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Degrees of freedom in social bonds of crested macaque females.

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Abstract

Social bonds between group members affect individual fitness and well-being. While the impact of bond strength is well studied, the consequences of bond predictability and equitability are often overlooked. Similarly, whether bonds reflect short-term contingencies and/or long-term social strategies remains understudied. We investigated these questions in female crested macaques (*Macaca nigra*), which display a tolerant social style within a nepotistic hierarchical social structure. We analysed the structure of social bonds by testing whether similarity within dyads – in kinship, dominance and age – predicted the strength, predictability and equitability of bonds. We then tested the value of social bonds by analysing the effect of their characteristics on three fitness-related behaviours: coalitionary support, feeding-in-proximity and aggression. We found that the bond characteristics of females differed substantially from those of other species with comparable data: bonds were of average strength, of moderate endurance and relatively balanced. Stronger bonds were more equitable but less predictable than weaker bonds. Closely-ranked females, but not kin or age peers, had stronger, more predictable and more equitable bonds than others. Coalitionary support was not related to any of the bond characteristics, feeding-in-proximity was positively associated with strength and predictability and aggression was positively linked to strength and negatively to equitability. These results highlight the complex picture of the benefits of social bonds in this species. They reflect the degrees of freedom tolerant macaque females can express in their social relationships within their stable social structure, a pattern that may not be given enough consideration in stable nepotistic hierarchical societies. Comparative research is necessary to establish whether these patterns are more general than previously thought or a specific feature of tolerant macaques. Investigating various characteristics of bonds together is paramount in order to appreciate the dynamics of social relationships and to better understand the social components of fitness.

Keywords

behavioural strategy, equitability, predictability, primates**,** social bonds, social dynamics, strength

Introduction

Social bonds are positive social relationships amongst pairs of individuals of the same group (Silk, Cheney, & Seyfarth, 2013; Silk 2007a). They are defined in a multidimensional space of relationship qualities such as relative strength, predictability (or magnitude of change over time) and equitability (the balance of social exchanges within a dyad) (Silk et al., 2013; Whitehead, 2008). Variation in these components can affect individual fitness inasmuch as individuals with more numerous, stable or stronger bonds experience enhanced survival, greater reproductive success or improved general well-being compared to others (Cameron, Setsaas, & Linklater, 2009; Frère et al., 2010; McFarland & Majolo, 2013; Silk et al., 2009, 2010; Uchino 2006; Young, Majolo, Heistermann, Schülke, & Ostner, 2014). For individuals, the value of social bonds is also related to the direct or indirect benefits they may obtain from daily social exchanges, e.g. in reconciliation after conflicts (e.g. Fraser & Bugnyar, 2011), or for better access to food resources (e.g., Smith, Memenis, & Holekamp, 2007), which ultimately may impact their fitness and well-being (Ostner & Schülke, 2014; Silk, 2007a).

In order to understand the function and value of social bonds, i.e. which benefits can be obtained by forming and maintaining them, it is also crucial to investigate their underlying structure, i.e. the characteristics of the dyads forming particular bonds. In many animal societies, individuals that are similar in terms of genetic relatedness, dominance status, personality, reproductive state or energetic needs are more likely to form strong and enduring social bonds than others (Armitage & Schwartz, 2000; Carter, Seddon, Frère, Carter, & Goldizen, 2013; Godde, Côté, & Réale, 2015; Hirsch, Staton, & Maldonado, 2012). Each of these characteristics can be uniquely important in influencing the formation and maintenance of a bond. For instance, although close kin are obvious coalition partners, kin-based coalitionary support may not be advantageous if such kin are low-ranking (Chapais, 2006), in which case establishing a bond with a higher-ranking non-relative may be more valuable (Schino, 2007; Smith et al., 2010). Similarly, pregnant or early lactating female chacma baboons were less likely to become involved in coalitions and, thus, were not reliable cooperation partners for both kin and non-kin (Barrett & Henzi, 2001).

Research on the benefits of social bonds amongst same-sex adult group members has so far mostly considered how bond characteristics at the extreme positive end of the spectrum, e.g. preferred associates (Frère et al., 2011) or top three partners (Silk et al., 2006a), affect measures of fitness, health or well-being. However, animals may have a variety of options for regulating the consequences of bonds. First, establishing and maintaining predictable and/or equitable bonds may bring as much, if not more, benefits as having strong bonds (e.g. the sheer amount of research on cooperation and reciprocity: Nowak, 2006; Trivers, 1971, 2006). In addition, "weak" bonds within a social network may be as important as "strong" bonds, inasmuch as weak bonds contribute to stabilising the overall network or to enhancing the propagation of information or innovation (Bakshy, Rosenn, Marlow, & Adamic, 2012; Granovetter 1973). Finally, it has been shown that variance in bond strength rather than absolute strength itself actually predicts fitness (e.g., Barocas, Ilany, Koren, Kam, & Geffen, 2011; Wey, Burger, Ebensperger, & Hayes, 2013). Studies integrating the different dimensions of social bonds simultaneously and on a continuous scale are therefore indispensable for deepening our understanding of the link between sociality and fitness.

Individuals may thus use varying social strategies reflecting certain degrees of social freedom according to social context, the spatial or temporal availability of partners, or environmental conditions, even when living in stable organised societies. Consequently, it has been argued that social bonds are likely to be formed and maintained based on contingencies (short-term, opportunistic tactics) rather than, or in addition to, long-term, fixed strategies (Barrett & Henzi, 2006). For instance, female chacma baboons did not sustain constant differentiated relationships with other females over time but changed cyclically between "brief associations", "casual acquaintances" and "constant companionships" according to food availability in the environment (Barrett & Henzi, 2006). Although this seems rather straightforward in animal societies that display flexibility in their social structure, such as in fission-fusion societies, variation in social strategies only recently began to be considered in species with a stable nepotistic hierarchical social structure such as those of many primates, hyenas or elephants (Barrett & Henzi, 2001, 2006; Henzi, Lusseau, Weingrill, van Schaik & Barrett, 2009; Ilani, Booms, & Holekamp, 2015; Sick et al., 2014).

Macaques (genus *Macaca*) are an ideal candidate for the investigation of such variation in social strategies. Although they share the same social organisation (philopatric females organised in stable matrilineal dominance hierarchies), the different macaque species are described as more or less socially tolerant depending on the degree of nepotism, power asymmetries, conciliatory tendencies and counter-aggression in social relationships (Thierry, 2007, 2013). Regardless of how such patterns emerged (see Thierry, 2004; van Schaik, 1989), such social variation can be expected to influence the structure and function of social bonds (Butovskaya, 2004; Thierry, 1990). Specifically, when power asymmetries are moderate and the degree of nepotism is weak, as in more tolerant macaques, individuals are able to interact with diverse partners and to develop a great diversity and number of social bonds (Butovskaya, 2004; Cooper & Bernstein 2008; Duboscq et al., 2013; Thierry, 1990). In contrast, less tolerant macaques are more constrained in their behavioural options and may rely on a relatively low number of strong, predictable and equitable partnerships instead. Thus, the degrees of freedom that individuals have in their relationships within their group could be assessed through the size and diversity of their social network in relation to the influence of dominance and kinship on an individual's social options – or lack thereof (Butovskaya, 2004; Thierry, 1990).

