Title

Female macaques compete for ‘power’ and ‘commitment’ in their male partners

Abstract

The formation of male-female social bonds and the resulting competition among females for male partners is a core element of human societies. While female competition for a male partner *outside* the mating context is well studied in humans, evidence from non-human primates is scarce, and its evolutionary roots remain to be explored. We studied two multi male – multi female groups of wild Assamese macaques (*Macaca assamensis*), a species where females gain benefits from selectively affiliating with particular males. Using a behavioral data set collected over several years, we tested whether females competed over access to male social partners, whether success in competition was driven by female dominance rank, and which male traits were most attractive for females. We found assortative bonding by dominance rank between females and males, which together with females initiating and maintaining contact suggests direct female competition over males. Two male traits independently predicted male attractiveness to females: (1) current dominance rank, a measure of “power” or a male’s ability to provide access to resources, and (2) prior male affiliation with immatures, a measure of a male’s potential paternal proclivity or “commitment” to infant care. Both traits have been consistently identified as drivers of female partner choice in humans. Our study adds to the evidence that female competition for valuable male partners is not unique to humans, suggesting deep evolutionary origins of women’s mate choice tendencies for ‘power’ and ‘commitment’.

Keywords

Female competition, assortative bonding, male traits, dominance rank, male care, human pair bond

1 Introduction

The formation of male-female bonds is a core element of human societies (Alexander & Noonan, 1979; Chapais, 2008). Male provisioning of females during energetically demanding phases (e.g. gestation, lactation), the development of paternal care, and the division of labor are all implicated in the evolution of the human pair bond (Alexander & Noonan, 1979; Hawkes, 2004; Lovejoy, 1981; Marlowe, 2000; Quinlan & Quinlan, 2007, 2008). The precise evolutionary pathways and causal relationships between these factors are still being debated, but there is broad agreement that they have favored the evolution of large brains, elaborate cognitive abilities, and the unparalleled ecological success of humans (Kaplan et al., 2000, 2009; Chapais, 2013; Coxworth et al., 2015; Fletcher et al., 2015). If male behavioral traits (e.g. provisioning, paternal care) enhance offspring fitness, females should choose males based on these traits to increase their reproductive success. If males that feature desirable traits are scarce, females should compete for valuable male partners (Slagsvold & Lifjeld, 1994; Stockley & Campbell, 2013).

Sexual selection theory was long interpreted in terms of female mammals predominately competing for resources pertinent to nutrition and survival, and males primarily competing for access to female mating partners (Clutton-Brock, 1989; Clutton-Brock & Harvey, 1978; Emlen & Oring, 1977; Tobias, et al., 2012; Trivers, 1972). Whereas evidence for female competition over access to mating partners is accumulating (Baniel et al., 2018a, 2018b; Bro-Jørgensen, 2002; Buss, 1988; Rosvall, 2011; Stockley & Bro-Jørgensen, 2011; Stockley & Campbell, 2013), less is known about female competition for male long-term bond partners based on resources or 'services' males may provide.

Reproductive success in female mammals is constrained primarily by the availability of energy resources to sustain the high energetic demands of gestation and lactation (Bongaarts, 1980; Sadleir, 1969; Schneider, 2004), and by individual differences in infant mortality (Clutton-Brock, 1988). Consequently, females compete directly for food and other resources related to reproductive performance, such as nest sites (Emlen & Oring, 1977; Pusey & Schroepfer-Walker, 2013; Stockley &

Bro-Jørgensen, 2011; van Schaik, 1989; Wrangham, 1980). If males provide resources to females that vary in quantity or quality (access to food: Haunhorst et al., 2017; protection against infanticide: Baniel et al., 2018a; Engh et al., 2006; Hawkes, 2004; Opie et al., 2013; Palombit, 2009; Paul et al., 2000; van Schaik & Kappeler, 1997), bonding with particular males could be an indirect manifestation of resource competition (Campbell, 2004; Emlen & Oring, 1977; Stockley & Bro-Jørgensen, 2011). In this case, females should select males based on their quality.

The competitive superiority of higher-ranking males improves their ability to successfully enhance access to energy resources (Hamilton & Bulger, 1990; Watts, 2010). Competitive ability will also determine the ability to protect offspring against conspecifics, but a male's propensity to provide such support may vary independently, or may even be inversely related (Huchard et al., 2013). Thus, females may increase their reproductive success primarily by bonding with high-ranking males or males that have provided infant care in the past (Fernández-Duque, Valeggia, & Mendoza, 2009). This pattern observed in nonhuman primates is mirrored in human female mate choice with women being attracted to (among other traits) high status males and males perceived high in their affinity to infants (Buss & Shackelford, 2008; Rooney et al., 2006). Consequently, women compete for men that exhibit 'power', i.e. high social status, and access to valuable resources, and 'commitment', i.e. loyalty towards women and her children (Campbell, 2004), thus, a man's ability to invest and his proclivity for parenting (Buss & Shackelford, 2008).

Relevant comparative data on female competition over male social partners mainly come from different species of baboons. In hamadryas baboons (*Papio hamadryas*) that live in one-male units, female-male grooming time is a function of female dominance rank suggestive of female competition for access to the leader male (Colmenares et al., 2002). By frequent grooming, females reduce the threat of aggression from the leader male, enhance their access to resources, and gain protection against harassment by other group members (Colmenares et al., 2002). In chacma baboon (*Papio ursinus*) multi-male multi-female groups, females compete for access to the most likely sire of their offspring, who provides protection from potentially infanticidal males (Palombit et al., 2001), and these male-female relationships break up upon the infant´s death (Palombit et al., 1997). Consistent with female competition over males, aggression among lactating females peaks in periods of social instability when risk of infanticide is highest (Baniel et al., 2018a) and may lead to reproductive suppression in estrus females (Baniel et al., 2018b). Only a few other studies identified female competition for males outside the mating context in non-human primates (Archie et al., 2014; Lemasson et al., 2008; Smuts, 1985). In order to complement the comparative data set, we tested whether Assamese macaque females compete for access to male social partners, and which male qualities they compete over.

