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Degrees of freedom in social bonds of crested macaque females.

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Abstract

Social bonds between group members can 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 dyadic 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 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.

1 Degrees of freedom in social bonds of crested macaque females.

2

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30 **Abstract**

31

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

54

55 **Keywords**

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

57

58 **Introduction**

59

60 Social bonds are positive social relationships amongst pairs of individuals of the same group
61 (Silk, Cheney, & Seyfarth, 2013; Silk 2007a). They are defined in a multidimensional space of
62 relationship qualities such as relative strength, predictability (or magnitude of change over time) and
63 equitability (the balance of social exchanges within a dyad) (Silk et al., 2013; Whitehead, 2008).
64 Variation in these components can affect individual fitness inasmuch as individuals with more
65 numerous, stable or stronger bonds experience enhanced survival, greater reproductive success or
66 improved general well-being compared to others (feral horses (*Equus caballus*), Cameron, Setsaas, &
67 Linklater, 2009; bottlenose dolphins (*Tursiops sp.*) Frère et al., 2010; talapoin monkeys (*Miopethicus*
68 *talapoin*), Keverne, Martensz, & Tuite, 1989; Barbary macaques (*Macaca sylvanus*), McFarland &
69 Majolo, 2013; Young, Majolo, Heistermann, Schülke, & Ostner, 2014; chacma baboons (*Papio*
70 *cynocephalus ursinus*), Silk et al., 2009, 2010; humans (*Homo sapiens*), Uchino 2006). For
71 individuals, the value of social bonds is also related to the direct or indirect benefits they may obtain
72 from daily social exchanges (primate males: Ostner & Schülke, 2014; mammalian females: Silk,
73 2007a), e.g. reciprocation of social grooming, reduction of aggression, increased coalitionary support
74 during conflicts, or better access to food resources (ravens (*Corvus corax*), Fraser & Bugnyar, 2011;
75 baboons (*P. ursinus*), King, Clark, & Cowlshaw, 2011; spotted hyenas (*Crocuta crocuta*), Smith,
76 Memenis, & Holekamp, 2007), which ultimately may impact their fitness and well-being.

77 In order to understand the function and value of social bonds, i.e. which benefits can be
78 obtained by forming and maintaining them, it is also crucial to investigate their underlying structure,
79 i.e. the characteristics of the dyads forming particular bonds. In many animal societies, individuals
80 that are similar in terms of relatedness, dominance status, personality, reproductive state or energetic
81 needs are more likely to form strong and enduring social bonds than others (yellow-bellied marmots
82 (*Marmota flaviventris*): Armitage & Schwartz, 2000; chacma baboons: Barrett & Henzi, 2001;
83 giraffes (*Giraffa camelopardalis*), Carter, Seddon, Frère, Carter, & Goldizen, 2013; mountain goats
84 (*Oreamnos americanus*), Godde, Côté, & Réale, 2015; rhesus macaques (*M. mulatta*), de Waal &

85 Lutrell, 1986; ring-tailed coatis (*Nasua nasua*), Hirsch, Staton, & Maldonado, 2012). Each of these
86 characteristics can be uniquely important in influencing the formation and maintenance of a bond. For
87 instance, although close kin are obvious coalition partners, kin-based coalitionary support may not be
88 advantageous if such kin are low-ranking (Chapais, 2006), in which case establishing a bond with a
89 higher-ranking non-relative may be more valuable (primates: Schino, 2007; hyenas: Smith et al.,
90 2010).

