiter.

Coalitionary recruitment, in our study examining the situational availability of potential supporters, seemed to be based on these two independent criteria (dominance rank and social bond strength), corroborating previous studies, on the same species, each considering only one mechanism (Berghänel, Ostner, Schröder, et al., 2011; Bissonnette et al., 2009). Males in the study by Bissonnette et al. (2009) possibly attempted to maximize feasibility in many all-up (levelling) coalitions (81% all-up) by recruiting high-ranked males but the effect of social bonds was not investigated. Another study on the same group with a lower, but still substantial proportion (41%) of all-up coalitions (Berghänel et al., 2010) found social bond strength to be predictive of coalition formation among males (Berghänel, Ostner, Schröder, et al., 2011), but did not consider the role of partner rank in support selection. In the same semi-free-ranging population males supported their maternal kin over nonkin highlighting again that more than hierarchal position may be considered when supporting in coalitionary aggression (Widdig et al., 2000). Indeed, studies in other cercopithecines have previously highlighted that several factors can play a role in decision making and the relationships of other group members may be classified simultaneously by different criteria (Bergman et al., 2003; Schino et al., 2006). Our study adds to these findings by showing males may use their social knowledge flexibly depending on the context of the contest during recruitment decisions.

Partner recruitment has been suggested to be a by-product of spatial assortment by rank within social groups (Hemelrijk & Puga-Gonzalez, 2012; Puga-Gonzalez et al., 2009). As we recorded all spatially available bystanders within a 15 m radius for each recruitment event and still found effects of rank and social bonding, spatial proximity alone did not seem to drive this effect. On a more fine-grained spatial scale, we found that in almost two-thirds of recruitment events the spatially closest male was not selected by the recruiter, again suggesting that supporter selection was not solely based on spatial factors. Noë and Sluijter (1995) argued that estimates of male association may be inflated by coalitionary behaviour as this leads males to associate more frequently in close proximity. For species characterized by large male power asymmetries, high reproductive skew, consortship by high-ranked males and infrequent affiliation, such as yellow baboons, coalition formation may be opportunistic in nature and based on both the intrinsic fighting abilities of partners and the identity of the target (Noë, 1992, 1994; Noë & Völkl, 2013). Partner recruitment may occur on a short-term, situation-specific basis dependent on the current needs of the participants to break up consortships and gain immediate access to consorted females (Noë, 1992, 1994; Pandit & van Schaik, 2003). Males can gain short-term benefits through levelling coalitions and long-term social bonds may not have been selected for because of a more dynamic male group composition associated with high-contest conditions (Kulik et al., 2012; Ostner & Schülke, 2014; van Noordwijk & van Schaik, 2004). This is reflected in our study, in which we found that males may attempt to maximize the feasibility of levelling coalitions. Owing to the more opportunistic nature of these coalitions and contest over a highly prized resource (access to a female) males may require a partner with the strongest fighting abilities for these one-shot polyadic contests.

However, coalitionary activity does not occur only over direct access to females; males can utilize rank-changing coalitions leading to changes in the dominance hierarchy (van Schaik et al., 2004, 2006), which may require many aggressive events. In these species reproductive skew may be medium to low with longer male coresidency and thus social bonding is more likely to develop (Kulik et al., 2012; Ostner & Schülke, 2014; van Noordwijk & van Schaik, 2004). Males may recruit partners based on previous experience but over a longer time frame based on both previous coalitionary activity and affiliative behaviour (Ostner & Schülke, 2014; Schino & Aureli, 2010; Schülke et al., 2010; Young et al., 2014). Cooperating in aggressive encounters is risky: defection by one ally can leave its partner in a vulnerable position with an increased risk of injury (van Schaik et al., 2006). Males can use frequent affiliation to strengthen social bonds and these bonds may act to advertise a willingness to cooperate in the future (Perry, 2012; Perry et al., 2004; Silk, 1992). Our results support this idea, because the probability of rejecting an invitation to support was negatively related to social bond strength, i.e. a closely bonded male would rarely reject a call for help. If males base their recruitment decisions on their previous social interactions and experiences (Campennì & Schino, 2014; Fruteau, Lemoine, Hellard, Van Damme, & Noë, 2011; Noë & Völkl, 2013; Schino, 2007; Schino & Aureli, 2009, 2010) both successful coalitions and affiliative behaviour are likely to be intertwined in a positive feedback mechanism ultimately enhancing reliability and trust of both partners. Defection during a coalition or rejection of recruitment may then lead to a negative association with the defector and, if defection persists, to a termination of future cooperation (Schino & Aureli, 2009; van Schaik et al., 2006). In species with strong social bonds individuals may be able to show behavioural flexibility, utilizing a strongly bonded partner for coalitions with a rank-related function while maximizing feasibility of short-term opportunistic, levelling coalitions basing recruitment decisions on the rank of the bystanders available, as we saw in our study.

