Report

Social Bonds Enhance Reproductive Success in Male Macaques

Oliver Schülke,[1,2,*] Jyotsna Bhagavatula,[2,3] Linda Vigilant,[3] and Julia Ostner[1,2]
[1]Courant Research Centre Evolution of Social Behaviour, Georg August University, Göttingen, 37077 Göttingen, Germany
[2]Integrative Primate Socio-Ecology Group
[3]Department of Primatology
Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

Summary

For animals living in mixed-sex social groups, females who form strong social bonds with other females live longer and have higher offspring survival [1–3]. These bonds are highly nepotistic, but sometimes strong bonds may also occur between unrelated females if kin are rare [2, 3] and even among postdispersal unrelated females in chimpanzees and horses [4, 5]. Because of fundamental differences between the resources that limit reproductive success in females (food and safety) and males (fertilizations), it has been predicted that bonding among males should be rare and found only for kin and among philopatric males [6] like chimpanzees [7–9]. We studied social bonds among dispersing male Assamese macaques (*Macaca assamensis*) to see whether males in multimale groups form differentiated social bonds and whether and how males derive fitness benefits from close bonds. We found that strong bonds were linked to coalition formation, which in turn predicted future social dominance, which influenced paternity success. The strength of males' social bonds was directly linked to the number of offspring they sired. Our results show that differentiated social relationships exert an important influence on the breeding success of both sexes that transcends contrasts in relatedness.

Results

We used data from wild male Assamese macaques at Phu Khieo Wildlife Sanctuary in Thailand collected over a 2 year period (subdivided into three consecutive study periods based on changes in male dominance hierarchy; see Experimental Procedures) to investigate how sociality influences coalition formation, how coalition formation affects future dominance status, and how status is related to paternity. Males formed strongly differentiated social relationships with other males (see Supplemental Experimental Procedures). Close bonds were not confined to potential kin. Across dyads, the strength of social bonds (composite sociality index, CSI [2], based on association and grooming frequencies) was not predicted by mitochondrial DNA sequence identity in any of the three study periods (Spearman's row-wise matrix correlations period 1: 12 males, $R_r = -755$, $r_{rw, av} = -0.10$, $p = 0.81$; period 2: 12 males, $R_r = -600$, $r_{rw, av} = -0.08$, $p = 0.72$; period 3: 11 males,

$R_r = 526.5$, $r_{rw, av} = 0.12$, $p = 0.22$). More than half of the top three social bonds per male (59%, 62%, 54% in periods 1–3) involved males with dissimilar haplotypes who must represent maternally unrelated males.

Social partner preferences were linked to contest for social status within the group. Males frequently formed agonistic coalitions ([10], 0.11/hr) in which joint aggression is displayed by two or more males against a common male target. The stronger the bond between two males, the more often they cooperated in conflicts (Spearman's row-wise matrix correlation period 1: $R_r = 4941.8$, $rho_{rw, av} = 0.43$, $p = 0.001$; period 2: $R_r = 2777.5$, $rho_{rw, av} = 0.49$, $p = 0.0005$; period 3: $R_r = 224.5$, $rho_{rw, av} = 0.35$, $p = 0.015$). If the adaptive function of coalition formation is to increase and maintain both allies' social dominance, then coalition formation should be linked to dominance in the future. Accordingly, the total number of coalitions a male formed was related to his future dominance success measured by the normalized David's score [11] (nDS), a continuous measure of dominance (Pearson correlation of coalitions period 1 and nDS period 2: $r = 0.69$, $n = 12$, $p = 0.019$; coalitions period 2 and nDS period 3: $r = 0.58$, $n = 11$, $p = 0.059$). Predictability increased with increasing time depth (coalitions period 1 and nDS period 3: $r = 0.73$, $n = 11$, $p = 0.011$). Our analyses suggest that any coalition provides benefits to both partners, i.e., dominants also benefit from cooperating with or supporting subordinates.

