



Strong, equitable and long-term social bonds in the dispersing sex in Assamese macaques



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In multimale multifemale primate groups, the strength and stability of affiliative relationships have been shown to affect an individual's long-term fitness such as offspring survival and longevity. Studies investigating the fitness benefits of close social relationships and the underlying mechanisms have mainly focused on the philopatric sex. The strong relationships of philopatric chimpanzee males and baboon females share important characteristics with human friendships in that increased strength of affiliative relationships is associated with increased equitability in service exchanges and relationship stability. So far, it has remained unclear whether the strong relationships of dispersing males share these characteristics as well and can thus be labelled as social bonds. Here we provide results on the variation in affiliative relationship strength and its relation to equitability and relationship stability from two wild groups of male Assamese macaques, *Macaca assamensis*, at Phu Khieo Wildlife Sanctuary, Thailand collected over 2 and 7 years, respectively. Our analyses of almost 9000 h of focal animal data show that males formed differentiated affiliative relationships and that the strength of a relationship affected how likely males returned a grooming service within a single bout and how equally males were responsible for the maintenance of close proximity. Partner stability among the three strongest relationships was higher than among weaker relationships which suggests that top partners were not retained simply because of a lack of alternatives. Together, these results suggest that dispersing male Assamese macaques form differentiated affiliative relationships that increase in equitability and stability with increasing relationship strength. This is the first study showing long-term partner stability in males as the dispersing sex. Our results thus add to the growing body of literature indicating that nonhuman animals form close social relationships similar to human friendships.

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Living in a social group entails costs and benefits for each individual. On the one hand, close proximity to and daily repeated interactions with conspecifics within a group increase feeding and mating competition, the risk of disease transmission and, in some species, the risk of infanticide (Altizer et al., 2003; Krause & Ruxton, 2002; Lukas & Clutton-Brock, 2014; Ostner, Heistermann, & Schülke, 2011; Palombit, Seyfarth, & Cheney, 1997; van Schaik & Aureli, 2000; Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987; Wittig & Boesch, 2003). On the other hand, animals can derive benefits from sociality such as lower predation risk, better access to food resources, more effective territory defence and increased access to mating

partners (Connor, 2000; Frère et al., 2010; Silk, Alberts, & Altmann, 2003; Silk et al., 2009; Weidt, Hofmann, & König, 2008). In gregarious species within-group variation in sociality may be associated with variation in coalition formation (Langergraber, Mitani, & Vigilant, 2007; Pope, 1990; Schülke, Bhagavatula, Vigilant, & Ostner, 2010), co-feeding tolerance, (Huchard et al., 2010) and buffering against environmental and social stressors (McFarland & Majolo, 2013; Young, Majolo, Heistermann, Schülke, & Ostner, 2014). This in turn may lead to increased reproductive success and longevity for individuals (Archie, Tung, Clark, Altmann, & Alberts, 2014; Brent et al., 2013; Frère et al., 2010; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Silk et al., 2010a).

One mechanism linking partner preferences within a social group and fitness is the formation of social bonds that serve as reliable alliances in competitive situations and help to attain and maintain high social status which in turn regulates access to resources and safety (Connor, Smolker, & Richards, 1992; Heesen,

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Macdonald, Ostner, & Schülke, 2014; Ostner & Schülke, 2014). If bonds evolved for alliance formation, selection favoured an individual's ability to form a few very strong affiliative relationships (Hinde, 1976) for the exchange of support (Ostner & Schülke, 2014) rather than an individual's overall level of affiliation. Thus, differentiation into weaker and stronger affiliative relationships is crucial (Massen, Sterck, & deVos, 2010; Ostner & Schülke, 2014; Silk, 2002). Furthermore, strong affiliative relationships may be more equitable and longer lasting than weaker ones which makes them similar in kind to human friendships (Lehmann & Boesch, 2009; Massen et al., 2010; Mitani, 2009; Ostner & Schülke, 2014; Silk, 2012). Consequently, strength, equitability, and stability have been suggested as defining characteristics of a social bond (Ostner & Schülke, 2014).

In the past three decades, several studies have investigated characteristics of affiliative relationships separately. First, variation in the strength of social relationships, which emerges by biased allocation of affiliation towards specific group members, has been described for a broad range of animal taxa, for example guppies, *Poecilia reticulata*, and sticklebacks, *Gasterosteus aculeatus* (Croft et al., 2005), great tits, *Parus major* (Aplin et al., 2013), mice, *Mus domesticus* (Weidt et al. 2008), bats, *Myotis bechsteinii* (Kerth, Perony, & Schweitzer, 2011), feral goats, *Capra hircus* (Stanley & Dunbar, 2013), nonhuman primates (Aureli, Fraser, Schaffner, & Schino, 2012), kangaroos, *Macropus giganteus* (Carter, Macdonald, Thomson, & Goldizen, 2009), male bottlenose dolphins, *Tursiops truncatus* (Parsons et al., 2003), female African elephants, *Loxodonta africana* (Archie, Moss, & Alberts, 2006) and giraffes, *Giraffa camelopardalis* (Carter, Seddon, Frère, Carter, & Goldizen, 2013). Affiliation is often biased towards maternal and paternal kin and individuals similar in age or dominance rank (e.g. female giraffes, Carter et al., 2013), female yellow baboons, *Papio cynocephalus* (Silk, Altmann, & Alberts, 2006), female vervet monkeys, *Chlorocebus aethiops* (Cheney, Seyfarth, & Smut, 1986), female macaques, *Macaca* spp. (Cheney et al., 1986; Schülke, Wenzel, & Ostner, 2013; Widdig, Nürnberg, Krawczak, Streichl, & Bercovitch, 2001) and male chimpanzees, *Pan troglodytes schweinfurthii* (De Waal, 1991; Mitani, 2009).