Female Assamese macaques exhibit concealed ovulation and no reliable sexual signals of fertility (Fürtbauer et al., 2011). Consequently, and in contrast to baboons, paternity concentration in the alpha male is low (29%) and, despite being rank-related, paternity is distributed across a number of different males in the group (Sukmak et al., 2014). Assamese macaques form stable opposite-sex social bonds which are not equally distributed across all males (Haunhorst et al., 2016) and, despite a promiscuous mating system (Fürtbauer et al., 2011a), may last across reproductive seasons and throughout several years (Haunhorst et al., 2016; Ostner et al., 2013). Males of all dominance ranks can be top social partners of more than one female (Haunhorst et al., 2016) and derive direct benefits in form of increased mating success from associating with a specific female ('friends with benefits hypothesis', Ostner et al., 2013). Male-female association in the mating season predicts future male-infant association which, in turn, predicts male agonistic support for the respective infant (Minge et al., 2016; Ostner et al., 2013), indicating a certain degree of male care. Infanticide has been directly observed (Kalbitz, Ostner, Schülke, unpubl.), yet the risk from within the group is low given that ovulation is concealed from males and females mate synchronously (Fürtbauer et al., 2011a, 2011b). In addition to male care for their offspring, females directly benefit from bonding with a male through male agonistic support and increased food intake rates in the male's presence (Haunhorst et al., 2017). Above and beyond the preferential agonistic support for closely bonded female partners, the frequency of male support is predicted by male dominance rank (Haunhorst et al., 2017). Hence, based on the strength of opposite-sex dyadic affiliative relationships male Assamese macaques provide resources for females that may enhance a female´s reproductive success. Females with higher rates of affiliation with males during the mating season have reduced glucocorticoid metabolite levels pointing towards beneficial effects of male-female affiliation in this species (Fürtbauer et al., 2014).

With this study, we do not propagate Assamese macaque as a model for hominin evolution. Instead, we aim to draw attention to a specific combination of reproductive and social traits observed in some primate species, including Assamese macaques, that is shared with humans (Alexander & Noonan, 1979; Marlowe & Berbesque, 2012) and may be the historical basis for the human pair bond and thus should be of high relevance to the study of human social evolution. These traits include large group sizes or dispersed females combined with concealed ovulation making it difficult for males to monopolize several females, and thus leading to alternative male reproductive tactics such as male-female social bonds embedded within multi male – multi female social groups (van Schaik, 2016). Here, we first confirmed the occurrence of competition for male partners and then tested three predictions regarding female competition for males in this system. Since dominance hierarchy is a predictor for access to resources (or access to male partners, e.g.: Colmenares et al., 2002; Palombit et al., 2001), female dominance rank should predict relationship strength to high ranking males, leading to rank-based assortative bonding (prediction 1). For females who share the same top partner (i.e. a 'competitive situation'), the strength of their affiliative relationships to the male should be correlated with the females' dominance rank (prediction 2). Finally, we predicted the strength of a male's affiliative relationships with females to increase with (i) his dominance rank, i.e. "power", and thus his ability to provide resources, and (ii) his time spent affiliating with immatures in the preceding six months, i.e. "commitment" (prediction 3).

2 Methods

2.1 Study site and population

We conducted our study in Phu Khieo Wildlife Sanctuary (PKWS; >1600sqkm, 16°5´ - 35´ N, 101°20´ - 55´ E, 300-1300m) in north-eastern Thailand (Schülke et al., 2011). The study area is covered by hill evergreen forest, dry evergreen forest, dry dipterocarp forest, and bamboo stands (Borries et al., 2002). PKWS is part of an interconnected system of eight protected areas, the 6500sqkm Western Isaan Forest Complex (Grassman et al., 2005) in Chaiyaphum and harbors a diverse community of large mammals and predators indicating low levels of habitat disturbance.

We studied two wild groups (AS, AO) of fully habituated Assamese macaques. Assamese macaques are seasonal breeders, with a mating season (ms) from October through January and a non-mating season (nms) from February to September. Most infants are born between April and June (Fürtbauer et al., 2010). At any time, both groups included several adult males, several adult females and a large number of immatures (Table 1).

2.2 Behavioral data collection

On approximately n=20 days per month, we followed the two study groups from dawn to dusk. We observed a total of n=28 individual adult males and n=33 adult females in 30 min focal animal protocols using continuous and instantaneous recording (Table 1; Altmann, 1974). We used six two-hour time-blocks between 06:00 AM and 06:00 PM to distribute focal observations evenly across time of the day and individuals. We observed all adult males in group AS continuously from 2009 through 2014, and in group AO from 2012 onwards. All adult females in the respective study groups were observed during the same period, with the exception of two 4-month periods when data were collected on males only (Table 1).

Table 1: Average focal animal observation hours per season and focal animal sex [mean ± SD, hrs], and number of adult individuals in the group. All adult individuals were observed if not specified otherwise. AS and AO refer to the two study groups.