The quality of a male's social relationships, measured as the combined strength of his top three social bonds, is directly linked to his future dominance success (CSI period 1 and nDS period 2: $r = 0.60$, $n = 12$, $p = 0.036$; CSI period 2 and nDS period 3: $r = 0.72$, $n = 11$, $p = 0.013$; CSI period 1 and nDS period 3: $r = 0.75$, $n = 11$, $p = 0.007$; Figure 1), but not to his current dominance success (within period 1: $r = 0.51$, $n = 12$, $p = 0.16$; period 2: $r = 0.54$, $n = 12$, $p = 0.087$; period 3: $r = 0.31$, $n = 12$, $p = 0.35$). Moreover, the reverse correlations, i.e., between current dominance success and future social bonds, were also not significant (Pearson correlation nDS period 1 and CSI period 2: $r = 0.31$, $n = 12$, $p = 0.34$; nDS period 1 and CSI period 3: $r = 0.009$, $n = 11$, $p = 0.98$; nDS period 2 and CSI period 3: $r = 0.13$, $n = 11$, $p = 0.71$), which collectively suggests a causal link between sociality and dominance, and not vice versa. We focused on the cumulative strength of the top three closest bonds per male in order to keep the number of bonds constant and evaluate the influence of their strength instead (following research on bonding in females [1, 2]). But we also found that our results remained unchanged if strength of all bonds, instead of the top three bonds, was used to predict future status (data not shown).

In order to further investigate the dynamics underlying male social bonding, we extended our analysis to include a fourth period (the nonmating season following period 3) for which data on ordinal ranks were available (top rank = 1). When individual sociality changed, future dominance rank did not change randomly but followed similar trajectories in most individuals. Specifically, the distribution of individual correlation coefficients between sociality and future ordinal rank was significantly different from a normal distribution
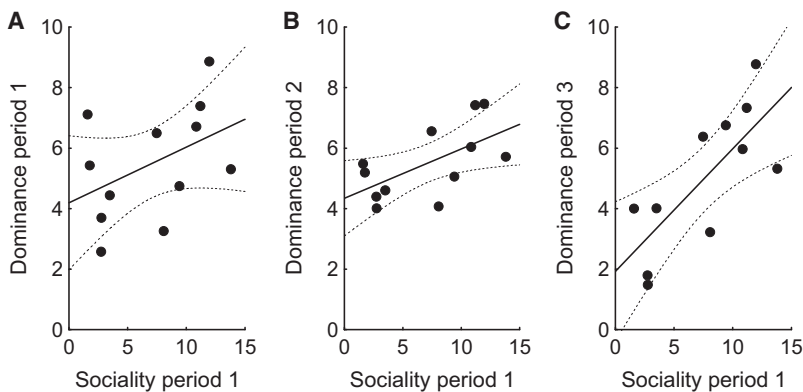
*Correspondence: oschuel@gwdg.de

Figure 1. Link between Sociality and Dominance Success

(A–C) Sociality, measured as the cumulative strength of the top three closest bonds of a male, predicts future (B and C) but not current (A) dominance success. The pattern did not result from all high-ranking males being more social than low-ranking ones, as was predicted by older models on grooming distribution in primates [19]. For most males, increases in sociality were associated with increased future status, and vice versa. These trajectories were not easily explained by changes in male age. Males with strong bonds increased their dominance success or maintained high status, whereas high-ranking males that failed to bond dropped in rank or stayed at the bottom of the hierarchy (see Results for statistical results).