Second, of the goods and services that are exchanged within dyads allogrooming is perhaps the best studied behaviour. In several species grooming is often reciprocated in the sense that the more grooming an individual provides to a partner the more it receives from the same individual in return (Connor, 1995; Fruteau, Lemoine, Hellard, van Damme, & Noë, 2011; Gomes, Mundry, & Boesch, 2009; Kaburu & Newton-Fischer, 2015; Lewis, Harris, Prigmore, & Wanless, 2007). So far, the relationship between grooming equitability and the strength of the partners' affiliative relationship, the second characteristic of social bonds, have only been investigated in a few studies (e.g. bonnet macaques, *Macaca radiata*, Adiseshan, Adiseshan, & Isbell, 2011; chimpanzees, Mitani, 2009; savanna baboons, Silk, Alberts, & Altmann, 2006; chacma baboons, *Papio ursinus*, Silk et al., 2010b). In humans, affiliative physical contact (e.g. cuddling) is an important predictor of the value of a relationship. Here friends touch each other more often than partners with a weaker affiliative relationship (Dunbar, 2010). Hence, it is important to study similar behaviours such as grooming in animals (Massen et al., 2010). Finally, empirical data on the relative temporal stability of affiliative relationships, the third characteristic of social bonds, are scarce. In philopatric male chimpanzees (Mitani, 2009) and female chacma baboons, stronger affiliative relationships were more stable over time than weaker ones (Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012), albeit partner choice for their strongest relationship was not consistent among female chacma baboons of a different population (Henzi, Lusseau, Weingrill, Schaik, & Barrett, 2009). In female yellow baboons, mothers, daughters and maternal sisters formed the

strongest and also most enduring relationships suggesting that stronger relationships were also more stable (Silk, Alberts, et al., 2006). The same pattern has been observed in male chimpanzees. Here both the strength of an affiliative relationship and its stability were positively related to grooming symmetry (Mitani, 2009) which suggests that stronger relationships were also more stable. In contrast, stronger affiliative relationships were not more stable than weaker ones in dispersing female chimpanzees. Females' preferences for association partners were much more stable than preferences for grooming partners (Lehmann & Boesch, 2009). It remains to be shown whether the long-term stability of affiliative relationships varies with their strength in the dispersing sex in which group membership and dominance relationships are more fluid.

We have previously shown for the dispersing sex with a smaller sample of 12 adult individuals observed over 2 years that affiliative relationships of male Assamese macaques, *Macaca assamensis*, are differentiated in strength and that in general the amount of grooming given is correlated with the amount of grooming received across all possible dyads (Schülke et al., 2010). The strength of affiliative relationships also predicted cooperation in agonistic within-group coalitions against other males. This coalitionary support helped males attain and maintain higher social status in the future and ultimately translated into increased paternity success (Schülke et al., 2010; Sukmak, Wajjwalku, Ostner, & Schülke, 2014). Our previous analyses did not, however, answer the question whether stronger affiliative relationships differ in their grooming symmetry and stability from weaker relationships, and hence fulfilling the three characteristics of social bonds. Here, we investigated whether the affiliative relationships formed by the dispersing sex of Assamese macaques qualify as social bonds. Our study is based on almost 9000 h of focal animal data collected over 7 consecutive years to test whether dispersing male Assamese macaques form strong, equitable and stable social relationships that qualify as social bonds.

METHODS

Study Site and Subjects

This study was carried out in the Phu Khieo Wildlife Sanctuary (PKWS; 16°5'–35'N, 101°20'–55'E) which is part of the ca. 6500 km² interconnected and well-protected Western Isaan forest complex in northeast Thailand (Borries, Larney, Kreetiyutanont, & Koenig, 2002). The hilly forest comprises dense, mostly evergreen vegetation and harbours a diverse community of predators (Borries et al., 2002). Behavioural data were collected on two fully habituated multimale multifemale groups. All adult males of the AS group were followed from 2006 until 2013. Data from the AO group were collected from May 2012 until September 2013. Both groups were observed almost daily. The AS group had on average \pm SD 51.4 \pm 4.7 group members, 10.1 \pm 1.9 males and 13 \pm 1.9 females, and the AO group had 45.1 \pm 2.0 members, 10.6 \pm 0.5 males and 10.6 \pm 0.5 females. Changes in group composition occurred due to immigration, emigration and death. Across the entire study period 17 individual adult males lived in the AS group and 10 in the AO group.

Data Collection

All adult males, from both groups, were subject to 30 min focal animal sampling, yielding a total of 8952.82 h (AS: 7200.40 h; AO: 1752.42 h) of focal animal data. For a more detailed overview on observation hours per male and per period see the Appendix (Tables A1 and A2). An effort was made to equally distribute focal sampling across males and for each male across time of the day. By

using continuous sampling (Martin & Bateson, 2007) we recorded frequencies and durations as well as the actor and receiver of all affiliative (grooming, body contact), submissive (bare teeth, give ground, make room) and aggressive (e.g. lunch, slap, bite) behaviours and approaches into and departures from a 1.5 m radius around the focal individual (referred to below as ‘close proximity’) (Ostner, Heistermann, & Schülke, 2008). In addition we recorded agonistic interactions between males other than the focal animal by ad libitum sampling (Altmann, 1974).

Data Analysis

To make our results comparable to previous studies on relationship strength, equitability and stability we broke our data down into yearly periods (e.g. Silk, Alberts, et al., 2006; Silk, Altmann, et al., 2006). We defined one observation period as 1 year from the start of the mating season (October) until the end of the subsequent nonmating season (September) (Fürtbauer, Schülke, Heistermann, & Ostner, 2010). The observation periods were not the same as in our previous analyses (Schülke et al., 2010). The first observation period of the AO group spanned 5 months only.