In this study, we aimed to investigate these degrees of freedom and the interplay between the structure and the value of social bonds in wild female crested macaques (*Macaca nigra*), which express a tolerant social style (Duboscq et al., 2013; Petit, Abegg, & Thierry, 1997). Crested macaques live in a relatively predictable and safe ecological environment (low predation risk and abundant food year round; O'Brien & Kinnaird, 1997) while facing dynamic social conditions, e.g. male migration and hierarchical changes, which are a potential source of social instability in the group (Marty, Hodges, Agil, & Engelhardt, 2015; Neumann, 2013). Females reproduce year round (Kerhoas et al., 2014), which is another potential source of fluctuation in the amount of time and attention females can devote to their female social partners (Bardi, Shimizu, Fujita, Borgognini Tarli, & Huffman, 2001; Barrett & Henzi, 2001; Brent, MacLarnon, Platt, & Semple, 2013; D'Amato, Troisi, Scucchi, & Fuccillo, 1982). Previous studies on the same population showed that female crested macaques form highly diverse affiliative social networks (Duboscq et al., 2013). On the one hand, the strength of female-female social bonds was positively linked to predator deterrence, suggesting that

strong bonds play a role in enhancing survival (Micheletta et al., 2012). On the other hand, bond strength did not affect the occurrence and frequency of reconciliation, an important conflict management strategy (Duboscq, Agil, Engelhardt, & Thierry, 2014). Nonetheless, other relationship qualities, such as equitability and predictability, increased the likelihood of reconciliation (Duboscq et al., 2014). As such, it seems that social bond characteristics have different values depending on the context of the social benefits to be gained in this species and we would expect that females express great degrees of social freedom in their choice of social partners and the patterning of their social bonds.

Specifically, since macaques form stable matrilineal hierarchical societies, kin and adjacently-ranked dyads are expected to form the strongest, most predictable and most equitable bonds (Silk, 2007b). However, given the tolerant social style of crested macaques and their expected great degrees of social freedom, we hypothesised that these dyad characteristics would not predict social bond characteristics. To test this prediction and to quantify the structure of bonds, we analysed the relationship between three measures of dyadic similarities (relatedness, similarity in age and dominance rank) and three social bond characteristics, namely strength, predictability and equitability. Furthermore, under the hypothesis that social bond characteristics are linked to fitness in a positive predictable way (Silk, 2007a, b), variation in these characteristics is expected to substantially explain the occurrence or frequency of behaviours directly or indirectly linked to fitness benefits, such as a reduction in aggression, increased coalitionary support during conflicts or better access to food resources. However, again given the tolerant social style of crested macaques and their expected great degrees of social freedom, we hypothesised that the characteristics of social bonds would not predict the occurrence of these fitness-related behaviours. To test this prediction and to establish the value of bonds, we tested the extent to which each social bond characteristic influenced coalitionary support, feeding-in-proximity and aggression. By taking a more integrated perspective of social bonds in a species with a tolerant social style, we address the concept of individuals' degrees of social freedom within their stable network of social relationships (Butovskaya, 2004; Thierry, 1990).

Methods

Ethical Note

This research adheres to all legal requirements and guidelines of the German and Indonesian governments and institutions (permit numbers 1240/FRP/SM/VI/2008 and SI-101/Set-3/2008) and to the ASAB/ASB (2012) guidelines for the Treatment of Animals in Behavioural Research and Teaching. No trapping or tagging was done as this is a wild population of critically endangered animals. The study animals were fully habituated to human observers at least one year before the start of data collection. Habituation consisted of following the group silently each day and for the entire day wearing a project-specific t-shirt until observers could approach any individual to within 5m without them reacting. All adult monkeys could be individually identified based on physical characteristics alone (scars and old injuries (e.g. a limp), facial features, body shape, etc.). Binoculars were used to ensure accuracy in identification and data collection. All observers followed the same rules: no more than five observers were assigned to a group on a given day; no observers were to approach the monkeys to within two meters; no observers were to interact with the animals in any way; and no observers were to disturb the natural behaviour of the subjects in any way. Furthermore, observers showing signs of sickness were not allowed in the forest until they produced a medical note certifying they were clear of infection, and all waste produced during observation was either buried or brought back to camp.

Behavioural data collection and analysis

Field site, study animals and data collection

Crested macaques are critically endangered and endemic to the island of Sulawesi, Indonesia (Sugardjito et al., 1989). The study population inhabits the Tangkoko Reserve, North Sulawesi (1º33'N, 125º10'E; e.g. Duboscq, Neumann, Perwitasari-Farajallah, & Engelhardt, 2008), broadly classified as a lowland rainforest with seasonal variation in rainfall and fruit abundance (O'Brien & Kinnaird, 1997). The study was part of the Macaca Nigra Project, a long-term field project on the

196 biology of crested macaques that started in 2006. We studied two groups, "PB" and "R1", comprised
197 of ca. 60 and 80 individuals respectively.

198 JD and two field assistants collected behavioural data between October 2008 and May 2010
199 on all adult females (15 – 18 in PB, 21 – 24 in R1) using focal animal sampling (Martin & Bateson,
200 1993) (interobserver reliability: Cohen's kappa = 0.69–0.90, correlation coefficients between
201 behavioural variables = 0.79 – 0.98). We collected 30 minute-point-sample observations for activity
202 (foraging (searching for and manipulating food), feeding (putting food to mouth and chewing),
203 socialising (being involved in social interactions including aggression), resting (staying immobile
204 eyes closed), and travelling (moving in a decided direction)). Every second minute, we also noted the
205 identity of neighbours in three proximity categories: in body contact, within one body-length, and
206 within five body-lengths (based on the maximum average body-length of a female crested macaque,
207 55cm (Zinner et al., 2013)). We recorded focal social events continuously, including the start and end
208 time of interactions, the sequence of all behaviours, as well as the identity and behaviours of all social
209 partners. This study included a total of 2,480 hours of focal data focusing on the 35 females that were
210 continuously present during the entire study period (median_{PB} = 68 hours per female, range_{PB}: 65 – 78,
211 N_{PB} = 14; median_{R1} = 66 hours per female, range_{R1}: 59 – 71, N_{R1} = 21). By doing so, we deliberately
212 focused on general patterns and a stable core of individuals to make our study comparable to others.
213 Behavioural interactions were expressed as duration (e.g. social grooming) or frequency (e.g.
214 approach) per focal and per dyad (sum of two focal individuals) observation time over the whole
215 study period (i.e. 19 months).

216 Additionally, for genetic relatedness determination, we collected at least three faecal samples
217 from all females opportunistically (N = 140, median per female = 4, range = 3 - 4). We followed a
218 two-step alcohol-silica storage protocol (Nsubuga, et al., 2004), after which the samples were stored
219 at room temperature until DNA extraction.

220

221 *Dyad characteristics*

222 Dominance difference: To account for power asymmetries between females, we used Elo-
223 rating (R package EloRating, Neumann & Kulik, 2014), which reflects an individual's success in

224 agonistic interactions and is based on temporal sequences of decided (clear winner and loser)
225 agonistic interactions (Albers & de Vries, 2001; Neumann et al., 2011). We made use of direct
226 aggressive interactions (i.e. threats, hits, chases, bites) and displacements (i.e. one individual
227 approaches another one without any threatening behaviour and the other leaves without protesting; for
228 further definitions and more details, see Duboscq et al., 2013, Thierry et al., 2000) taken from all
229 agonistic data collected during focal observations and *ad libitum* data. At the beginning of the
230 observation period, each individual in a group starts with a rating of 1000, which is updated, i.e.
231 increased or decreased, after each agonistic interaction based on the outcome of the interaction (won
232 or lost), the previous ratings of both opponents and a determined factor, k (here k = 100, following
233 Neumann et al., 2011). As we aggregated all other behavioural data over the entire study period, we
234 used the female Elo-rating at the end of the study period. We then computed the absolute difference of
235 the Elo ratings (hereafter termed Elo difference) between the two members of a dyad.