Observation period	Season	mean ± SD duration [hrs]		Number of adult individuals per study group	
		Male	Female	Male	Female
Oct 2009 – Jan 2010	ms	49.1 ± 7.8	no obs.*	AS: 10	AS: 15
Feb 2010 – Sep 2010	nms	49.4 ± 21.4	49.7 ± 5.3	AS: 10	AS: 15
Oct 2010 – Jan 2011	ms	49.4 ± 6.0	39.0 ± 4.5	AS: 10	AS: 15
Feb 2011 – May 2011	nms	15.3 ± 1.7	24.3 ± 3.3	AS: 10	AS: 15
Oct 2012 – Jan 2013	ms	19.6 ± 5.9	no obs.*	AS: 7; AO: 10	AS: 11; AO: 11
Feb 2013 – Sep 2013	nms	81.1 ± 10.4	46.5 ± 3.0	AS: 7; AO: 10	AS: 10; AO: 12
Oct 2013 – Jan 2014	ms	53.5 ± 12.6	27.8 ± 5.9	AS: 8; AO: 10	AS: 11; AO: 12
Feb 2014 – Sep 2014	nms	82.8 ± 18.4	19.4 ± 2.4	AS: 7; AO: 6	AS: 11; AO: 10

*during this period data females were not observed; data collection on adult males only

During a total of n=7,757 hours of focal animal observation, we recorded in the continuous protocol the frequency and duration of three affiliative behaviors: (i) close proximity (< 1.5 m), (ii) body contact, and (iii) grooming. An approach into close proximity was defined as an individual approaching another within at least 1.5 m and staying in this distance for at least 10 seconds. We recorded a departure when one of the individuals left the 1.5 m proximity of the other individual. We recorded body contact when two individuals were standing, sitting or lying close to each other so that part of their bodies touched. We defined an interaction in close proximity or body contact whenever one individual started the behavior, and the time spent performing a behavior as the total duration of the interaction. We recorded grooming when one individual manipulated with its fingers the fur of another individual, removing dirt or parasites. We defined a grooming interaction as one continuous bout of one individual grooming another that was not interrupted by more than 10 seconds by either pausing, the performance of other behaviors, or a change in the actor and recipient roles. Additionally, we recorded all dyadic agonistic interactions within the continuous protocol. We defined agonism as one individual showing aggressive (lunge, chase, slap, push-and-pull, bite, ground slap, open mouth) or submissive (make room, silent bared teeth, flee, crouch) behavior towards another (Ostner et al., 2008). Additionally, agonistic interactions were recorded ad libitum. Dominance hierarchies were constructed for males and females separately and were based on decided, dyadic interactions only. We also recorded all individuals in the focal animal´s 5 m proximity every ten minutes.

2.3 Behavioral data analysis

We used the dyadic composite sociality index (CSI: Haunhorst et al., 2016; Silk et al., 2006) as a measure of the strength of the affiliative relationship between a male and a female relative to the group's average across all male-female relationships for a given group and period (mating season (ms) vs. non-mating season (nms) within a given year). For each dyad, we included the total duration (time spent performing a behavior) and frequency (number of interactions) of three behaviors: being in close proximity (<1.5 m), body contact, and grooming. We subtracted the duration of grooming from the duration of body contact and the duration of body contact from the duration of close proximity, as those behaviors are nested into each other. We controlled for biases due to varying observation times by dividing the behaviors by the total observation time of the dyad. To standardize on the level of the social group, we divided each resulting behavior by the average across all dyads in the group in a given period. We calculated the index as follows:

$$CSI_{xy} = \frac{\sum_{i=1}^{b} \left(\frac{f_{ixy}}{f_i} + \frac{d_{ixy}}{d_i}\right)}{2b}$$

Here *b* is the number of behaviors that contribute to the index, f_{ixy} is the frequency of behavior *i* for the dyad *xy*, f_i is the mean of the frequency of behavior *i* across all male-female dyads, d_{ixy} is the total duration of behavior *i* for the dyad *xy*, and d_i is the mean of the total duration of behavior *i* across all male-female dyads. The index has a minimum of 0, a mean of 1 and increases with the strength of the dyadic affiliative relationship (Silk et al., 2013). We ran row-wise matrix correlations in R (version 3.1.2, R Core Team 2014) for all combinations of the six behavioral measures and found components of the CSI to be significantly positively correlated (15 correlations; all $p < 0.001$; range of average, row-wise Spearman´s rho 0.47 - 0.98; mean ± SD row-wise average rho = 0.70 ± 0.14).

To compute dominance hierarchies, we used all dyadic agonistic interactions including clear submissive signs (make room, silent bared teeth, unprovoked give ground; Ostner et al., 2008) from both continuous focal protocols and ad libitum data. We calculated hierarchies separately for males and females, based on the normalized David´s Score (Schmid & De Vries, 2013) for each period of data collection (Table 2). In our analyses, we used standardized dominance ranks (ranging from 0 to 1) to control for the number of individuals in the group and sex. The standardized dominance rank translates into the highest-ranking individual as 1 and the lowest ranking individual as 0, and other individuals distributed evenly in between. This approach allows for comparison of dominance hierarchies of varying group sizes and compositions. We calculated the similarity or difference in dominance rank between males and females as the absolute value of male standardized dominance rank minus female standardized dominance rank. The difference in dominance rank could vary between 0 and 1, with 0 indicating no difference in dominance rank (i.e. highest ranking male with highest ranking female, or lowest ranking male with lowest ranking female) and 1 with the highest possible difference in dominance rank (i.e. highest ranking male with lowest ranking female, or vice versa).

Table 2: Details on male and female dominance hierarchies with mean and standard deviation (mean ± SD) across observation periods and groups.