Dominance hierarchy

For the purpose of this study, we calculated a dominance hierarchy for each observation period from decided dyadic agonistic interactions (Ostner et al., 2008) recorded during continuous and ad libitum sampling (Martin & Bateson, 2007). A winner/loser matrix of these interactions was used to calculate the standardized normalized David’s score (nDS) using DomCalc (Schmid & de Vries, 2013). These David’s scores were utilized to calculate a continuous measure of rank distances (Table A3).

Strength of Affiliative Relationships

We investigated the strength of affiliative relationships between adult males by following Silk, Altmann, et al. (2006) and computing the composite sociality index (CSI) for each male dyad each year. This index quantifies the extent by which each dyad deviates from the average male dyad in the same group during the same period (Silk, Altmann, et al., 2006). We used as components both the frequency and duration of grooming, body contact and time spent in close proximity ≤1.5 m. The time a dyad spent in close proximity while also in body contact or grooming was deduced from the proximity time; similarly, time spent grooming was deduced from time spent in body contact. All components were highly correlated in row-wise matrix correlations with 10 000 permutations using Spearman rank correlations (mean rho_{rw,ave} = 0.92 ± 0.01; range rho_{rw,ave} = 0.88–0.97). To control for partner availability, we divided per dyad each component by the number of hours each of the partners was observed to give a frequency per hour of observation or duration in minutes per hour of observation. Then values for an individual dyad (ij) were divided by the mean value of this component across possible male-male dyads.

Then the CSI was calculated as follows:

$$CSI = \left[\frac{FP_{ij} + FB_{ij} + FG_{ij} + DP_{ave} + DB_{ave} + DG_{ij}}{FP_{ave} + FB_{ave} + FG_{ave} + DP_{ave} + DB_{ave} + DG_{ave}} \right] \times 6$$

The first term represents the hourly frequency of time spent in close proximity (frequency in proximity, FP) per dyad (ij) divided by the average hourly frequency in close proximity (FP_{ave}) across all dyads. The second and third term represent the ratio between dyadic frequency of body contact (FB_{ij}) and of grooming (FG_{ij}) and average frequencies of both parameters across all dyads (FB_{ave} and

FG_{ave}). The last three terms represent the hourly duration of close proximity (DP_{ij}), body contact (DB_{ij}) and grooming (DG_{ij}) for each dyad (ij) divided by their averages (DP_{ave}, DB_{ave} and DG_{ave}) across all dyads. The values of the six terms are then summed and divided by the number of behaviours used, i.e. six in this case. The average CSI score across all dyads is by definition always one. Values ≥1 reflect dyads that share a stronger affiliative relationship, while values between zero and one (excluding one) suggest that the relationship is weaker (Silk, Altmann, et al., 2006). Descriptive statistics for the CSI and the components are provided in the Results section. It has been shown in other primates that individuals close in dominance rank may form stronger relationships than individuals ranking further apart (Silk, Altmann, et al., 2006). To assess whether dominance rank drives the pattern of social relationship strength in male Assamese macaques, we tested for a possible relationship between dyadic CSI score and dominance rank difference using a linear mixed model (LMM; Model 1). The response variable was the CSI value of each dyad in each year and the predictor variable was the nDS difference. Actor and receiver identity as well as group and period were included as random factors to control for nonindependent repeated measures across the same individuals within the same periods.

Equitability of affiliative relationships

We assessed the equitability of affiliative relationships in several ways. We calculated the grooming symmetry index (GSI; Silk, Alberts, et al., 2006) based on the duration of grooming given (G_{ij}) and received (G_{ji}) by each male within a dyadic grooming bout and across grooming bouts. A grooming bout can contain one or several grooming interactions if grooming is reciprocated immediately.

$$GSI = 1 - \text{abs} \left(\frac{G_{ij} - G_{ji}}{G_{ij} + G_{ji}} \right)$$

A GSI of one indicates a perfect balance between grooming given and grooming received whereas a GSI of zero indicates that all grooming went only one way. Relationships with a more symmetric exchange of grooming are more equitable.

Additionally, we assessed imbalances in responsibility for the maintenance of close spatial proximity of <1.5 m by calculating the Hinde index (HI; Hinde & Atkinson, 1970) of approaches into and departures from a 1.5 m radius.

$$HI = \left(\left(\frac{A_{ij}}{A_{ij} + A_{ji}} \right) \times 100 \right) - \left(\left(\frac{D_{ij}}{D_{ij} + D_{ji}} \right) \times 100 \right)$$

The HI ranges from 0 to 100 and increasingly high indices indicate an increasing imbalance in the relationship (Hinde & Atkinson, 1970). Since small deviations from zero may result from sampling, e.g. because odd numbers of approaches or departures always generate an imbalance, it has been suggested that one should refrain from interpreting the variation in values below 10 (Hill, 1987). We therefore excluded all dyads with HIs below 10 from further analyses.

To assess whether the strength of affiliative relationships affected within-bout grooming symmetry and the likelihood of grooming reciprocation, we built two models. First, we used a generalized linear mixed model (GLMM; Baayen, 2008) to examine whether the dyadic CSI affected the likelihood of grooming being reciprocated at all within a bout (irrespective of the amount of grooming returned). Thus, in this model (Model 2) the response was binomial: is grooming reciprocated within the same bout yes or no? To control for dominance rank distance effects (Schino, 2001), we included the absolute nDS difference as a fixed control

factor. Second, to assess whether the dyadic CSI affected the GSI within a grooming bout we ran an LMM (Model 3; Baayen, 2008) with GSI as the response, CSI score as the predictor and nDS difference as the fixed effect. In models 2 and 3, actor and receiver identity, dyad, observation periods and group were included as random factors to control for nonindependence of repeated measures across the same individuals within the same periods. We were unable to run an LMM to investigate whether CSI and rank differences affect grooming symmetry across bouts as the assumption of normality of residual distribution and homogeneous residuals were not fulfilled (Quinn & Keough, 2002).