236 Kinship: DNA was extracted from 100–150 mg of faeces with the GEN-IAL® All-tissue
237 DNA extraction kit following the manufacturer's instructions. We amplified 12 short-tandem repeats
238 (or microsatellites - 10 tetranucleotide loci and 2 dinucleotide loci), proven to be informative in
239 humans and other primates (see appendix). We used a two-step multiplex chain polymerase reaction
240 (PCR) approach (Arandjelovic et al., 2009). In the first step, all loci were amplified in a single
241 reaction in an Eppendorf® Master Gradient machine following cycles of denaturation, annealing and
242 elongation (see appendix). We followed multiplex PCRs with singleplex PCRs, using the same
243 protocol but for each primer separately (see appendix). Singleplex PCR products were then sequenced
244 in an ABI 3130xL sequencer. Allele sizes were finally read into PeakScanner (Applied Biosystems®).
245 Given that we had several samples per individual, allele sizes were considered definitive when at least
246 two different samples of the same individual produced the same results in at least four amplifications
247 for heterozygotes and six for homozygotes (multi-tubes approach, Taberlet et al., 1996). Consensus
248 genotypes were found for a median of 12 loci (range = 6 – 12) and processed using COANCESTRY®
249 software, which provides two likelihood methods and five moment estimators of relatedness (Wang,
250 2011). We chose the dyadic maximum likelihood (DML) estimator of Milligan (2003) because it
251 proved to be the most reliable estimator of the mother-infant's theoretical degree of relatedness 0.5

(mean ± SD = 0.51 ± 0.12, N = 60 mother-infant pairs). DML between adult females ranged between 0 and 0.72 with a median of 0.05 ($median_{PB}$ = 0.05, $range_{PB}$ = 0 – 0.53; $median_{R1}$ = 0.05, $range_{R1}$ = 0 – 0.72).

Age difference: We estimated the age category (young, middle-aged or old) females belonged to based on their reproductive history (e.g. number of dependent infants or cycling status) known since 2006, the shape of their nipples (e.g. short or long) indicative of nursing history, the presence of physical injuries and their general appearance (both linked to age rather than rank due to mild level of aggression between females in this species). Based on these categories, we then scored dyads as belonging to the same or to different age classes.

Bond characteristics

The strength of dyadic social bonds was quantified with the Composite Sociality Index or CSI (Silk et al., 2006b). It is built from matrices of dyadic social interactions and was calculated as follows:

$$\mathrm{CSI}_{ij} = \left[\left(\frac{Gij}{G}\right) + \left(\frac{Pij}{P}\right) + \left(\frac{P_{posij}}{P_{pos}}\right)\right]/3,$$

where Gij is the grooming rate (duration of grooming given and received in minutes per hour of dyadic observation time) between individual i and j and G is the mean grooming rate across all dyads in the group; Pij is the rate of close proximity (number of instances females were within one body-length of each other per hour of dyadic observation time) between individual i and j and P the mean proximity rate for all dyads in the group and P_{posij} is the rate of positive outcome upon approach (number of close proximity approaches followed by affiliation (e.g. grooming, embracing, lipsmacking) per hour of dyadic observation time) between individual i and j and P_{pos} the mean rate of positive outcome upon approach for all dyads in the group (Duboscq et al., 2013). In subsequent analyses, we used the actual CSI values and only separated our data into artificial categories to describe them in a way that is comparable with previously published studies.

Bond temporal variation (hereafter predictability) was assessed over three periods of six months each. Sampling efforts (i.e. observation time) per individual in each period were very similar.

Six months is the maximum number of months after which all dyads have been seen in proximity at least once, thus characterising relatively accurate and robust matrices of interactions. We calculated the CSI again for each dyad for each period, then computed the coefficient of variation (CV, standard deviation divided by the mean) over the three CSIs for each dyad (Majolo, Ventura, & Schino, 2010). For statistical analysis, we multiplied the CV by -1 so that the lower (i.e. the more negative) the CV, the lower the predictability of the relationship across the three periods, i.e. the more CSI values varied across the three periods. Note that, in this way, even weak but stable bonds will be considered predictable.

Bond equitability represents how balanced social exchanges are within a dyad (Silk et al., 2013). The Equitability Index (EI) was calculated as a composite symmetry index (Silk et al., 2013), computed from symmetry indices of the behaviours composing the CSI and was calculated as:

$$\mathrm{EI}_{ij} = -\left[\left(1 - \left|\frac{Gij - Gji}{Gij + Gji}\right|\right) + \left(1 - \left|\frac{Pij - Pji}{Pij + Pji}\right|\right) + \left(1 - \left|\frac{P_{posij} - P_{posji}}{P_{posij} + P_{posji}}\right|\right)\right]/3,$$

where G is grooming duration, P the rate of being in close proximity, P_{pos} the rate of positive outcome upon approach, and i and j the individuals in the dyad. An index of 1 indicates perfect equitability between the two individuals in the dyad, while 0 indicates that one individual alone was responsible for all grooming and proximity interactions. Note that this index takes into account the directionality of interactions.

Fitness-related behaviours

We defined coalitionary support as a focal female intervening aggressively (e.g. by threatening or chasing away one of the opponents) or peacefully (e.g. by embracing or lipsmacking at one of the opponents) in support of another female or receiving such an intervention herself during an aggressive interaction with another individual (Duboscq et al., 2014; Petit & Thierry, 1994). We calculated the frequency of support as the number of support instances over the total number of aggressive interactions each member of the dyad was separately involved in (Duboscq et al., 2014). Due to the low frequency of occurrences, for subsequent analyses we transformed this variable into a binary variable, i.e. the behaviour did or did not occur within the dyad (Duboscq et al., 2014). We

calculated the frequency of feeding in proximity as the number of point samples spent feeding while other females were within 5-body-length proximity, controlling for overall dyadic proximity and observation time. Hourly frequencies of aggression were taken from Duboscq and colleagues (2013).

Statistical analyses

Structure of social bonds

We first tested for correlations between the three bond characteristics to assess their relationships with each other and to test the prediction that stronger bonds would be more predictable and equitable than weaker bonds. We built symmetric matrices of the CSI scores, the CVs and the EIs before running matrix correlations in MatMan v1.1 (de Vries et al., 1993) with 1,000 permutations between those matrices two-by-two. We then built three (generalised) linear mixed models (GLMM, Bolker et al., 2008), one for each of the social bond characteristic as response variable, and including relatedness (DML), absolute Elo-rating difference (Elo difference) and age difference (as a categorical variable same/different) as test predictors and member 1 and member 2 of the dyad (i.e. female identities randomly assigned to either variable) independently nested in group as random effects. We ran simulations in which female ID was randomly assigned to either member 1 or member 2, model parameters were recalculated and compared to the original results. This showed that this random assignment did not affect our conclusions (see Tables A1-6, Figures A1-6 in appendix).

Function of social bonds

We built three more models to investigate the value of social bonds, with the occurrence of coalitionary support, feeding-in-proximity rate and aggression rate as response variables and bond strength (CSI), predictability (CV), equitability (EI) as test predictors. In these models we included as control predictors (that will be included in the null model) relatedness (DML), absolute Elo-rating difference (Elo difference) and age difference, and member 1 and member 2 of the dyad (i.e. female identities randomly assigned to either variable) independently nested in group as random effects (see appendix for identical simulations than previously).

All analyses were done in R version 3.2.1 (R Development Core Team, 2015). We implemented GLMMs with a Gaussian (and Maximum Likelihood) or binomial error structure using the function "lmer" and "glmer" from the package "lme4" (v. 1.1-11, Bates, Maechler, Bolker, & Walker, 2015). We transformed numerical variables whenever necessary (log, square-root or fourth root) and standardised all numeric variables to a mean of 0 and a standard deviation of 1. For all models, we checked a variety of assumptions and diagnostics (normally distributed and homogeneous residuals, variance inflation factors < 2, Cook's distance, dfbetas; Field, Miles, & Field, 2012). No obvious violation of assumptions was detected. Using likelihood ratio tests (LRT), we tested the final full model (including all fixed and random effects) against null models. For the three models on bond structure these null models were intercept-only models. For the three models on bond function we included control variables (absolute Elo difference, DML, and age difference) into the null models. We used 95% confidence intervals to assess whether a predictor significantly contributed to explaining the response variable (interval excluding 0).