	Number of dyads	Number of conflicts	Linearity index h’	Unknown relationships (%)	Directional consistency	Two-way relationships (%)	Ties (%)
Male	37.3±13.9	232.3±52.1	1±0	8.27±5.97	0.96±0.02	10.0±5.8	1.53±1.16
Female	79.3±20.4	453.7±82.3	0.82±0.06	10.6±1.36	0.98±0.02	4.4±3.1	0.33±0.47

To assess male “attractiveness” to females, we ranked, for each female, all males by their CSI value from a female´s perspective. We standardized these values like the dominance ranks by assigning a value of 1 to the strongest and a value of 0 to the weakest relationship and spreading all others equally in-between. From these values, we calculated an average CSI position across all females for each male (CSI-position hereafter). The highest CSI-position indicates the highest “attractiveness” to females.

To assess a male´s affiliation with immatures, as an approximation of paternal quality, we computed, for each male, a male-immature affiliation index by adding the time spent in three affiliative behaviors (close proximity, body contact, and grooming; see above) with all immatures below three years of age during the six months preceding the respective period (mean ± SD: 21.3 ± 3.5). We did not include immatures older than 3 years to avoid confusion with other motivations for affiliation than male care since age at first birth for female Assamese macaques is five years (Fürtbauer et al., 2010). We included the total time of each affiliative behavior without subtraction from each other (unlike the calculation of the CSI), thereby weighing time spent in body contact over close proximity and grooming over the other two behaviors, respectively, resulting in males grooming immatures being scored as more social than males that spent the same time in proximity to immatures but never groomed them. We standardized the sum of the three behaviors on the level of the respective period across all males in the group by dividing a male´s value by the average value of the group in the respective period, to eliminate the effect of the number of resident males and immatures present at times and seasonal dependent behavioral changes. The standardized index varies between 0 and ∞, with high values indicating males spending increasing amounts of time affiliating with immatures.

2.5 Statistical analysis

2.5.1 General procedure

We fitted all models in R (version 3.2.2; R Core Team 2014) using the functions ‘lm’, ‘lmer’ and ‘glmer’ of the R-package ‘lme4’ (Bates et al., 2014). In the case of linear mixed models with Gaussian error link function and generalized linear mixed models with binomial error link function (LMM and GLMM, respectively; Baayen, 2008) we followed the procedure as follows. Prior to analysis, we transformed variables if necessary, to achieve an approximately normal distribution of residuals (reported in detail below). We z-transformed all predictors and fixed effects (to a mean of zero and a standard deviation of one), hence all estimates reported are standardized betas. We checked for whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting Q-Q plots and the residuals plotted against fitted values. We checked for model stability by excluding subjects one at a time from the data (functions provided by Roger Mundry, Leipzig). To rule out collinearity of fixed effects, we derived Variance Inflation Factors (VIF, Field, 2005) using the function ‘vif’ of the R-package ‘car’ (Fox & Weisberg, 2011) applied to a standard linear model excluding the random effects. We found no obvious influential cases, nor obvious deviations from the assumptions of normality and homogeneity of residuals (Field, 2005; Forstmeier & Schielzeth, 2011). We established the significance of the full model as compared to the null model (comprising only fixed control and random effects) using a likelihood ratio test (R function ‘ANOVA’ with argument test set to "Chisq"; Dobson, 2002; Forstmeier and Schielzeth, 2011). To allow for a likelihood ratio test we fitted the models using Maximum Likelihood (rather than Restricted Maximum Likelihood; Bolker et al., 2009). P-values for the individual effects were based on likelihood ratio tests comparing the full with respective reduced models (Barr et al., 2014; R function drop1). All full models reported in the results were different from the respective null model (Table 3). For all models we calculated the ‘conditional’ R^2, a measure for how well the model fits the data. It represents the variance of the results explained by the model (i.e., fixed control and random effects) using the function ‘MuMIn’.

2.5.2 Prediction 1: Assortative bonding

To test the prediction of assortative bonding, we used a LMM including CSI as response and dominance rank difference (diff.rank) as predictor (Table 3). We added male dominance rank, female dominance rank and reproductive season (ms/nms) as fixed effects to control for potential behavioral changes associated with dominance rank or the respective seasons. We included the dyadic, male and female identification, as well as group ID (AS vs. AO) and year as random effects. We power-transformed CSI by 0.3 and dominance rank similarity by 0.5 prior to analysis to achieve approximately symmetric distribution and avoid influential cases. Both male and female dominance rank were approximately symmetrically distributed.

2.5.3 Prediction 2: Effect of dominance rank within a competitive situation

We further established the occurrence of female competition for males by evaluating the situation from each male´s perspective, considering only those females that shared the same male as top partner (highest CSI; Haunhorst et al., 2016). A competitive situation was defined as two or more females sharing the same male as top partner. As competition is mediated by dominance hierarchy, with the higher ranking individual having priority in gaining access to resources (Barton, 1993; Barton & Whiten, 1993; van Noordwijk & van Schaik, 1987; Whitten, 1983), we expected that the higher ranking a female, the stronger the affiliative relationship with a male would be compared to other females competing over the same male. Hence, we ordered females within a competitive situation by 1) the strength of their relationship with the male from the male´s perspective and 2) their dominance rank. In this study, the maximum number of females in a competitive situation (i.e. sharing the same male as top partner, see above) was five. In this case, we sorted these five competing females 1 to 5 in both relationship strength and dominance rank, respectively. We ran a linear regression with the order of relationship strength as the response and the dominance rank within the competitive situation as a predictor (Table 3).