We built a fourth LMM (Model 4) with the HI as a response and the dyadic CSI and nDS difference as predictors; actor, receiver, dyad, group and observation period were included as random factors to control for nonindependent repeated measures across the same individuals within the same periods in the same group. The predictors in all models were z-transformed and the response log transformed to achieve a normal distribution. All models were run in R (version 3.0.2, R Core Team, 2013) using the function 'lmer' of the R package 'lme4' (Bates, Mächler, Bolker, & Walker, 2015). For model validation we checked that the assumption of normality of residual distribution and homogeneous residuals were fulfilled by visually inspecting scatter plots of the residuals plotted against the fitted values and a qq-plot (Quinn & Keough, 2002). We checked for the stability of each model by excluding data points one by one from the data and comparing the estimates derived with those obtained for the full model (Quinn & Keough, 2002). We present the outcome of the models run with the full data set.

For each model we first determined the significance of the full model against a null model comprising only the random factors and the intercept. All three models were significant (see Results). We then derived the *P* value for each predictor in each model using the R function 'drop1' (Barr, Levy, Scheepers, & Tily, 2013). Variance inflation factors were calculated for each predictor by using the function 'vif' of the R package car (Fox & Weisberg, 2010). VIF values below five indicate that collinearity between the predictors is not a problem (Bowerman & O'Connell, 1990). In all our models VIFs were below 2.2.

Stability of Affiliative Relationships

To assess the overall stability of male social relationships over time, we compared the CSI scores per dyad between observation periods using Kendall's tau row-wise matrix correlations computed in MatMan 1.1.4. (De Vries, Netto, & Hanegraaf, 1993) with 10 000 permutations. Each period was compared to the following period and the first to the last. Within the analysis the average Kendall's tau of adjacent periods was calculated based only on CSI values of dyads that were present in both periods, meaning dyads that were only present in one of the respective periods were not considered in this matrix correlation. To specifically test whether relationship stability differed between stronger and weaker affiliative relationships we used the partner stability index (PSI; Silk, Alberts, et al., 2006) for all males present for at least two observation periods as follows:

$$\text{PSI} = \left(\frac{ns - u}{ns - s} \right)$$

where *n* is the number of periods the individual was present in the group, *s* is the number of top partners considered and thus always equals three in our analyses and *u* is the number of unique partners, i.e. different males that were among the individual's top three affiliation partners ordered by their CSI values across periods. Male partners had to be present continuously; no gap between periods was allowed. For a male that always had the same top three

partners across periods the PSI equals one. If a male changed all its top three partners between periods the PSI equals zero. We determined whether male partner choice was stable over time, by comparing observed PSIs to expected PSI values based on random partner choice. The top three partners were randomly chosen 10 000 times from all males residing in the group and PSIs were calculated for each permutation (Silk et al., 2012) using Microsoft Excel 2010. Partner stability was considered different from random when the observed PSI score of a given male was higher than 95% of all the simulated PSI values. To test specifically whether the strength of affiliative bonds affected their stability we used a matched-sample test comparing across males an individual's PSI for his top three affiliation partners with the PSI for his weaker partners ranking fourth to sixth in affiliation strength. In addition, we ran a Pearson correlation of male partner stability and the sum of the CSI values of a male's top three partners. We only included males that were resident in the group for at least 3 years.

RESULTS

The number of coresident male dyads in the same group varied across observation periods between 21 and 66 (mean ± SE = 45.2 ± 5.3) due to male maturation, immigration, emigration and death.

Variation in the Strength of Affiliative Relationships

For a general description of relationship differentiation we computed one composite sociality index (CSI) for each coresident dyad in each group across all years (*N* = 407 dyads). The distribution of these scores provides a measure of how evenly male affiliative behaviour was distributed across same-sex dyads. This distribution was strongly right-skewed which indicates highly differentiated social relationships between males (Fig. 1). Most dyads formed weak affiliative relationships i.e. they had below average rates and durations of affiliative interactions. One-third of dyads (34%, *N* = 138) exhibited above average CSI values indicating strong affiliative relationships. The top 10% (*N* = 41) of values were above 2.34. The percentage of CSI values above 1 was 34% on average across all periods with a range between 21% and 44%.

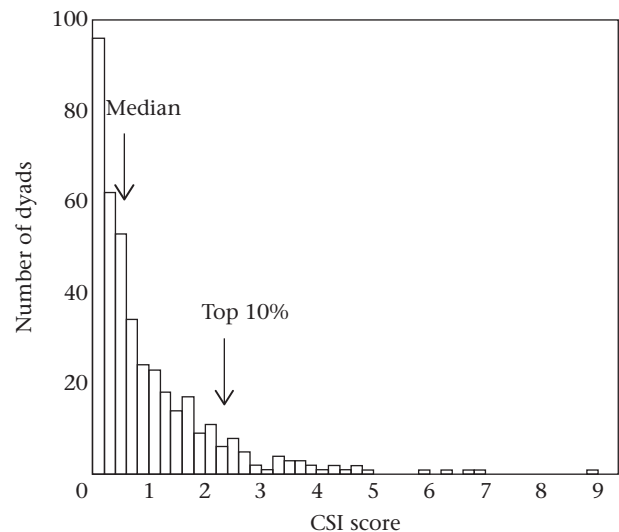


Figure 1. Distribution of the strength of dyadic male–male affiliative social relationships measured as the composite sociality index (CSI). Data from both groups are pooled and one value is included for each coresident dyad across the entire study period (mean = 1, median = 0.56, range 0–8.83).