Testing the effect of kinship measured by a microsatellite-based estimator

Microsatellite-based relatedness estimators have been deemed unreliable for accurately measuring genetic relatedness in populations without pedigree information (Csilléry et al., 2006; van Horn, Altmann, & Alberts, 2008). We tackled this issue by using the approach suggested by Tinsley Johnson and colleagues (2014) of controlling for measurement error in relatedness estimates by running models repeatedly with a random amount of error added to the observed relatedness value of a given dyad. In our data, the maximum observed difference between the estimated relatedness (DML) and the true theoretical relatedness (r = 0.5) of all 60 known mother-infant pairs was 0.41. We therefore introduced an error taken from an uniform distribution of numbers between -0.41 and +0.41, which we feel is conservative as 95% of the DML values for known mother-infant pairs were within 0.25 of the pairs' true relatedness (r = 0.5). Our custom simulation proceeded in four steps: 1/ add an error from an uniform distribution between -0.41 and +0.41 to the DML index of all female-female dyads in the dataset, 2/ run the models again with the modified DML index, 3/ perform a likelihood

ratio test between the full model with modified DML and a reduced model excluding modified DML and 4/ determine the number of simulations in which the significance of the effect of the modified DML index on the response variable was different from the tests with the original models with the original data. The DML index was not a significant predictor of the response variable in 96% to 100% of the 1,000 simulations, depending on the response variable, which indicates that our results are relatively robust against errors in relatedness estimations (Table A7, appendix).

Results

The structure of social bonds

CSI scores ranged from 0.05 to 3.54 in the R1 group and from 0.16 to 4.99 in the PB group, with a median of 0.89 and 0.88 respectively (Figure 1). The distribution of CSI scores, giving an assessment of how skewed dyadic affiliative behaviours are, was less asymmetrical than what is typically observed in other species (Figure 1). 45.7% (96/210 in R1) and 40% (42/105 in PB) of female dyads had a CSI score above the average of the group (i.e., above 1) and the mean CSI score of the top 10% of dyads was 2.34 in both groups (Figure 1). Females had a median of 9 (range 2–13) above-average (CSI > 1) relationships in R1 and 6 (range 2–11) in PB.

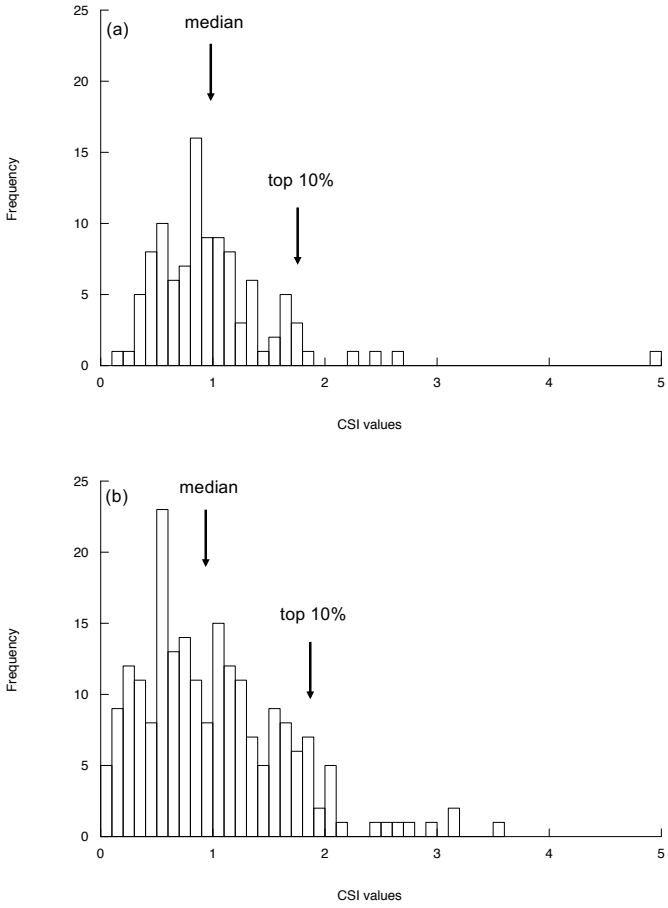

Figure 1: Distribution of overall CSI scores of female-female dyads in the two study groups, (a) PB and (b) R1. The arrows indicate the median and the limit of 10% of the strongest CSI scores. The fact that the distribution is only moderately skewed to the left (i.e. towards 0) indicates how average most of the bonds between females are contrary to what is known for other species where similar data are available.

The mean coefficient of variation indicated moderate to low bond strength predictability across the three 6-months periods (mean CV_{R1} = 0.66 ± 0.01 SD, mean CV_{PB} = 0.70 ± 0.14 SD; Figure 2). 94% of all females had at least one recurring partner over at least two periods amongst their three top partners and 47% of all females had at least one recurring partner over all three periods amongst their top three partners but no female had the same three recurring top partners across all three periods (Figure 2).

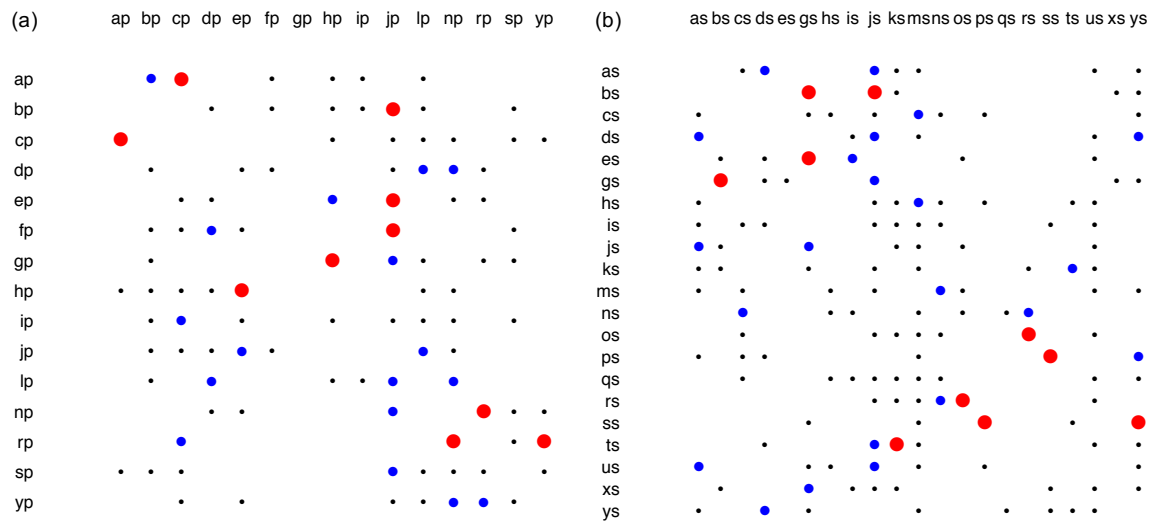

Figure 2: Variation in CSI scores of female-female dyads in the two study groups, (a) PB and (b) R1, across three six-months-periods. Row and column labels represent female identities. A circle denotes that the female in the column was amongst the top three partners of the female in the row at least once (small black), twice (medium blue) or three times (big red) across the three periods. The presence of few red circles but many black dots illustrate how bond strength changes across periods and lacks predictability.

Bond equitability was overall relatively moderate (mean EI_{R1} = 0.22 ± 0.47 SD, mean EI_{PB} = 0.27 ± 0.13 SD), indicating relatively balanced social exchanges amongst the two members of a dyad.