In conclusion, we have built on previous knowledge of male affiliation and coalitionary activity, helping to fill in some of the gaps and open questions of previous studies. We corroborated findings for Barbary macaques by Berghänel, Ostner, Schröder, et al. (2011) and Berghänel, Ostner, and Schülke (2011) on the role of social bonds in supporter selection for coalitions. We largely ruled out that the correlation is driven by spatial proximity alone and added a long-term perspective of male social relationships showing that strong social bonds are equitable and stable for 2 years in wild groups. We corroborated results from the Bissonnette et al. (2009) study by showing that supporter selection was related to relative supporter rank. Our results are in line with the decision rule suggested by Bissonnette et al. (2009), i.e. always select the highest ranking supporter available, and we went beyond the previous study by only considering those males as potential supporters that were present during the recruitment event. Previous findings (Perry et al., 2004; Schino et al., 2006) suggested that primates categorize group members by more than one characteristic, e.g. hierarchically by rank and kinship (Bergman et al., 2003). We extended this conclusion to dispersing male macaques and showed that males flexibly use this cognitive ability by implementing one of two selection criteria when recruiting support in different agonistic contexts.

Acknowledgments

We are grateful to Professor Mohamed Qarro (Ecole Nationale Forestière d'Ingénieurs, Morocco) for his support in the field and the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification of Morocco for research permission. We are also grateful to the Editor and three anonymous referees for insightful comments which improved the manuscript. We also thank Michael Madole, Dave Thomas, Sofia Santos, Maria Thunström, Tom Smith, Josephine Msindai and Sabine Hähndel for assistance in the field. We thank Laëtitia Maréchal, Cédric Girard-Buttoz and Rebecca Rimbach for helpful comments, Christof Neumann for statistical advice and Andreas Berghänel and Annie Bissonnette for fruitful discussions. Financial support was provided by the Max Planck Society, the Christian Vogel Fonds and Georg-August University Göttingen through funds from the German Initiative of Excellence.

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Appendix

Male Social Bonds: Strength, Stability and Equability

Methods

To measure the strength of male affiliative relationships we adopted the following approach. We determined eight behaviours of male affiliation to be highly correlated: duration of time spent in close proximity (s/h the dyad was observed), number of friendly/neutral approaches per h per dyad (excluding approaches resulting in agonistic behaviour), duration of male–infant triadic interactions (s/h dyad was observed), number of male–infant triadic interactions per h per dyad, number of grooming interactions per h per dyad, duration of grooming (s/h dyad was observed), number of friendly body contact interactions per h per dyad (usually sitting in body contact) and duration of body contact (s/h dyad was observed). During the mating season there was a pronounced drop in grooming and body contact activity between males. For example, males in the Green group spent 0.47 min/h grooming other males in the premating period versus 0.02 min/h in the mating season with the average grooming bout length reduced from 32 to 10 min on average. Because grooming and body contact were so rare in the mating season the frequency and duration estimates must have had large measurement errors and we excluded these behaviours from the CSI calculations. Although there were fluctuations in the rates of the other affiliative behaviours between periods they were never as rare as grooming in the mating season. Rates of affiliative behaviours were higher in general during nonmating season periods (e.g. Green group PostMS10: number of approaches/h: mean = 0.085; number of male–infant triadic interactions/h: mean = 0.151) than during the mating season (e.g. Green group MS10: number of approaches/h: mean = 0.025; number of male–infant triadic interactions/h: mean = 0.035).

Social bond equability was measured as follows. Male–infant triadic interactions have previously been shown to be an affiliative social behaviour between Barbary macaque males that leads to the formation and maintenance of social bonds (Berghänel, Ostner, Schröder, et al., 2011; Deag & Crook, 1971; Henkel et al., 2010; Paul et al., 1996). This ritualized behaviour is always bidirectional with both partners simultaneously involved in teeth-chatter and grasping of the infant (Hesler & Fischer, 2007). These exchanges are always equitable.