2.5.4 Prediction 3: Male attractiveness

To assess the qualities in males that females compete for, we ran a GLMM with CSI-position as the response and the time affiliating with immatures in the six months preceding the respective observation period (see above) and male dominance rank as main predictors (Table 3). Because behavior may change due to changes in social and sexual interactions or the presence of infants (Fürtbauer et al., 2014; Haunhorst et al., 2016), we included the reproductive season (ms vs. nms) as additional fixed effect. To control for individual and group-specific differences, we included male ID and group ID (AS vs. AO) as random factors.

Table 3: Summary of models with response, predictors and fixed control factors with comparison of full vs. null models.

Model name	**Response**	**Predictors**	**Control factors**	X^2	**df**	***P***
Assortative bonding	CSI	Difference in dominance rank	Female dominance rank; Male dominance rank; Season	574.7	3	< 0.001
Rank effects in a competitive situation	Order of relationship strength	Dominance rank within competitive situation	*Not applicable here (linear regression)*			
Male attractiveness	CSI-position	Male dominance rank; Immature affiliation	Season	162.9	3	< 0.001

3 Results

3.1 Assortative bonding

Overall, we tested N=835 male-female dyads. The difference in dominance rank within a dyad had a negative effect on relationship strength (CSI): the more similar a male and a female were in dominance rank, e.g. both ranking very high in the respective male or female hierarchy, the stronger was the relationship between them (β ± SE: -0.21 ± 0.05, t = -4.10, p < 0.001; Fig. 1). Additionally, both male (β ± SE: 0.33 ± 0.08, t = 4.40, p = 0.001) and female (β ± SE: 0.17 ± 0.06, t = 2.95, p = 0.003) dominance rank were significantly positively associated with affiliative relationship strength. The higher the dominance rank of an individual, the stronger its dyadic relationships to an opposite-sex partner. Relationship strength was significantly lower in the non-mating than in the mating season (β ± SE: -0.08 ± 0.02, t = -3.51, p < 0.001). The complete model explained 28% of the variance in relationship strength (R^2 = 0.28).

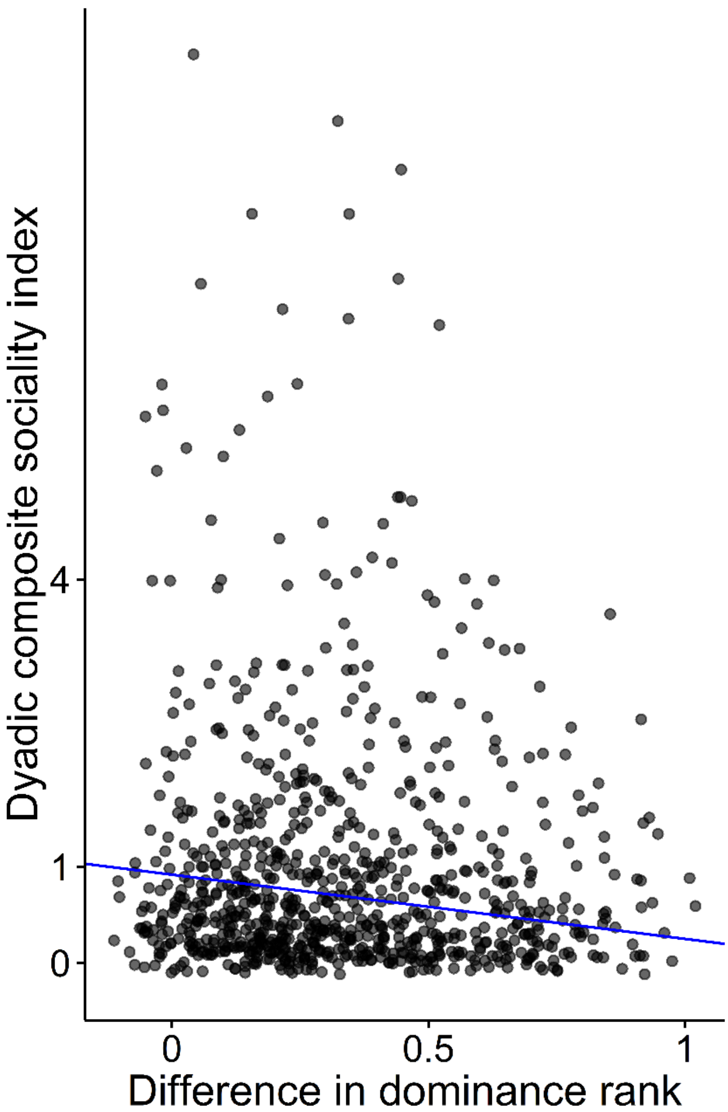


Figure 1: The strength of male-female affiliative relationships (expressed as dyadic composite sociality index; CSI) as predicted by the partners' difference in dominance rank. Male and female dominance ranks are measured on separate scales and a difference of zero indicates that the female occupies the same position in the female dominance hierarchy as the male in the male dominance hierarchy. The blue line indicates the relationship between the difference in dominance rank and the strength of a relationship predicted by a LMM. Note that the LMM controlled for effects of season, male and female dominance rank, which are not shown.

3.2 Dominance rank effects within a competitive situation

The number of males in competitive situations (*n* = 26) varied widely across the study period with 2 to 6 males being top partner of 2 to 5 females, adding up to n = 70 data points. Males in competitive situations held all possible dominance ranks from the highest (alpha) to the lowest ranking position (n = 18 males from the upper half of hierarchy; *n* = 8 males from lower half). The strength of a female's relationship to the male compared to others in the same competitive situation was strongly associated with her rank in the female dominance hierarchy (Figure 2; estimate ± SE = 0.49 ± 0.10; z = 5.13; $p < 0.001$). In 50% of the 26 cases, a female was ordered highest in both categories (dominance rank and bond strength order). Only 11% of cases were below the predicted regression line, showing that few cases ran counter the prediction.