Since the CSI is a dimensionless index we provide here some descriptive statistics of its components. Each male featured on average \pm SE 3.2 ± 0.21 (range 0–8) relationships with CSI values above 1. Male dyads spent on average \pm SD 25 ± 36 s/h ($N = 407$, range 0–263 s) in close proximity. Males sharing a closer than average affiliative relationship ($CSI \geq 1$) spent 52 ± 48 s/h ($N = 138$) in close proximity compared to 10 ± 12 s/h ($N = 269$) in males with a weaker than average relationship ($CSI < 1$). Across all possible male dyads, males spent on average \pm SD 5 ± 13 s/h in body contact ($N = 407$, range 0–113 s) with closely affiliated males spending 13 ± 15 s/h ($N = 138$) and weakly affiliated males spending 2 ± 3 s/h ($N = 269$) in body contact. Finally, dyadic male-male grooming time averaged 7 ± 12 s/h ($N = 407$, range 0–92 s) with closely affiliated males grooming 17 ± 16 s/h ($N = 138$) and weakly affiliated males 2 ± 3 s/h ($N = 269$). All statistical analyses were run on continuous measures of relationship strength.

The dominance rank asymmetry between two males was negatively associated with the strength of their affiliative relationship (Model 1, Table 1). For this analysis we used the CSI score per dyad per period and controlled for potential differences between periods. The full model, with CSI as the response and rank differences as a predictor, was significantly different from the null model with the random factors ($\chi^2 = 17.26$, $P < 0.001$).

Equitability

We observed 1845 grooming interactions (within 1198 grooming bouts) across both groups. Only 58 of 91 possible male dyads in the AO group and 132 of a possible 316 in the AS group engaged in grooming, indicating that male Assamese macaques were selective in their choice of grooming partners. The grooming interactions were directly reciprocated by the partner in only a quarter of all grooming bouts (294 of 1198, 24.62%). We found a significant and positive effect of the CSI score on the likelihood of reciprocating grooming during a given bout ($N = 1198$, Model 2, Table 2), indicating that the stronger the affiliative relationship between two males the more likely reciprocation occurred within a bout. Dominance rank distance did not significantly affect the likelihood of reciprocation (Table 2). The full model (GLMM) of grooming reciprocation was significantly different from the null model with the control variable and the random factors ($\chi^2 = 16.75$, $P < 0.001$).

Across all grooming bouts in which grooming was reciprocated ($N = 294$ bouts, over 190 dyads) the GSI ranged from 0.01 to 0.99 (mean \pm SE = 0.6 ± 0.02). The within-bout GSI was predicted by the

CSI score and the dominance score difference between the partners ($N = 294$, Model 3, Table 3, Fig. 2). The stronger the affiliative relationship between two males, the more balanced was their grooming exchange within a bout. Also, the closer males were in rank the more balanced were their grooming exchanges, independent from the CSI effect (Table 3). Variation inflation factors below 2.2 indicate that covariation between CSI and rank difference did not affect model outcome. The full model (LMM, Model 3) of grooming symmetry was significantly different from the null model ($\chi^2 = 4.11$, $P = 0.043$).

Finally, an LMM (Model 4), examining whether the HI of a dyad was driven by relationship strength and dominance score differences was significantly different from the null model (Table 4). The higher the CSI score of a dyad the more balanced the responsibility for maintaining close spatial proximity was, independent of the effect of rank difference (Table 4).

Stability

At the group level, patterns of affiliation were stable over time. CSI score matrices were correlated with each other from one observation period to the next (all row-wise, average Kendall's taus between 0.38 and 0.74 and all $P < 0.001$) and even from the first period to the last period, 7 years later ($\tau_{rw,ave} = 0.6$, $P < 0.001$; Fig. 3). Residence time of individual males varied between 1 and 7 years due to maturation, death and emigration.

Of 17 adult males, 16 resided for at least two periods in the AS group and were thereby included in the analysis of partner stability. Since we observed the AO group for only 1.5 periods, this group was not included in this part of the analysis. The tendency of males to keep their preferred top three affiliation partners ranked by CSI was significantly higher than expected from random partner choice among all males of the group (Wilcoxon signed-rank test: $V = 130$, $N = 16$, $P < 0.001$). Three-quarters of all males had a PSI score for their top three partners above 0.5. Across all 16 males the mean $PSI \pm SE$ was 0.57 ± 0.05 and ranged between 0 and 0.8 (Fig. 4) in the AS group. Of these 16 males, nine kept at least one of their top three partners across their entire 2–7-year residence time. Half of the males retained two of their top three partners. Partner stability was much lower for weaker partners ranking fourth to sixth in affiliation strength; only 37.5% of the males had a PSI score above 0.5 ($PSI_{ave} \pm SE = 0.41 \pm 0.05$, range 0–0.7, $N = 16$; Fig. 4). Thus, the strength of the affiliative relationship affected their stability. Males had significantly more stable relationships with their top three affiliation partners than with their weaker partners (Wilcoxon signed-rank test: $V = 65$, $N = 16$, $P = 0.045$). Differences in PSI between top and weaker partners were not related to male rank (Spearman rho = 0.08, $N = 16$, $P = 0.78$) nor to the number of years a male resided in the study group (Spearman rho = -0.14 , $N = 16$, $P = 0.61$).