All three characteristics were correlated in both groups (Mantel tests, PB: N = 105 dyads: strength-predictability: Pearson's r = -0.50, Z = 27.7, P < 0.001; strength-equitability: Pearson's r = 0.80, Z = 77.6, P < 0.001; predictability-equitability: Pearson's r = -0.71, Z = 20.7, P < 0.001; R1: N = 210 dyads: strength-predictability: Pearson's r = -0.55, Z = 133.6, P = 0.001; strength-equitability: Pearson's r = 0.79, Z = 143.0, P < 0.001; predictability-equitability: Pearson's r = -0.72, Z = 85.6, P < 0.001), indicating that stronger bonds were more equitable but less predictable over time than weaker bonds and that more predictable bonds were less equitable than less predictable ones.

Female dyads with smaller dominance differences had significantly stronger, more predictable and more equitable social bonds than those with greater dominance differences (strength: $LRT_{full\text{-}null}$: χ^2_3 = 40.67, P < 0.001; β ± SE [95% CI] = -0.33 ± 0.06 [-0.44 – -0.22]; predictability: $LRT_{full\text{-}null}$: χ^2_3 = 10.31, P = 0.016; β ± SE = -0.14 ± 0.05 [-0.24 - -0.04]; equitability: $LRT_{full\text{-}null}$: χ^2_3 = 23.06, P < 0.001; β ± SE = -0.26 ± 0.06 [-0.37 - -0.13]; Table 1; Figure 3). None of the tested bond

416 characteristics were significantly related to the relatedness and age difference of the dyads (Table 1,

417 Figure 3).

418

419 **Table 1:** Dyad characteristics and social bond components

	Bond strength		Bond predictability		Bond equitability	
LRT Null vs. full	$\chi^2_3 = 40.67$, $P < 0.001$		$\chi^2_3 = 10.31$, $P = 0.016$		$\chi^2_3 = 23.06$, $P < 0.001$	
Variables	β ± SE	95% C.I. [lower upper]	β ± SE	95% C.I. [lower upper]	β ± SE	95% C.I. [lower upper]
Intercept	0.06 ± 0.12	[-0.24 0.22]	0.28 ± 0.43	[-0.16 0.29]	0.06 ± 0.13	[-0.19 0.32]
Elo difference	-0.33 ± 0.06	[-0.44 -0.22]	-0.14 ± 0.05	[-0.24 -0.04]	-0.26 ± 0.06	[-0.37 -0.13]
DML	0.08 ± 0.05	[-0.02 0.19]	-0.05 ± 0.05	[-0.15 0.03]	0.08 ± 0.06	[-0.01 0.21]
Age difference	-0.14 ± 0.11	[-0.37 0.08]	-0.11 ± 0.10	[-0.31 0.08]	-0.04 ± 0.12	[-0.27 0.19]

420 Results of GLMMs testing the influence of dominance difference (Elo difference), degree of genetic
421 relatedness (DML) and age difference on bond strength, bond predictability and bond equitability (N
422 = 286). LRT – likelihood ratio test, β ± SE = estimate and standard error, C.I. = confidence intervals.
423

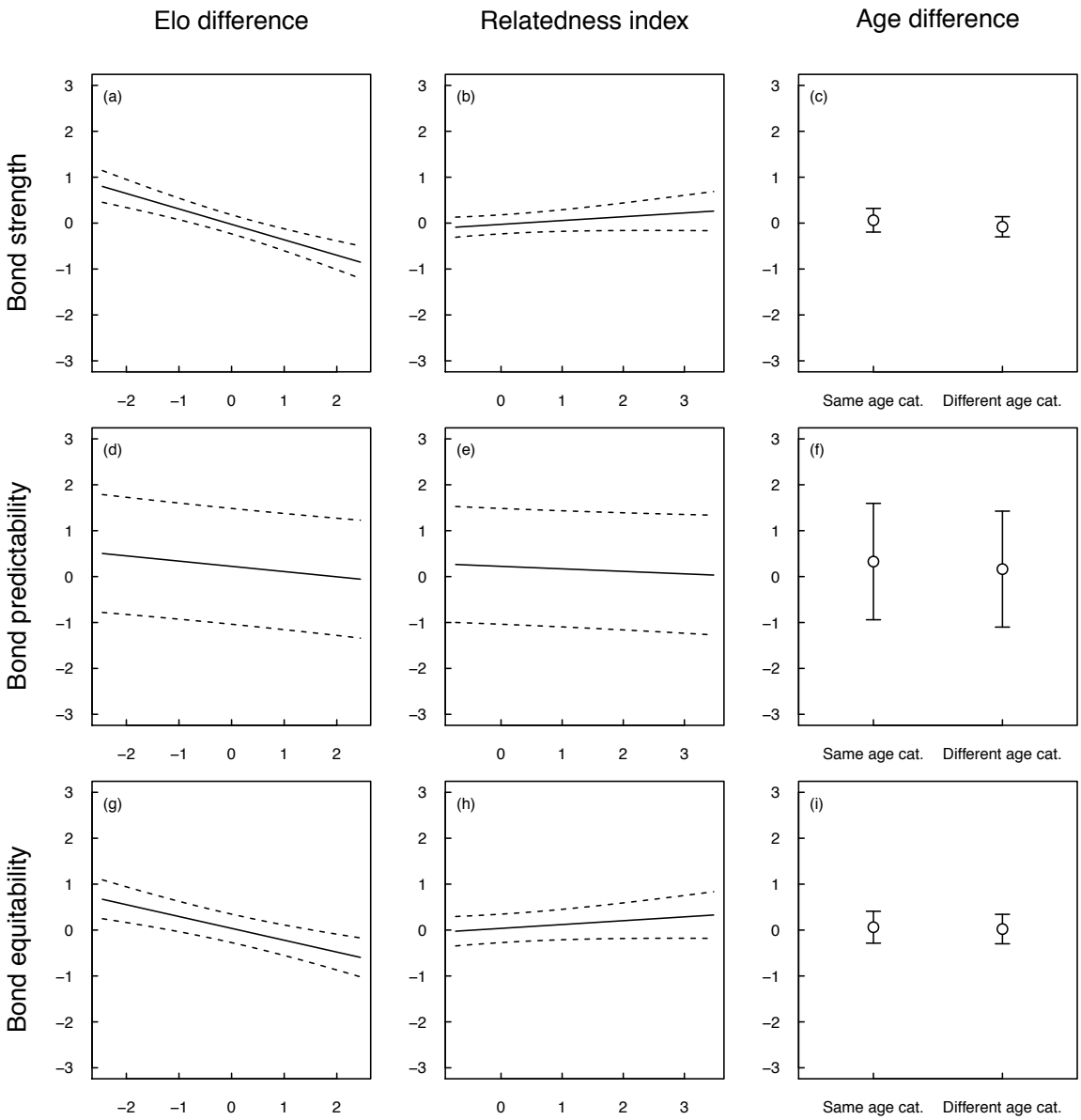

Figure 3: Effect of Elo difference ((a), (d), (g), from left to right = smaller to greater difference), relatedness ((b), (e), (h), from left to right = smaller to greater difference) and age difference ((c), (f), (i)) on bond strength ((a) to (c), from bottom up = weak to strong scores), bond predictability ((d) to (f), from bottom up = low to high predictability), and bond equitability ((g) to (i), from bottom up = from low to high equitability). The straight full line represents the estimate variation as predicted by the model, the dotted lines are the associated lower and upper 95% confidence intervals of the estimate.

The value of social bonds

Rates of support between adult females were low; we recorded a total of 206 coalitionary events (48 peaceful interventions, 158 aggressive ones) in the two groups over a total of 3,208 aggressive interactions. A female was found to be feeding in the proximity of another female around

once in every ten times she was found in proximity with that female (median = 0.11, range = 0.00 – 0.39, feeding scan per proximity scan). Females engaged in aggressive interactions with each other about once every two hours (for details see Duboscq and colleagues (2013)).