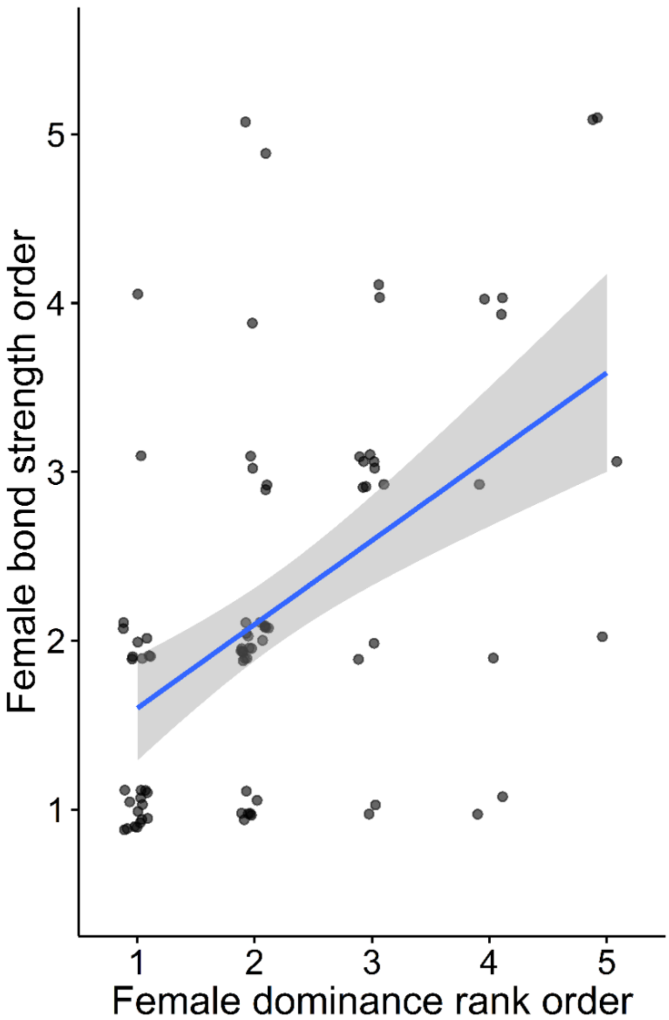


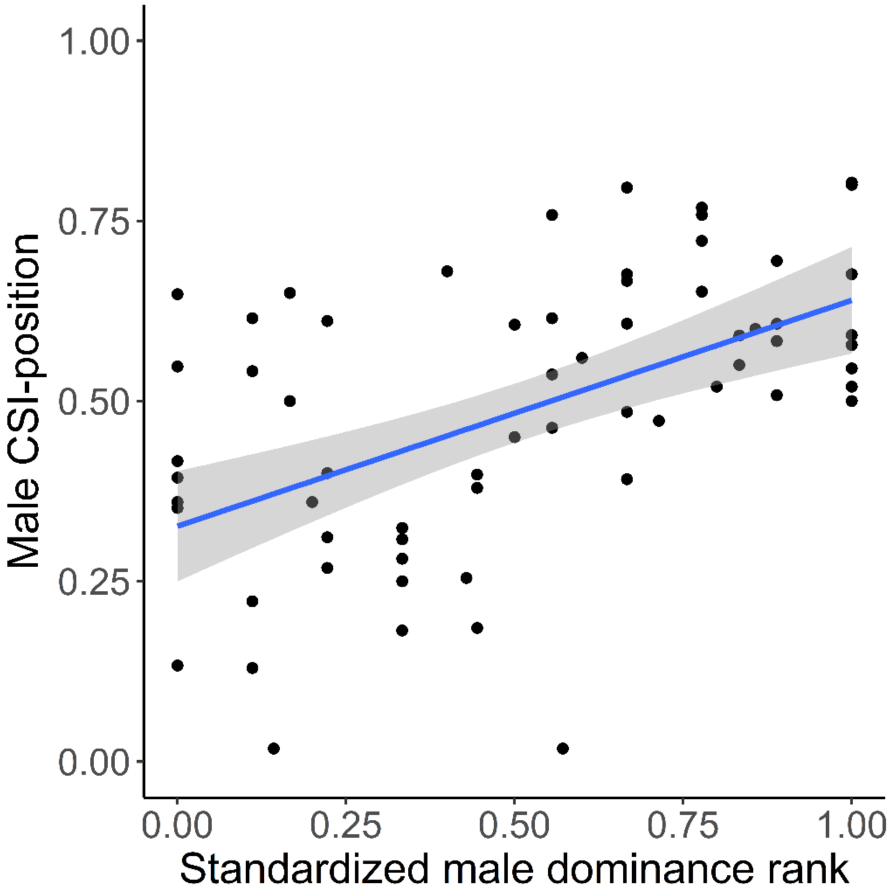
Figure 2: Female affiliative relationship to a male (CSI; from 1 strongest bond) predicted by female relative dominance rank within a competitive situation. The blue line indicates the predicted linear regression and the grey area the standard error.