In further support of the link between the strength and the stability of affiliative relationships, the PSI and the sum of CSIs for the top three affiliation partners were positively correlated among males from the AS group that were resident for at least three periods (Pearson correlation: $r_9 = 0.68$, $P < 0.05$).

Table 1
Estimates \pm SE, Z and P values for the LMM (Model 1) run to test the effect of rank differences on relationship strength

Predictors	Estimate \pm SE	t	P
Intercept	1.000 \pm 0.087	11.520	<0.001
Rank difference	-0.044 \pm 0.010	-4.369	<0.001

Number of dyads = 407.

Table 2
Estimates \pm SE, Z and P values for the GLMM (Model 2) run to test the effect of affiliative relationship strength and dominance rank asymmetry on the likelihood of grooming reciprocation

Predictors	Estimate \pm SE	Z	P
Intercept	-1.546 \pm 0.56	-2.775775	0.005
CSI	0.518 \pm 0.144	3.587587	<0.001
Rank difference	0.002 \pm 0.115	0.025	0.979

Table 3
The effect of affiliative relationship strength on the symmetry of the grooming relationship between the same males (Model 3, LMM)

Predictors	Estimate \pm SE	t	P
Intercept	0.510 \pm 0.025	20.310	<0.001
CSI	0.041 \pm 0.018	2.288	0.041
Rank difference	-0.044 \pm 0.017	-2.588	0.011

Number of observation bouts = 294.

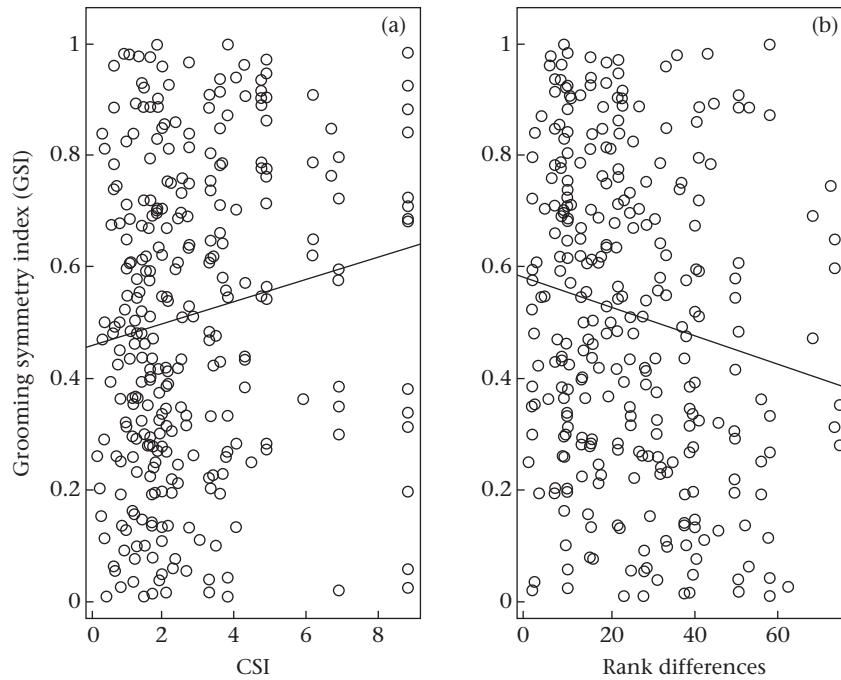


Figure 2. Within-bout grooming symmetry (GSI) as a function of (a) the strength of the partners' affiliative relationship (CSI) and (b) the absolute dominance score difference. The plots show the prediction from the LMM and the raw data of 190 dyads formed by 26 males. On average \pm SD a male had 7.3 ± 3.0 different grooming partners. Meaningful interpretation requires acknowledgment of all significant factors in the LMM.

Table 4
Estimates \pm SE, *t* and *P* values for the LMM (Model 4) run to test whether the CSI and dominance score difference have an impact on the Hinde Index

Predictors	Estimate \pm SE	T	P
Intercept	2.482 \pm 0.035	71.93	<0.001
CSI	-0.072 \pm 0.028	-2.51	0.017
Rank difference	0.058 \pm 0.027	2.13	0.047

Number of observations = 155. Null versus full model: $\chi^2_2 = 12.48, P < 0.002$.

DISCUSSION

Our study provides the first empirical evidence that males, the dispersing sex in Assamese macaques, form social bonds, defined as strong, equitable and long-lasting affiliative relationships. Adult males biased their affiliative behaviour towards a few male partners. The stronger an affiliative relationship between two males was the more likely they reciprocated a grooming act immediately and the more balanced was the grooming exchanged within a grooming bout. Furthermore, the stronger the affiliative relationship was the