We also examined the grooming equitability as follows. For each dyad the amount of grooming given and received was measured during focal protocols, controlling for the number of hours both individuals were observed. We compared the frequency of grooming given by each dyad member for the total duration each dyad was observed outside the mating season to give an estimate of grooming reciprocity (grooming equitability score).

Social bond stability was examined between male dyads. For each male, we identified who their top three social partners were during each time period (those with the greatest CSI score). We then determined the proportion of time periods an individual appeared as a top three partner. Thus, for each dyad we were able to determine how frequently they were a top three partner and accordingly how stable their social bond was, creating a stability score for each dyad.

Statistical analysis

To investigate the stability of social bonds between males we compared the CSI scores of all dyads between observation periods using row-wise Kendall's matrix correlations of symmetric matrices of CSI scores with MATMAN 1.1.4 controlling for repeated measurements from the same individual. For this analysis we included additional data on CSI scores from the PreMS11 and MS11 periods for the Green group (Young, Hähndel, et al., 2013), allowing us to investigate the stability of social bonds from September 2009 to December 2011 for the Green group. Data collection protocol for the time period July–December 2011 differed slightly and bystander information during coalition formation was unavailable for this time and, thus, these data were not included in any other analyses. Grooming frequencies for each dyad (grooming given versus grooming received) were compared for each group separately using row-wise matrix correlations to examine grooming equitability.

Results

In total, 64 dyads showed a CSI score of 1 or above (36.16%; Fig. 1). The top 10% of dyads were above a score of 2.46. A male had on average ± SD 0.71 ± 0.94 very strong bonds (CSI score in the top 10%). We found the CSI scores between all time periods showed a significant correlation in both groups (Tables A1, A2), including the two periods furthest apart, which were separated by 2 years (Green group, MS09–MS11).

Social bonds were considered to be equitable because of the frequent and reciprocal affiliative behaviour of male–infant triadic interactions (see above) which was one of the main components of our CSI score. Additionally, we also found grooming given by males to be correlated with grooming received from the same partner throughout the study (excluding the mating season) in both groups (Kendall row-wise matrix correlation: Green group: $\tau_{rw} = 0.723$, $P < 0.001$, proportion of dyads that did not groom = 0.14; Scarlet group: $\tau_{rw} = 0.754$, mean $P < 0.001$, proportion of dyads that did not groom = 0.40). We found a male's top three strongest bonded partners to be stable over time with a mean stability score ± SD of 0.674 ± 0.283, range 0–1.

Table A1

Stability of CSI scores of the Green group across time periods

	PostMS09	PreMS10	MS10	PostMS10	PreMS11	MS11
MS09	τ_{rw}=0.681 P<0.001	τ_{rw}=0.710 P<0.001	τ_{rw}=0.499 P<0.001	τ_{rw}=0.780 P<0.001	τ_{rw}=0.630 P<0.001	τ_{rw}=0.769 P<0.001
PostMS09		τ_{rw}=0.743 P <0.001	τ_{rw}=0.481 P<0.001	τ_{rw}=0.780 P<0.001	τ_{rw}=0.670 P<0.001	τ_{rw}=0.780 P<0.001
PreMS10			τ_{rw}=0.497 P<0.001	τ_{rw}=0.648 P<0.001	τ_{rw}=0.760 P<0.001	τ_{rw}=0.692 P<0.001
MS10				τ_{rw}=0.729 P<0.001	τ_{rw}=0.632 P<0.001	τ_{rw}=0.824 P<0.001
PostMS10					τ_{rw}=0.670 P<0.001	τ_{rw}=0.868 P<0.001
PreMS11						τ_{rw}=0.751 P<0.001

Kendal row-wise matrix correlation comparing the CSI scores between time periods for the Green group, including the PreMS11-MS11 time periods. The τ_{rw} value and P value for the comparison of two time periods are shown.

Table A2

Stability of CSI scores of the Scarlet group across time periods

	MS10	PostMS10
PreMS10	τ_{rw}=0.745 P<0.001	τ_{rw}=0.857 P=0.003
MS10		τ_{rw}=0.571 P=0.023

Kendal row-wise matrix correlation comparing the CSI scores between time periods for the Scarlet group. The τ_{rw} value and P value for the comparison of two time periods are shown.