91 Research on the benefits of social bonds amongst same-sex adult group members has so far
92 mostly considered how bond characteristics at the extreme positive end of the spectrum affect
93 measures of fitness, health or well-being, e.g. preferred associates (Frère et al., 2011) or top three
94 partners (Silk et al., 2006a). However, animals may have a variety of options for regulating the
95 consequences of bonds. First, the predictability and equitability of an individual's social relationships
96 may be as important as their strength (e.g. the sheer amount of research on cooperation and
97 reciprocity: Nowak, 2006; Trivers, 1971, 2006). In addition, "weak" bonds, as opposed to "strong"
98 bonds, within a social network may also be important. For example, weak bonds contribute to
99 stabilising the overall network in *Escherichia coli* (Csermely, 2004). In humans, although a few
100 strong bonds are individually more influential, more numerous weak bonds enhance the propagation
101 of novel information (Bakshy, Rosenn, Marlow, & Adamic, 2012). Finally, it has been shown that
102 variance in bond strength is actually more predictive of fitness than strength itself (longevity in rock
103 hyraxes (*Procavia capensis*), Barocas, Ilany, Koren, Kam, & Geffen, 2011; pup production in degus
104 (*Octodon degus*), Wey, Burger, Ebensperger, & Hayes, 2013). Studies integrating the different
105 dimensions of social bonds simultaneously and on a continuous scale are therefore indispensable for
106 deepening our understanding of the link between sociality and fitness.

107 It has also been argued that social bonds are likely to be formed and maintained based on
108 contingencies (short-term, opportunistic tactics) rather than, or in addition to, long-term, fixed
109 strategies (Barrett & Henzi, 2001, 2006). For instance, female chacma baboons did not sustain
110 constant differentiated relationships with other females across time but changed cyclically between
111 "brief associations", "casual acquaintances" and "constant companionships" according to food
112 availability (i.e. between food-abundant and food-scarce periods) (Henzi, Lusseau, Weingrill, van

113 Schaik & Barrett, 2009). In addition, pregnant or early lactating female chacma baboons were less
114 likely to become involved in coalitions and, thus, were not reliable cooperation partners for both kin
115 and non-kin (Barrett & Henzi, 2001). Therefore, individuals may use varying social strategies
116 reflecting certain degrees of social freedom according to social context, the spatial or temporal
117 availability of partners, or environmental conditions, even when living in stable organised societies.
118 Although this seems rather straightforward in animal societies that display flexibility in their social
119 structure (i.e. group membership and group size regularly changing, such as in fission-fusion
120 societies), variation in social strategies only recently began to be considered in species with a stable
121 nepotistic hierarchical social structure such as those of many primates, of hyenas or African elephants
122 (Barrett & Henzi, 2001; Ilani, Booms, & Holekamp, 2015; Sick et al., 2014).

123 Macaques (genus *Macaca*) are an ideal candidate for the investigation of variation in social
124 strategies. Although the different macaque species share the same social organisation (philopatric
125 females organised in stable matrilineal dominance hierarchies), macaque species are described as
126 more or less socially tolerant depending on the degree of nepotism, power asymmetries, conciliatory
127 tendencies and counter-aggression in social relationships (Thierry, 2007; Thierry, 2013). Such social
128 variation can be expected to influence the structure and function of social bonds (Thierry, 1990;
129 Butovskaya, 2004). Specifically, when power asymmetries are pronounced and the degree of
130 nepotism is high, as in less tolerant species, individuals' options regarding who to interact with and
131 how are limited. These constraints may lead to individuals having a relatively low number of strong,
132 predictable and equitable partnerships within a social group. In contrast, when social rules are more
133 relaxed, i.e. when power asymmetries are moderate and the degree of nepotism is weak, as in more
134 tolerant macaques, individuals are able to interact with diverse partners and develop a greater
135 diversity and number of social bonds (Thierry, 1990; Butovskaya, 2004; Cooper & Bernstein 2008;
136 Duboscq et al., 2013). Thus, the degrees of freedom that individuals have in their relationships within
137 their group can be assessed through the size and diversity of their social network in relation to the
138 influence of dominance and kinship on an individual's social options – or lack thereof (Thierry, 1990;
139 Butovskaya, 2004).