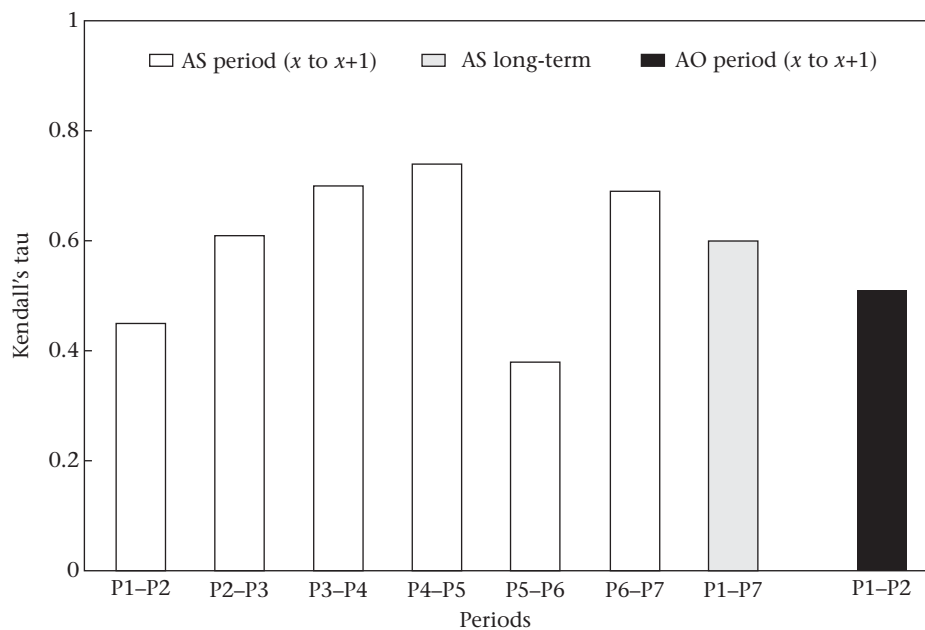


Figure 3. Group-wide patterns of male affiliation across time. Bars are average correlation coefficients from significant row-wise matrix correlations of CSI values comparing consecutive observation periods as well as the first to the last period (grey). The black bar is for the AO group, all others for the AS group.

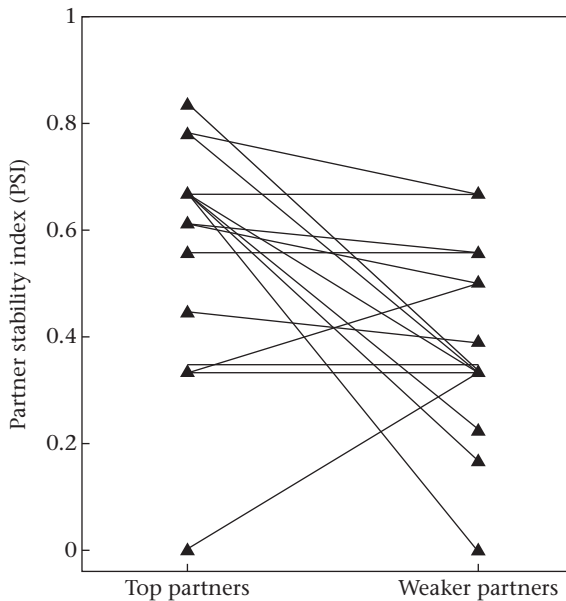


Figure 4. Stability of stronger relationships (top three partners) and weaker ones (partners 4 to 6 ranked by CSI). A triangle displays the PSI values. Each line (total 16) connects the PSI values (first, second and third partner on the left and fourth, fifth and sixth on the right) of one male.

less biased was the responsibility for maintaining close spatial proximity and the more stable was the relationship over time.

The degree of relationship differentiation we found in male Assamese macaques closely resembles that described for philopatric female baboons with the median CSI being close to 0.5 and only one-third of relationships being stronger than the average (Silk, Altmann, et al., 2006; Silk et al., 2010b). In contrast 'it is hard to detect what could be called a 'friendly' relationship in any pair of male baboons' (Noë, 1989, p. 219; cf. Silk, 1994) and males in many other species forming multimale groups either affiliate rarely or in an undifferentiated manner (Ostner & Schülke, 2014; Young, Majolo, Schülke, & Ostner, 2014). Males in our study formed fewer strong and more weak relationships than the female Assamese macaques in the same groups (Macdonald, Schülke, & Ostner, 2014). This is similar to the differences described for dispersing female chimpanzees compared to their more sociable philopatric male group mates (Langergraber, Mitani, & Vigilant, 2009).

As in the philopatric sex of several primates, dominance was an important feature structuring male relationships (Mitani, 2009; Schülke et al., 2013; Silk, Altmann, et al., 2006; Widdig et al., 2001). The stronger affiliative relationships were the closer males were in rank. Our previous work suggests that rank similarity is the consequence rather than the cause of close affiliative relationships; close partners support each other in rank-changing coalitions effectively pulling each other to similar ranks (Schülke et al., 2010). Similarly, female philopatric primates form their strongest relationships with their closest maternal kin which they support in rank acquisition resulting in close affiliation partners occupying adjacent ranks (Chapais, 1992; Lea, Learn, Theus, Altmann, & Alberts, 2014; Silk, Alberts, & Altmann, 2004; Silk, Altmann, et al., 2006). The degree to which kinship structures male Assamese macaque affiliative relationships remains largely unknown, but males sharing mtDNA haplotypes formed strong relationships as often as males with different haplotypes (Schülke et al., 2010). Expectations for the equitability in exchanges between partners in stronger versus weaker affiliative relationships can go both ways (Massen, Sterck & deVos, 2010): either close partners exchange goods and services more equitably (Silk, Alberts, et al., 2006) or close relationships could

withstand more short-term inequality (Silk, 2002; Surbeck & Hohmann, 2015). If the properties of males' social relationships reflect their tendency to participate in coalitions, as well as the roles that they play in those coalitions (Silk, 1994), grooming relationships may reflect the partners' willingness to reciprocate aid. In wild Barbary macaques, *Macaca sylvanus*, for example, the closer the affiliative relationships between males the more equitable their grooming exchanges and the less likely it is that a partner ignores the other's recruitment for agonistic support in an ongoing conflict with another male (Young, Majolo, Schülke, et al., 2014). In the present study grooming equitability was also related positively to the similarity of the partners' dominance ranks. The fact that relationship strength and rank difference had independent effects may result from grooming having different functions in different dyadic relationships. For partners with a strong affiliative relationship grooming may function to strengthen and maintain their bonds whereas it may be traded for other commodities (e.g. tolerance or reduced aggression, Fairbanks, 1980; Silk, 1982) in less closely bonded ones. The view that not all grooming serves the same function is supported by observations in chimpanzees in which grooming with a close partner is associated with increased peripheral oxytocin levels, while oxytocin levels remain unchanged when two nonbonded individuals engage in the exact same grooming interaction (Crockford et al., 2013).