(Shapiro-Wilks test: W = 0.75, n = 7, p = 0.012), with a large negative median correlation coefficient at −0.84 (interquartile range: −0.99 to 0.03) indicating that males that became less sociable fell in rank and that males that became more sociable over time rose in rank. The sociality-rank trajectories were not age related. Age-rank relationships of males in nonprovisioned primate groups usually follow a bell curve [12, 13]. Age in period 1 did not predict future dominance (correlation with dominance period 3 polynomial fit: r = −0.47, n = 11, p = 0.15; dominance period 4 polynomal fit: r = −0.07, n = 11, p = 0.87). Males of the same age were as much as six and eight ranks apart in period 4, because some had risen to the top while some stayed at the very bottom of the hierarchy, indicating that males follow different routes as they age. Thus, for male macaques, strong social bonds predict high future social status, irrespective of age.

As the last step in our chain of evidence, we analyzed two years of paternity data and found that males of high ordinal dominance rank enjoy higher reproductive success (Spearman's rho = −0.85, n = 12 ranks, p = 0.0006; 12 infants sired in periods 1 and 3). More directly, we can show that the strength of male social bonds (in period 1) predicts the number of offspring sired in the subsequent mating season (period 3), when the benefits of bonding are manifest (Spearman's rho = 0.76, n = 11 males, p = 0.0102; five infants, Figure 2).

Discussion

Our highly consistent results linking a series of predicted relationships through several study periods suggest that the adaptive function of close male bonds arises from cooperation in competition for social status [14], which in turn determines reproductive success. Bonding provided benefits to both partners—dominant and subordinate—which may explain why males invest in affiliative relationships despite living in a society with strict dominance rank relationships [10] in which dominant males enjoy priority of access to the nonsharable resource of fertilizations [15]. As a case in point, the third-ranking male at the beginning of the study was one of the largest males in the group and was in excellent physical condition. However, he failed to form strong bonds with other males, participated in few coalitions, and subsequently dropped to rank 6 in period 2 and rank 8 in period 3. High-ranking males that invested in social bonds and formed coalitions—often with mid- or low-ranking individuals—maintained their high status. Hence, irrespective of rank, both partners may

inevitably benefit from forming social bonds and cooperating in coalitions [15].

Our results linking paternity success to participation in coalitions and alliances corroborate earlier findings on lions, horses, birds, and dolphins [16–20]. The situation in male Assamese macaques resembles that of female primates, including humans, in that they (1) base their partner choice on differentiated social bonds, (2) cooperate with only a few coresidents against other coresidents, and (3) live in closed groups, i.e., individuals cannot easily change from one group to another but usually stay in the same group for several years. In the cases in which an adaptive value of differentiated social bonds has been demonstrated, female primates bias their behavior toward kin [1–3]. Here we demonstrate for the first time a causal link between differentiated social bonds and fitness (1) in males and (2) in the absence of a strong kin bias. The existence of differentiated social bonds among both unrelated male and female chimpanzees [5, 9], together with our findings, suggests that the universal human tendency to engage in close social bonds may have evolutionary origins outside the context of the extended family.

Despite the similarities of male and female bonding behavior, the mechanisms that promoted the evolution of strong bonds seem to be fundamentally different. Female bonding is thought to promote the formation of agonistic alliances that increase an individual's access to limiting resources, thus immediately and directly increasing energy gain rates independent of dominance rank [21]. Rather than food, males compete over an even scarcer and ultimately indivisible resource, fertilizations. Our results suggest that bonding serves a political function in male Assamese macaque society, because males try to enhance their own status relative to that of others by manipulating social relationships [22] outside the context of mating competition. Thus, in large multimale primate groups, such political strategizing may be more important in the social lives of males than females.