140 In this study, we aim to investigate these degrees of freedom and the interplay between the
141 structure and the value of social bonds in wild female crested macaques (*M. nigra*), which express a
142 tolerant social style (Petit, Abegg, & Thierry, 1997; Duboscq et al., 2013). The study population of
143 crested macaques lives in a relatively predictable and safe ecological environment (low predation risk
144 and abundant food year round; O'Brien & Kinnaird, 1997) while facing dynamic social conditions,
145 e.g. male migration and hierarchical changes, which are a potential source of social instability in the
146 group (Neumann, 2013; Marty, Hodges, Agil, & Engelhardt, in press). Females reproduce year round
147 (Kerhoas et al., 2014), which is another potential source of fluctuation in the amount of time and
148 attention females can devote to their female social partners (D'Amato, Troisi, Scucchi, & Fuccillo,
149 1982; Bardi, Shimizu, Fujita, Borgognini Tarli, & Huffman, 2001; Barrett & Henzi, 2001; Brent,
150 MacLarnon, Platt, & Semple, 2013). Previous studies on the same population showed that female
151 crested macaques form highly diverse affiliative social networks (Duboscq et al., 2013). On the one
152 hand, the strength of female-female social bonds was linked to predator deterrence, suggesting that
153 strong bonds play a role in enhancing survival (Micheletta et al., 2012). On the other hand, bond
154 strength did not affect the occurrence and frequency of reconciliation, an important conflict
155 management strategy (Duboscq, Agil, Engelhardt, & Thierry, 2014). Nonetheless, other relationship
156 qualities, such as equitability and predictability, increased the likelihood of reconciliation (Duboscq et
157 al., 2014). As such, it seems that social bond characteristics have different values depending on the
158 context of the social benefits to be gained in this species and we would expect that females express
159 great degrees of social freedom.

160 Specifically, since macaques form stable matrilineal hierarchical societies (Cords, 2012), kin
161 and adjacently-ranked dyads are expected to form the strongest, most predictable and equitable bonds
162 (Silk, 2007b). However, given the tolerant social style of crested macaques and their expected great
163 degrees of social freedom, we made the hypothesis that these dyad characteristics would not predict
164 social bond strength, equitability and predictability. To test this prediction and to establish the
165 structure of bonds, we analysed the relationship between three measures of dyadic similarities (degree
166 of relatedness, proximity in age and dominance rank) and three social bond characteristics, namely
167 strength, predictability and equitability. Furthermore, under the hypothesis that social bond

168 characteristics are linked to fitness in a positive predictable way (Silk, 2007a, b), variation in these
169 characteristics is expected to explain a substantial amount of variation in the occurrence or frequency
170 of behaviours directly or indirectly linked to fitness benefits, such as a reduction in aggression,
171 increased coalitionary support during conflicts or better access to food resources. However, again
172 given the tolerant social style of crested macaques and their expected great degrees of social freedom,
173 we made the hypothesis that the characteristics of social bonds will not predict the occurrence of these
174 fitness-related behaviours. To test this prediction and to establish the value of bonds, we tested the
175 extent to which each social bond characteristic influenced coalitionary support, feeding-in-proximity
176 and aggression. By taking a more integrated perspective of social bonds in a species with a tolerant
177 social style, we address the concept of individuals' degrees of social freedom within their stable
178 network of social relationships (Thierry, 1990; Butovskaya, 2004).

179

180 **Methods**

181

182 Behavioural data collection and analysis

183

184 *Field site, study animals and data collection*

185 Crested macaques are critically endangered and endemic to the island of Sulawesi, Indonesia
186 (Sugardjito et al., 1989). The study population inhabits the Tangkoko Reserve, North Sulawesi
187 (1°33'N, 125°10'E; e.g. Duboscq, Neumann, Perwitasari-Farajallah, & Engelhardt, 2008), broadly
188 classified as a lowland rainforest with seasonal variation in rainfall and fruit abundance (O'Brien &
189 Kinnaird, 1997). The study was part of the Macaca Nigra Project, a long-term field project on the
190 biology of crested macaques that started in 2006. We studied two groups, "PB" and "R1", comprised
191 of ca. 60 and 80 individuals respectively. The monkeys were fully habituated to human observers and
192 all adults could be individually identified based on physical characteristics.