Furthermore, we found the affiliative relationships of male Assamese macaques to be rather stable. Half of the males retained two of three partners among their top three closest relationships throughout their residence time of up to 7 years. More specifically, the proportion of partners that was retained was higher for the three closest partners than for weaker relationships. This latter finding suggests that stability in top partner choice did not result directly from constrained partner availability due to small male group size. Interestingly, these findings mimic the situation in philopatric female baboons and male chimpanzees which is surprising because male Assamese macaques show natal and secondary dispersal (Ostner & Schülke, n. d.). Relationship stability is a crucial characteristic of social bonds if social bonds evolved for alliances in competition for social status (Ostner & Schülke, 2014). If male coalitions evolved for their function in rank attainment instead of more directly levelling the mating skew (van Schaik, Pandit, & Vogel, 2006), coalitionary partner choice requires a certain level of stability. After rank changes caused by coalitions within a group, more powerful males may come to rank below physically weaker but cooperative males. These situations are potentially very risky but can be managed if successful coalition partners maintain their relationship over time and defend their social status via defensive/conservative coalitions (Ostner & Schülke, 2014; Young, Schülke, & Ostner, 2014).

Together, our results show that male Assamese macaques form social bonds with a few coresident males which serve as reliable partners in cooperative attainment and maintenance of social status. Several lines of evidence suggest that social bonds are represented in nonhuman primates and variation in affiliation is not always simply the consequence of repeated identical partner choices in small groups. In many primates the probability that former opponents reconcile after a conflict is increased for closely bonded partners (Aureli et al., 2012), males base their coalition partner choice on relationships established in the past (Berghänel, Ostner, Schröder, & Schülke, 2011), individuals modulate their loud calls in reaction to the presence of bonded partners (Micheletta & Waller, 2012), females react with elevated glucocorticoid levels to the death of a partner compared to a nonbonded individual (Engh et al., 2006), and the stronger a male's social bonds the stronger the buffering effects they provide against increasingly strong stressors (Young, Majolo, Heistermann, et al., 2014). Thus, we may be dealing

with a phenomenon that is very similar to human friendships (Silk, 2002), which are also characterized by variation in relationship strength, equitability and stability (Allen-Arave, Gurven, & Hill, 2008; Gurven, 2006) and which may have evolved as within-group alliances (DeScioli & Kurzban, 2009). Future research is needed on relationship characteristics in nonprimate species to assess the generality of the phenomenon that animals establish relationships equivalent to human friendships.

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Appendix

Table A1

Total and average observation hours per period

Group_Period	Observation hours per period (mean±SD)
AS_P1	393 (35.67±4.19)
AS_P2	950 (86.36±16.37)
AS_P3	1816 (129.73±50.72)
AS_P4	779 (86.56±18.98)
AS_P5	887 (98.51±14.35)
AS_P6	1184 (118.40±45.04)
AS_P7	892 (127.43±5.06)
AO_P1	350 (38.91±14.54)
AO_P2	1397 (127±48.48)

Table A2

Total and average observation hours per male

Group	Male ID	Total no. of observation hours per male (mean±SD)	Residence time (years)
AS	mx08	782 (111.75±44.78)	7
AS	mx09	504 (126.03±34.94)	4
AS	mx10	672 (95.92±39.47)	7
AS	ms07	126	1
AS	mx11	628 (89.68±36.58)	7
AS	mx01	177 (59±39.77)	4
AS	mx12	396.18 (99.04±11)	3
AS	mx03	235 (78.44±31.06)	5
AS	mx13	652 (130.31±32.45)	4
AS	mx04	387 (96.67±66.66)	4
AS	mx14	772 (110.30±44.35)	7
AS	mx15	228 (75.83±37.30)	3
AS	mx05	143 (47.56±30.58)	3
AS	mx06	322 (47.56±74.74)	3
AS	mx20	134 (66.97±29.75)	2
AS	mx17	709 (101.27±43.39)	7
AS	mx07	143 (71.5±39.83)	2
AO	mx01	11.25	1
AO	ms09	123	1
AO	mx03	197 (98.45±92.78)	1.5
AO	mx22	133 (66.71±59.67)	1.5
AO	ms11	86 (43.14±40.76)	1.5
AO	mx27	149 (74.37±66.75)	1.5
AO	mx31	204 (101.85±73.73)	1.5
AO	mx26	208 (104.1±71.11)	1.5
AO	mx23	219 (109.45±77.85)	1.5
AO	mx24	214 (107.2±83.58)	1.5
AO	mx25	202 (101.13±79.01)	1.5

Table A3

Characteristics of male dominance hierarchies used in this study

Group	Period	No. of males	No. of conflicts	h'	Unknown relationships (%)	DC	Two-way relationships (%)	Ties (%)
AS	1	12	247	0.83	13.6	0.96	6.1	1.5
AS	2	12	361	0.82	12.1	0.93	13.6	0.0
AS	3	11	357	0.94	3.6	0.81	29.1	1.8
AS	4	9	240	0.87	13.9	0.94	13.9	2.8
AS	5	9	164	0.86	8.3	0.92	13.9	2.8
AS	6	9	191	0.97	2.8	0.90	13.9	0.0
AS	7	7	165	1.0	0.0	0.95	14.3	0.0
AO	1+2	11	292	0.9	10.9	0.99	1.8	1.8

Periods 1 and 2 of the AO group were combined, h' = corrected Landau's linearity index, DC = Directional Consistency Index.