3.3 Male attractiveness

Male CSI-position, after controlling for number of males in the group, ranged between 0.02 and 0.80 (mean ± SD: 0.49 ± 0.19; n = 65) with high values indicating that a male was a top partner for many females. In n = 24 cases, males were not a top partner for any female, with male dominance rank ranging from the highest to lowest ranking male (standardized male dominance rank, mean ± SD: 0.51 ± 0.33). The standardized time males spent affiliating with immatures ranged between 0 and 2.69, with 42% of males affiliating with immatures for longer than average (mean ± SD: 0.98 ± 0.55).

Our model of male traits predicting a male´s CSI-position explained 59% of the variance in the response (R^2 = 0.59). Independent of each other, both a male's dominance rank (*β ± SE*: 0.43 ± 0.13, *t* = 3.37, p = 0.001; Fig. 3a) and the time he spent affiliating with immatures (*β ± SE*: 0.26 ± 0.11, *t* = 2.34, p = 0.028; Fig. 3b) were significantly positively associated with his CSI-position with females. Season had no significant effect on the CSI-position (*β ± SE*: 0.25 ± 0.16, *t* = 1.50, p = 0.141). Thus, higher ranking males and males spending more time with immatures seemed more attractive to females.

a)


Male CSI-position
1.00
0.75
0.50
0.25
0.00
0.00
0.25
0.50
0.75
1.00
Standardized male dominance rank

b)

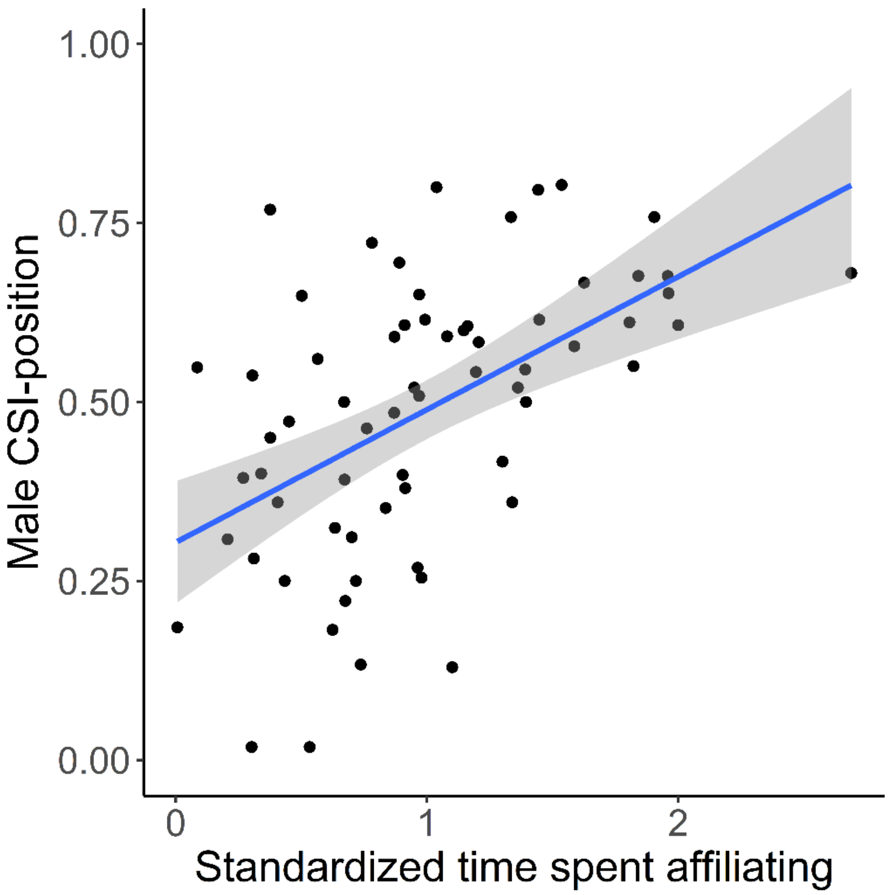


Figure 3: The effect of (a) a male's dominance rank and (b) the time a male spent affiliating with immatures on a male´s CSI-position across all adult females. Raw data before transformation is shown for better reading, though in the model all values were z-transformed. The blue lines represent the model-predicted standardized estimates with the shaded area showing the respective standard error.

4 Discussion

In the absence of behavioral data on early hominins, non-human primates, as our closest relatives, serve to elucidate human social evolution (Chapais, 2008; Coxworth et al., 2015; Strassmann, 1981; Swedell & Plummer, 2012; van Schaik, 2016). We investigated whether the typically human trait of female competition over male partners is found also in a non-human primate and suggest that female competition, not only for mating but also for social partners, has deep roots in human evolution.

While it is still unclear, whether the human pair bond evolved from a system of separated one-male units, a group composed of one-male units, or a multi-male – multi-female system with varying degree of cohesion (Chapais, 2013; van Schaik, 2016), there is increasing evidence for stable male-female affiliative relationships within multi-male – multi-female primate groups with varying levels of spatial cohesion. For example, in chimpanzees (*Pan troglodytes*) with a high degree of fission-fusion dynamics females selectively associate with particular males over extended periods of time and these socio-spatial associations together with male dominance rank predict male reproductive success (Langergraber et al., 2013). In Rwenzori Angolan colobus monkeys (*Colobus angolensis ruwenzorii*), a species exceptional among congeners in their multilevel social organization and high fission-fusion dynamics (Fashing, 2011), the strongest relationships among adults occur between the sexes and have been suggested to represent mating effort, possibly in association with later parental effort (Arseneau-Robar et al., 2018). Stable affiliative relationships outside the mating context have also been described for rhesus (*Macaca mulatta*) and Assamese macaques living in relatively cohesive multi-male – multi-female groups (Haunhorst et al., 2016; Massen & Sterck, 2013).