Coalitionary support was not explained by any of the tested bond characteristics ($LRT_{full-null}$: $\chi^2_3 = 2.14$, $P = 0.543$; Table 2; Figure 3). In contrast, dyads that had stronger and less predictable bonds fed more often in proximity than others ($LRT_{full-null}$: $\chi^2_3 = 13.56$, $P = 0.004$; strength: β ± SE [95% CI] = 0.17 ± 0.06 [0.05 - 0.30]; predictability: β ± SE [95% CI] = -0.20 ± 0.07 [-0.33 - -0.07]; Table 2; Figure 3). Finally, dyads that had stronger bonds were more frequently aggressive towards each other, while those with more equitable bonds fought less often than others ($LRT_{full-null}$: $\chi^2_3 = 24.79$, $P < 0.001$; strength: β ± SE [95% CI] = 0.28 ± 0.06 [0.16 - 0.40]; equitability: β ± SE [95% CI] = -0.19 ± 0.06 [-0.30 - -0.08]; Table 2; Figure 4).

Table 2: Bond components and fitness-related benefits

	Coalitionary support		Feeding in proximity		Aggression	
LRT Null vs. full	$\chi^2_3 = 2.14$, $P = 0.543$		$\chi^2_3 = 13.56$, $P = 0.004$		$\chi^2_3 = 24.79$, $P < 0.001$	
Variables	β ± SE	95% C.I [lower upper]	β ± SE	95% C.I [lower upper]	β ± SE	95% C.I [lower upper]
Intercept	-0.11 ± 0.50	[-1.10 0.88]	0.02 ± 0.21	[-0.40 0.43]	0.01 ± 0.12	[-0.25 0.23]
CSI	0.23 ± 0.17	[-0.10 0.57]	0.17 ± 0.06	[0.05 0.30]	0.28 ± 0.06	[0.16 0.40]
CV	0.05 ± 0.19	[-0.31 0.41]	-0.20 ± 0.07	[-0.33 -0.07]	-0.01 ± 0.06	[-0.12 0.11]
EI	-0.05 ± 0.16	[-0.36 0.26]	-0.02 ± 0.06	[-0.10 0.14]	-0.19 ± 0.06	[-0.30 -0.08]
Elo difference	-0.37 ± 0.17	[-0.70 -0.03]	0.02 ± 0.06	[-0.11 0.15]	-0.08 ± 0.06	[-0.20 0.04]
DML	-0.05 ± 0.15	[-0.34 0.24]	-0.00 ± 0.06	[-0.12 0.11]	-0.08 ± 0.05	[-0.18 0.03]
Age difference	0.73 ± 0.32	[0.10 1.35]	0.11 ± 0.12	[-0.13 0.35]	0.02 ± 0.11	[-0.20 0.24]

Results of GLMMs testing the influence of bond strength (CSI), bond predictability (CV), and bond equitability (EI) on coalitionary support, feeding in proximity and aggression, while controlling for dyad similarity characteristics, Elo difference, degree of genetic relatedness (DML) and age difference (N = 286). LRT – likelihood ratio test, β ± SE = estimate and standard error, C.I. = confidence intervals.

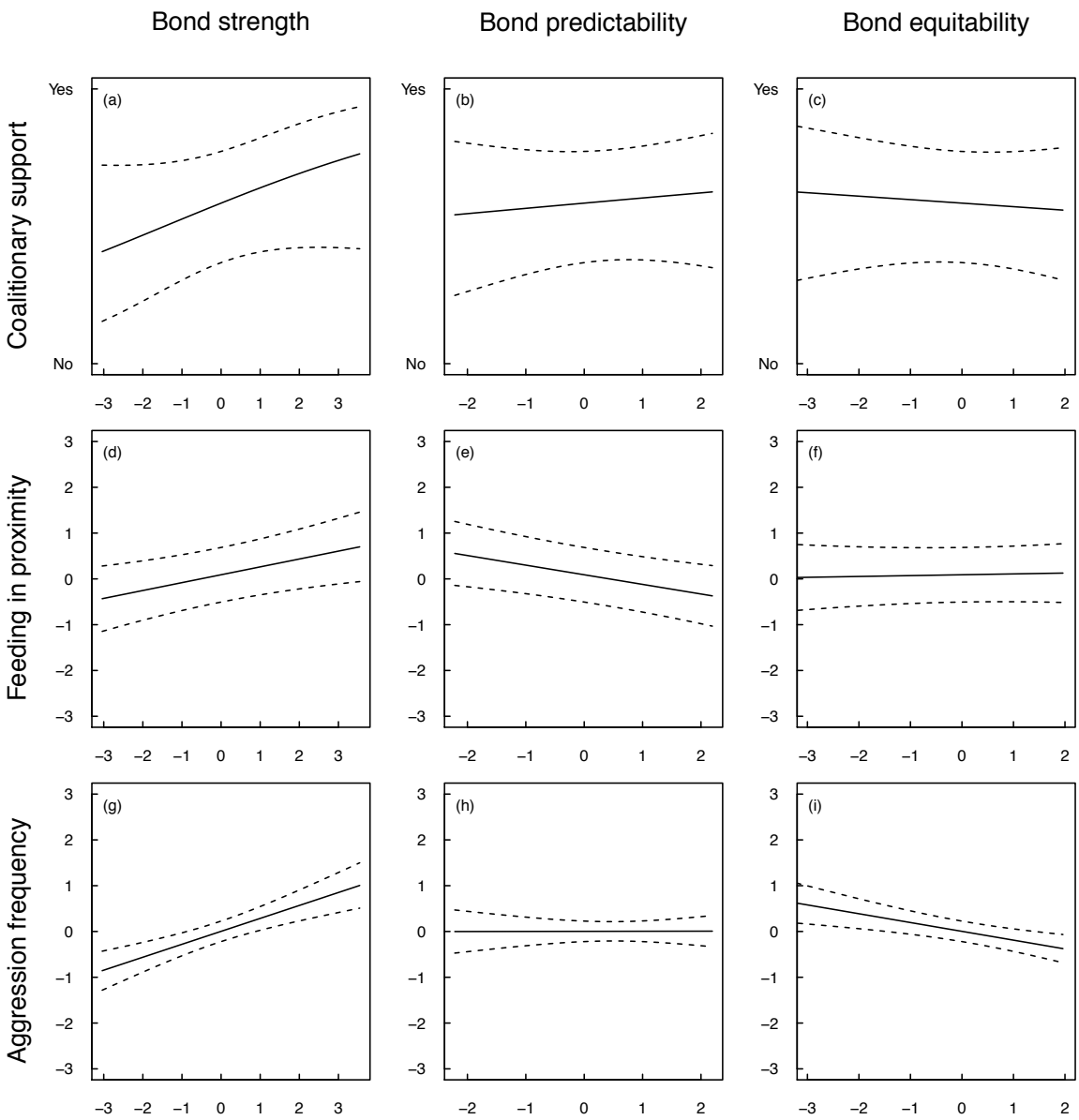

Figure 4: Effect of bond strength ((a), (d), (g), from bottom up = weak to strong scores), bond predictability ((b), (e), (h), from bottom up = low to high predictability), and bond equitability ((c), (f), (i)) (from bottom up = from low to high equitability) on coalitionary support ((a) to (c)), feeding in proximity frequency ((d) to (f), from bottom up = from low to high frequency), and aggression frequency ((g) to (i), from bottom up = from low to high frequency). The straight full line represents the estimate variation as predicted by the model, the dotted lines are the associated lower and upper 95% confidence intervals of the estimate.