Experimental Procedures

Study Site and Data Collection

The study was carried out at Huai Mai Sot Yai in the 1573 km^2 Phu Khieo Wildlife Sanctuary (16°05-35'N and 101°20-55'E) in Thailand [23, 24]. The main study period (October 2006–January 2008), comprising two mating seasons, was subdivided into three consecutive periods according to changes in the male dominance hierarchy. For a fourth period (February–May 2008), data on ordinal ranks were available. Data were collected in 20 or 30 min focal animal protocols on large males [10] using continuous
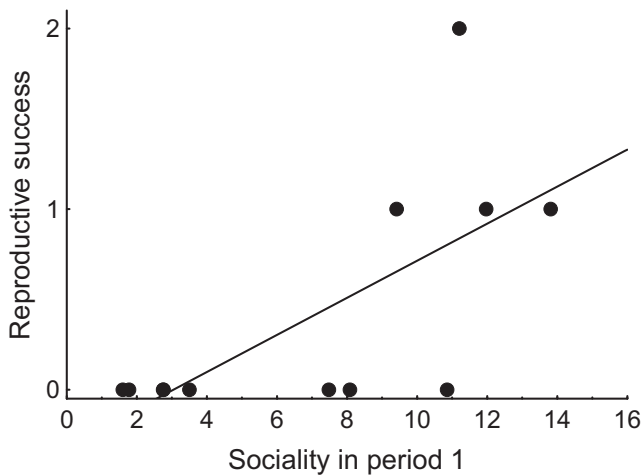
Figure 2. Male Sociality Predicts Reproductive Success
Each male formed strong bonds with only 3 of the 10 or 11 coresidents on average. The strength of the top three bonds predicted fitness outcomes (number of infants sired) that were measured in the subsequent mating season, when the effect of strong bonds on social status is manifest. The relationship remained significant when the three least-social males that did not sire offspring were excluded (n = 8 males, Spearman's rho = 0.72, p < 0.05).

recording of all social and approach-depart interactions into and from 1.5 m of the focal animal (1218 hr, 106.1 ± 5.5 standard deviation hours per male, excluding one male that emigrated during the study), as well as by ad libitum sampling of agonism [25]. Fecal samples for genetic analyses were collected opportunistically from all members of the habituated study group during behavioral observation (≥3 samples per individual) and opportunistically from other nonhabituated Assamese macaque groups. Preserved samples [26] were transported back to the laboratory, and genomic DNA was extracted from 0.1 g of fecal sample using a modified version [26] of the protocol provided with QIAamp DNA Stool Kit (QIAGEN) from 10–16 samples at a time. Blanks were included during extraction to monitor for contamination. Dominance success was measured from asymmetries in the exchange of subordination signals in dyadic conflicts among males using the corrected nDS, with high values indicating high dominance status [10, 11]. The CSI relates association (in less than 1.5 m) and grooming frequencies of two individuals to the averages across all dyads [2]. Age was estimated from body size and shape, dental morphology, skin condition, and testicular development. All statistical tests are two-tailed, with the alpha level set at 0.05 in Statistica 8 and MatMan 1.1.

Paternity Analyses
Genotyping reactions were carried out using the two-step multiplex polymerase chain reaction (PCR) protocol [27]. Primers were fluorescently labeled on the 5′ ends. We ran PCR products on an ABI 3100 genetic analyzer (Applied Biosystems) and used Genemapper (version 3.7) software to compare product sizes relative to the ROX HD400 internal size standard. DNA extracts were genotyped at the loci D5s1457, D10s676, D18s536, D3s1768, D1s1656, D9s910, D3s1766, D2s1768, D2s1363, D1s1675, D8s1106, D9s934, D6s1056, D17s804, D2s1326, and D14s306. Sex of individuals was confirmed or determined using a PCR-based sexing assay [28].

DNA concentration of the extracts was estimated using a real-time PCR assay [29]. A locus was accepted as heterozygous only if each allele occurred at least two times in independent PCR reactions. Using results from loci determined to be heterozygous, we estimated that the number of PCR replicates required to determine with >99% certainty that a given allele is homozygous and not a result of allelic dropout was 3 for extracts with ≤25 pg/μl of DNA and 2 for extracts with ≥26 pg/μl of DNA. Conservatively, we accepted a locus as homozygous only if the allele occurred independently at least four times in PCR reactions with DNA quantities ≤25 pg/μl or if it occurred independently at least three times for samples with ≥50 pg/μl.