In order to broaden the comparative knowledge on the evolution of social structure, we investigated whether wild female Assamese macaques compete for male social partners and if so, which male traits they compete for. If competition is costly and individuals differ in their ability to deal with the costs, poor competitors might benefit from avoiding high-quality partners and targeting low quality partners instead, leading to an assortment by dominance rank (Fawcett & Johnstone, 2003). Such condition-dependent preferences will emerge in both sexes as result of competition for high-quality partners and, if combined, can result in even stronger assortative partner choice (Buss, 1994; Buss & Barnes, 1986; Fawcett & Johnstone, 2003). Humans have been shown to assortatively bond and/or mate with the opposite sex based on similar mate values (Buss, 1994; Buss & Barnes, 1986; Kalick & Hamilton, 1986). The opportunity to form and maintain an affiliative relationship with a male may be a resource females compete for (Palombit et al., 2001), as it is constrained by a male's social time and tolerance towards females. In our study, male-female bonding among Assamese macaques was assorted by dominance rank, albeit not very strongly so, with males and females more similar in their respective dominance hierarchies forming stronger bonds. Additionally, whenever two or more females competed over the same male their success was dictated by their dominance rank. Such rank effects are generally interpreted as indicators of strong contest competition over access to a resource (Watts, 2010).

It is in the interest of a female to monopolize a male that is able and willing to provide valuable resources and to reliably support her and her offspring (Buss & Schmitt, 1993; Campbell, 2004). Male mountain gorillas (*Gorilla beringei beringei*) form close bonds with immatures (Rosenbaum et al., 2011), that persist across developmental stages (Rosenbaum et al., 2016) and are predictive of male reproductive success (Rosenbaum et al., 2018). In chacma baboons females gain protection for their offspring against infanticidal males (Moscovice et al., 2009; Palombit et al., 1997), and juveniles receive increased tolerance by biological fathers (Huchard et al., 2013). Female baboons compete for the male that most likely sired their offspring to ensure paternal investment (Palombit et al., 2001), and bonds are terminated after the highest threat of infanticide is over (Palombit et al., 1997). Female Assamese macaques benefit from social bonds with a particular male by increased support against conspecifics, increased food intake rate in the male´s presence (Haunhorst et al., 2017), male-offspring affiliation (Ostner et al., 2013) and male agonistic support of infants (Minge et al., 2016).

Consistent with these data and with our prediction, Assamese macaque females competed for both traits, i.e. male care for immatures and high male dominance rank independently. We have previously shown that Assamese macaque males preferentially support infants of mothers with whom they maintain a closer relationships (Minge et al., 2016; Ostner et al., 2013). Male protection of infants against non-lethal aggression from group members also seems to drive male-female(-immature) associations in yellow and olive baboons (Lemasson et al., 2008; Nguyen et al., 2009). The results of our study indicate that females bias their bonding towards males that generally are tolerant of and affiliate with immatures, which may be an indicator of paternal quality. For several reasons, this result is not a byproduct of differentiated association of males and females increasing a male’s chance to spend time in proximity of the female’s infant. First, our measurement of male care took male-immature affiliation into account that (i) went beyond pure spatial behavior (instead also including grooming and body contact), (ii) concerned immatures up to three years and thus well beyond the time an infant spends close to his mother and (ii) included all resident immatures instead of only the offspring of the male’s preferred partner. Across groups and years, a male on average affiliated with the large majority of available immatures (79% ± 18 of the 22 ± 3 available immatures; mean and standard deviation). When focusing on a male’s most strongly affiliated immature, only 15% were offspring of the respective males’ preferred female partner. Second, we have shown previously for the study population that immatures up to 20 months of age spend only 40% of their daytime activity within 5m of their mother and the probability of a male to be in the proximity of an immature is negatively related to the presence of the immature’s mother (Minge et al., 2016). Together, these considerations make it unlikely that it is the male-female association that drives a male’s propensity to care for immatures instead of the reverse, male care driving female preferences.

Apart from females bonding with males that spent a lot of time with immatures, Assamese macaque females preferentially affiliated with high ranking males. Although dominant Assamese macaques have priority of access to female mating partners (Ostner et al., 2011, 2013; Schülke et al., 2010), paternity skew is relatively weak with a 29% alpha male paternity concentration (Sukmak et al., 2014). A high dominance rank, however, puts a male in the position to provide his female partner with increased access to food resources and to more efficiently protect her and the offspring from conspecifics (Haunhorst et al., 2017). Thus, females may choose high-ranking males for their actual investment ability instead of choosing high rankers for their good genes. Female (mate) choice for males with high social status or resource acquisition indicators is a rather universal human trait (Buss, 1989) and has also been found in several species of nonhuman primates (reviewed in Small 1989; Paul 2002).

Our study suggests similarities between nonhuman primates and humans with respect to female competition for male social partners. Granted the human universal of socially recognized pair bonds in form of marriages with a tendency to exclusivity, also in humans, paternity skew within the larger group is low, due to concealed ovulation and extended receptivity, leading to permanent male-female bonds, male caretaking, provisioning of offspring and female partners, a reduced male-male competition for status, and increased male tolerance (Alexander & Noonan, 1979; Strassmann, 1981). Females compete for males that are able and willing to provide valuable resources that potentially enhance female reproductive success. Our study adds to the growing evidence for male care, a hallmark feature of human evolutionary success, to play a crucial role in female partner choice also in nonhuman primates. Our study provides further support for the hypothesis that the human pair bond results from co-evolution of male and female reproductive strategies enforced by female choice.

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