Discussion

Social bonds in the studied female crested macaques showed contrasting patterns in their structure and value compared to other species with nepotistic hierarchical societies for which comparable data are available. Bonds were mostly of average strength (i.e. median strength close to

the mean, 1, and relatively symmetric distribution), relatively equitable but only moderately enduring over the 19 months of the study. Social bonds were stronger, more predictable and more equitable amongst females close in dominance status than others, but not amongst kin or age peers. The three components of social bonds were correlated but had differential effects on the three fitness-related behaviours investigated. Thus, our predictions that dyad characteristics have little influence on social bond components and that these components have relatively weak effects on fitness-related behaviours were mostly fulfilled, showing the extent to which the studied females can express great degrees of freedom within their established network of relationships.

We observed a relatively weak influence of kinship on female social relationships; compared with less related females, more related females did not form significantly stronger, more predictable or equitable bonds, revealing a weakly nepotistic society. Several factors may contribute to the observed weak nepotism. First and foremost, the fact that we could not distinguish matrilines, due to the lack of a pedigree, and could not differentiate maternal from paternal relatives may have hidden kinship effects on behaviour. In several mammals, paternal relatives interact with each other substantially more often than with non-kin but also substantially less often than with maternal kin (Smith, Albers, & Altmann, 2003; Wahaj et al., 2004; Wenzel et al. 2013). Male reproductive skew and group tenure influence the proportion of paternal relatives in a group (Widdig 2013); high male reproductive skew and short male tenure, which is a characteristic of this population of crested macaques (Higham et al., 2012; Marty et al., 2015), can lead to a relatively high proportion of paternal relatives. These conditions have been hypothesised to be a strong driver for high social tolerance amongst female macaques (Schülke & Ostner, 2008). Indeed, a weak kin bias amongst numerous paternal relatives may blur a strong kin bias between fewer maternal relatives. A hint to that effect is the relatively consistent positive influence of small dominance differences (most likely maternal rather than paternal relatives) on social behaviour whereas age difference had little to no effect (peers are more likely to be paternal than maternal relatives). Another related factor is the use of a continuous measure of kinship, which may have obscured any distinction between kin categories (e.g. mother-daughter, sister-sister) that may be of greater significance for individuals (Kapsalis & Berman, 1996).

499 Notwithstanding these limitations, these results indicate that an overall weak kin bias in social
500 relationships constitutes a shared characteristic of tolerant societies, such as Barbary (*M. sylvanus*)
501 and Tonkean macaques (*M. tonkeana*), which contrasts with more despotic species of macaques and
502 other primates such as baboons (Cords, 2012; Paul, 2006; Thierry, 2007). This finding is also
503 consistent with predictions from the primate socioecological model (Sterck, Watts, & van Schaik,
504 1997); a weakly nepotistic hierarchy may indeed stem from the low profitability of kin support when
505 rank-related fitness benefits are not pronounced because direct competition for food is relatively low
506 (Chapais, 2004). The study population indeed lives in a felid-predator-free, food-abundant
507 environment (O'Brien & Kinnaird, 1997). Higher-ranking females appear to reproduce better than
508 low-ranking females, but this pattern varies with demographic and ecological conditions (Kerhoas et
509 al., 2014). The observed weak nepotistic pattern is common in other animal societies with high
510 cooperation levels and even more flexible social structures (e.g., meerkats: Clutton-Brock, 2009;
511 hyenas: East & Hofer, 2010; raccoons: Hirsch, Prange, Hauver, & Gehrt, 2013; chimpanzees:
512 Langergraber, Mitani, & Vigilant, 2007), which suggests great potential for relatively high degrees of
513 freedom in social relationships in the crested macaques too.

514 Overall, female-female bond strength did not show the typical asymmetrical distribution of
515 more despotic primate species (at least those for which similar data are available: Assamese macaque
516 males, Kalbitz, Ostner, & Schülke, 2016; chacma baboon females, Silk et al., 2006b; Barbary
517 macaque males, Young, Majolo, Schülke, & Ostner, 2014), indicating that female crested macaques
518 formed mostly bonds of median strength (close to the average of the group which is by definition
519 equal to 1), some weak and some strong bonds, and very few very strong bonds. This pattern is
520 strikingly different from the typical few strong-many weak bonds pattern found in the above
521 mentioned species and confirms the propensity of female crested macaques to form diverse and large
522 affiliative networks (Duboscq et al., 2013). Furthermore, bond strength and equitability were
523 negatively related to predictability, such that stronger and more equitable bonds were less predictable
524 than weaker and less equitable bonds. This result indicates the limited endurance of strong bonds
525 compared to average or weak bonds, which also contrasts with findings in other species in which
526 strong bonds appeared very stable over time (e.g., Kalbitz et al., 2016; Mitani, 2009; Silk et al.,

527 2006a; Young et al., 2014). The temporal variation found in bond strength suggests that preferred
528 associations of female crested macaques are of an opportunistic nature. Although the actual number of
529 strongest and weakest bonds a female has may remain constant, the identity of those partners and the
530 absolute values of CSI vary considerably. This is likely to be related to varying social contexts that we
531 did not address in our current study, such as the presence or absence of dependent infants (variable
532 throughout the year), social instability due to demographic changes (e.g. frequent male migration) or
533 changes in environmental conditions (e.g. massive seasonal fruiting of fig trees), all of which have
534 been shown to modulate relationships between group members (Barrett & Henzi, 2001; East & Hofer,
535 2010; Henzi et al., 2009; Wrangham & Rubenstein, 1986). Investigating the effect of these socio-
536 demographic events on bond formation and maintenance will be a fruitful endeavour in understanding
537 better social dynamics. Furthermore, we advocate using continuous social indices instead of
538 categories based on arbitrary cut-off points that are typically reported, such as three top partners
539 versus remaining partners. Until evidence accumulates that these cut-offs are meaningful to
540 individuals, we think it is prudent to move away from categorizations of social bonds into classes and
541 to take into account the full breadth of the network of social relationships in order to fully
542 comprehend the extent of social dynamics (see for example Young, 2016).

543 The most consistent finding in our study was the effect of dominance rank differences, i.e.
544 strong, predictable and equitable bonds were more likely to be formed by dyads with small
545 differences in dominance rank. In female primates and hyenas, the maintenance of these bonds has
546 been linked to competition for social partners, as females struggle for access to the highest-ranking
547 females and end up socialising most with affiliates of adjacent ranks due to competitive exclusion
548 (Seyfarth, 1977). However, because in the study population power asymmetries between females were
549 relatively moderate, counter-aggression frequent and affiliative and proximity networks quite diverse
550 (Duboscq et al., 2013), we argue that social competition was low and competitive exclusion was
551 ineffective so this hypothesis does not provide a satisfying explanation for our results. Social bond
552 formation and maintenance may instead involve the reciprocal exchange of social commodities if
553 adjacently-ranked partners were generally more similar – in terms of personality, energetic needs or
554 reproductive state – or competent partners in cooperation (Chapais, 2006; Schino & Aureli, 2009).

These reciprocal exchanges could be highly dynamic and opportunistic in a biological market susceptible to environmental and social conditions (Barrett & Henzi, 2006; Noë & Hammerstein, 1994), thereby generating a potential source of variation in the endurance of social bonds too.