Individual identities of the samples were confirmed by comparing the genotypes of known mother-and-offspring pairs. In addition, we genotyped

two or more independent DNA extracts, wherever available, from each identified individual in order to confirm the identity of the animals (∼1.9 samples/animal). Because several samples were also collected from nonhabituated groups comprised of unknown individuals, Cervus 3.0.3 [30] was used for a pairwise comparison of multilocus genotypes to identify unique genotypes that matched with one another across the loci genotyped. Genotypes matching exactly at six or more loci were combined into a consensus genotype.

Genotypes of potential fathers (n = 21) from within and outside of the group (including samples typed as male from the unhabituated groups) were used in paternity analyses. All mother-offspring pairs known from behavioral observation were confirmed to share an allele at each locus. We then used the likelihood method as implemented in Cervus 3.0.3 to identify the two most likely fathers (1% error rate, minimum number of loci typed 9, 21 candidate fathers, proportion of loci typed 0.86, proportion of candidate fathers sampled 0.7).

Genotypes were generated at a minimum of 7 loci and a maximum of 15 loci from 144 individuals (mean completion 81%). Using Cervus, we found that the mean number of alleles per locus was 7.2, mean polymorphism information content was 0.66, mean expected heterozygosity across all 15 loci was 0.71, and average observed heterozygosity was 0.72. Loci D2s1363 and D8s1056 depart from Hardy-Weinberg equilibrium, which is attributable to the presence of close relatives in the study group.

The individual probability of identity was 5.59×10^{-15}, and the sibling probability of identity $P(ID)sib$ is 2.53×10^{-6}, indicating that the chance of encountering siblings with identical genotypes is also extremely low. The $P(ID)sib$ even for the six least polymorphic loci was 1.57×10^{-2}. But, because we included in our analysis only those samples from which we could genotype a minimum of seven loci, the chance that the genotypes of two random individuals would be identical is infinitesimal. Paternity could be assigned with high positive LOD scores for 12 out of 13 offspring born during the study period.

Spearman rank correlations between reproductive success (i.e., the number of offspring) and either ordinal rank or CSI remained significant if the four or three lowest-ranking or least-social males, respectively, that also did not sire offspring were excluded from analysis (rank and reproductive success: n = 8, rho = −0.82, p < 0.05; CSI period 1 and reproductive success next mating season: n = 8, rho = 0.72, p < 0.05).

Relatedness Analysis
We examined which males were not maternally related using mitochondrial DNA (mtDNA) sequence information. For each of the 12 males in the group, a 470 bp segment of the HVR1 region of the mitochondrial DNA was PCR amplified with primers L15996 and H16498 [31]. PCR products were excised from agarose gel and eluted using the MinElute Gel Extraction Kit (QIAGEN) according to the manufacturer's recommendation. The eluted PCR products were cycle sequenced in both directions, employing the BigDye Terminator version 1.1 Cycle Sequencing Kit (Applied Biosystems), and sequenced on a 3730 DNA Analyzer (Applied Biosystems). Sequences were edited and aligned using BioEdit version 7.0.9.032 [32] and SeaView version 4.2 [33] and subsequently collapsed into haplotypes using FaBox [34].

MtDNA sequences could be obtained for 11 out of the 12 males sequenced. The 443 bp of the HVR1 region showed five variable sites defining two haplotypes found in five and six individuals, respectively. Paternal relatedness was not assayed because of the inaccessibility of the Y chromosome in nonmodel organisms [35], but it was assumed to be low, given the low reproductive skew among males (33% alpha male paternity), moderate female group size (12 females), and moderate interbirth intervals (median 22 months [36]) in our study on dispersing males [37]. From these results, we conclude that males with different haplotypes are maternally unrelated. Males bearing identical haplotypes may have a recent common ancestor, or relatedness may not exceed population baseline levels. Thus, the class of potentially related male-male dyads may include more unrelated males.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2010.10.058.

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