The potential opportunistic nature of these social bonds seems also apparent in the analyses of their potential adaptive value. Previous studies on the same population showed somewhat contrasting results. The strength of social bonds was related to anti-predator responses, indicating their importance in threatening situations (Micheletta et al., 2012). However, the equitability and predictability, rather than strength, of social bonds influenced the occurrence of conflict management behaviour (Duboscq et al., 2014). Furthermore, the occurrence of reconciliation – an important mechanism of social cohesion – appears to function as appeasement, a short-term tactic, rather than to repair relationships, a more long-term strategy (Duboscq et al., 2014). In the current study, variance in bond characteristics helped only to a certain extent to explain variation in three additional fitness-related behaviours. First, more strongly bonded females fed more often in proximity but also fought more often with each other than females with weaker bonds. This indicates that more strongly bonded dyads may be more resilient to disruptions of their bond (by aggression) over food than less strongly bonded dyads (Aureli, Fraser, Schaffner, & Schino, 2012). Second, this is consistent with the finding that partners with less predictable bonds also fed more often in proximity, as stronger bonds tended to be less predictable. The link between bond predictability and co-feeding frequency suggests either that partners with enduring relationships avoid endangering the stability of their relationship over feeding competition, or that the endurance of bonds is affected by another factor that we have not considered, for example female energetic needs (perhaps in relation to reproductive state). Third, the negative relationship between equitability and aggression rate could indicate that less equitable dyads often need to negotiate their relationship through engaging in agonistic interactions, which are often mild in this species (Duboscq et al., 2013). This could be the case if one partner gets frustrated to be at the lesser end of the social exchange, especially since less equitable bonds also tended to be weaker in strength. These results stress the need to consider more than one dimension of social bonds simultaneously in order to get a more integrative picture of how animals balance the costs and benefits of social bonds. Experiments involving cooperative tasks could help disentangle the

respective weight of bond characteristics in social decision-making in terms of partner choice, coalition formation, trust or punishment.

Overall, it appears that the female crested macaques under study generally form a dynamic number and large diversity of good average partners, rather than a tight network of enduring strong ones, perhaps similar to what has been suggested for males of the same species (Neumann, 2013; Neumann, Agil, Widdig, & Engelhardt, 2013). As such, females seem able to express great degrees of social freedom with regards to their dominance and kin relationships (Butovskaya, 2004; Thierry, 1990). Nevertheless, females also seem to specifically rely on certain partners, with whom they have strong, predictable or equitable bonds, in specific contexts (post-conflict interactions, Duboscq et al., 2014) or in especially challenging situations (predator deterrence, Micheletta et al., 2012). This "many-good-friends" strategy can be costly temporally and energetically, but it can also bring a wide range of benefits, including enhanced negotiation skills, improved collective decision-making, and facilitated cooperation in joint-action problems (Hare, Melis, Woods, Hasting, & Wrangham, 2007; McComb & Semple, 2005; Petit, Desportes, & Thierry, 1992; Sueur & Petit, 2008; Thierry et al., 2008).

The contrast between the stability of the social structure of macaques, in general, and the degrees of freedom shown by female crested macaques, in particular, in establishing and maintaining relationships leads to questions about the temporal dynamics of social bonds and the short- and long-term reciprocity of social exchanges within stable societies. It highlights the need to consider more carefully the whole network of bonds, weak and strong, in a more integrated continuous way as has been advocated by Granovetter already in 1973. More importantly, fitness-related behaviours, like coalitionary support, are presumably based on long-term alliances. Thus, to what extent patterns in so-called strategic behaviours can actually resist the magnitude of changes in social bonds is currently not clear. It is possible that females with stronger, more equitable, more predictable bonds or more numerous such partners benefit from a better extrinsic support network than others (Harcourt 1989; Silk 2007). This extrinsic power may not be "observable" as such because it often translates into conflict prevention or avoidance. Investigating this question could help to determine how dynamic societies actually are and whether species or population differences in dynamics exist. Fluctuations in

social networks are indeed pervasive in species with flexible (Schradin, 2013) or seasonal sociality (Blumstein, 2013; Brent et al., 2013; Prange, Gehrt, & Hauver, 2011). Whether our findings reflect a pattern more common than previously thought or are typical for this study population remains to be investigated and requires comparative studies. This is of tremendous importance to better understand the social components of fitness and the mechanisms linking sociality to fitness.

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Conflict of Interest

All authors declare they have no conflict of interest of any kind.

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941 **Appendix**

942

943 **Complete DNA analysis protocol**

944 We first measured DNA purity by absorbance of a subset of our samples to verify that extraction has
945 been successful and that samples were of good enough quality (Morin et al. 2001). We amplified 12
946 short-tandem repeats (or microsatellites), 10 tetranucleotide loci and 2 dinucleotide loci, proven to be
947 informative in humans and other primates (* or + indicates primers that have been modified
948 specifically for *Macaca fascicularis* or *M. nigra* respectively: D1s548, D3s1768*, D5s1457, D6s493^{+},
949 D6s501^{+}, D7s2204, D10s1432, D11s925, D12s67^{+}, D13s765*, D14s255^{+}, D18s536; Bayes et al.,
950 2000; Zhang et al., 2001; Engelhardt & Perwitasari-Farajallah, unpublished data). We used a two-step
951 multiplex chain polymerase reaction (PCR) approach (Arandjelovic et al., 2009). In a first step, all
952 loci were amplified in a single reaction with 4 µL of DNA extract (diluted 1:25 - 1:50) for each 20 µL
953 of reaction product, 2 µL H_2O, 2 µL QIAGEN enzyme buffer (25 mM Tris-HCl pH 8.0, 35 mM KCl,
954 0.1 mM EDTA, 1 mM DTT, 50% glycerol, 0.5% Tween 20, 0.5% Igepal CA-630 and stabilizers), 1
955 µL dNTPs 0.5 mM, 0.8 µL bovine serum albumine (BSA) 20 mg/mL, 0.4 µL MgCl 25 mM, 0.4 µL of
956 each primer unlabelled forward and reverse, 0.2 µL QIAGEN Hot Master Taq 5 U/µL) in an
957 Eppendorf ® Master Gradient machine.

958 We started with 2 min of denaturation at 94ºC, then ran 30 cycles of 20 sec. of denaturation at 94ºC,
959 30 sec. of annealing at 54ºC, 30 sec. of elongation at 70ºC and ended with 10 min of final elongation
960 at 70ºC. We followed multiplex PCR by singleplex PCRs, following the same protocol but with each
961 primer separated and different annealing temperatures specific to each primer. We included 1 µL of
962 multiplex PCR product and 19 µL of reaction product (14 µL H_2O, 2 µL QIAGEN enzyme buffer (25
963 mM Tris-HCl pH 8.0, 35 mM KCl, 0.1 mM EDTA, 1 mM DTT, 50% glycerol, 0.5% Tween 20, 0.5%
964 Igepal CA-630 and stabilizers), 1 µL dNTPs 0.5 mM, 0.8 µL BSA 20mg/mL, 0.5 µL of specific
965 fluorescently labelled (HEX or FAM) primer forward and reverse, 0.2 µL QIAGEN Hot Master Taq 5
966 U/µL). For primers D3s1768, D6s501, and D12s67, we also added 0.4 µL MgCl 25 mM for better
967 results, and consequently lowered the quantity of H_20 by the same amount. Singleplex PCR products

968 were then prepared for sequencing by diluting PCR products between 1:25 and 1:100, and mixing 1.5
969 µL of diluted product into 14 µL of HiDye Formamide buffer mixed with a size standard (HD400
970 from Applied Biosystems ®).
971
972 **Model randomizations**
973 In the following, we present results of a randomization procedure to assess the effects of assigning
974 individuals to ID1 and ID2 in our mixed models. Specifically, for each model we assigned the two
975 individuals of each dyad randomly to ID1 and ID2. This was done independently for each dyad. With
976 such a randomized data set, we refitted our models, extracted parameters and repeated this step 500
977 times for each of the six models.
978 For each of the six models, we calculated the following summary statistics across the 500
979 randomizations: (1) mean parameter estimates, (2) 90% and 10% percentiles of the parameter
980 estimates, (3) mean standard errors of the parameter estimates and (4) mean 95% confidence intervals.
981 Overall, the results from this procedure suggest that the assignment of individuals within dyads had
982 no consequences as far as our conclusions are concerned and that our models were stable with regards
983 to variation in our random effects structure.
984 PLEASE CONTACT THE CORRESPONDING AUTHOR FOR MORE DETAILS OR SEE THE
985 COPY-EDITED PAPER.