193 JD and two field assistants collected behavioural data between October 2008 and May 2010
194 on all adult females (15 – 18 in PB, 21 – 24 in R1) using focal animal sampling (Martin & Bateson,
195 1993) (interobserver reliability: Cohen's kappa = 0.69–0.90, correlation coefficients between

196 behavioural variables = 0.79 – 0.98). We collected 30 minute-point-sample observations for activity
197 (foraging, feeding, socialising, resting, and travelling). Every second minute, we also noted the
198 identity of neighbours in three proximity categories: in body contact, within one body-length, and
199 within five body-lengths. We recorded focal social events continuously, including the start and end
200 time of interactions, the sequence of all behaviours, as well as the identity and behaviours of all social
201 partners. This study included a total of 2,480 hours of focal data focusing on 35 females that were
202 present during the entire study period (median_{PB} = 68 hours per female, range_{PB}: 65 – 78, N_{PB} = 14;
203 median_{RI} = 66 hours per female, range_{RI}: 59 – 71, N_{RI} = 21). Behavioural interactions were expressed
204 as duration (e.g. social grooming) or frequency (e.g. approach) per focal and per dyadic (sum of two
205 focals') observation time over the whole study period (i.e. 19 months).

206 Additionally, we collected at least three faecal samples from all females opportunistically (N
207 = 140, median per female = 4, range = 3 - 4). We followed a two-step alcohol-silica storage protocol
208 (Nsubuga, et al., 2004), after which the samples were stored at room temperature until DNA
209 extraction.

210

211 *Dyad characteristics*

212 Dominance difference: To account for power asymmetries between females, we used Elo-
213 rating (R package EloRating, Neumann & Kulik, 2013), which reflects an individual's success in
214 agonistic interactions and is based on temporal sequences of decided (clear winner and loser)
215 agonistic interactions (Albers & de Vries, 2001; Neumann et al., 2011). We made use of direct
216 aggressive interactions (i.e. threats, hits, chases, bites) and displacements or supplantations (i.e. one
217 individual approaches another one without any menacing behaviour and the other leaves without
218 protesting; for further definitions and more details, see Duboscq et al., 2013, Thierry et al., 2000)
219 taken from all agonistic data collected during focal observations and *ad libitum* data. At the beginning
220 of the observation period, each individual in a group starts with a rating of 1000, which is updated, i.e.
221 increased or decreased, after each agonistic interaction based on the outcome of the interaction (won
222 or lost), the previous ratings of both opponents and a determined factor, k (here k = 100, following
223 Neumann et al., 2011). As we aggregated all other behavioural data over the entire study period, we

224 used the female Elo-rating at the end of the study period. We then computed the absolute difference of
225 the Elo ratings (hereafter termed dominance difference) between the two members of a dyad.

226 Kinship: DNA was extracted from 100–150 mg of faeces with the GEN-IAL® All-tissue
227 DNA extraction kit following the manufacturer’s instructions. We amplified 12 short-tandem repeats
228 (or microsatellites - 10 tetranucleotide loci and 2 dinucleotide loci), proven to be informative in
229 humans and other primates (see Appendix). We used a two-step multiplex chain polymerase reaction
230 (PCR) approach (Arandjelovic et al., 2009). In the first step, all loci were amplified in a single
231 reaction in an Eppendorf® Master Gradient machine following cycles of denaturation, annealing and
232 elongation (see Appendix). We followed multiplex PCRs with singleplex PCRs, using the same
233 protocol but for each primer separately (see Appendix). Singleplex PCR products were then
234 sequenced in an ABI 3130xL sequencer. Allele sizes were finally read into PeakScanner (Applied
235 Biosystems®). Given that we had several samples per individual, allele sizes were considered
236 definitive when at least two different samples of the same individual produced the same results in at
237 least four amplifications for heterozygotes and six for homozygotes (multi-tubes approach, Taberlet et
238 al., 1996). Consensus genotypes were found for a median of 12 loci (range = 6 – 12) and processed
239 using COANCESTRY® software, which provides two likelihood methods and five moment
240 estimators of relatedness (Wang, 2011). We chose the dyadic maximum likelihood (DML) estimator
241 of Milligan (2003) because it proved to be the most reliable estimator of the mother-infant’s
242 theoretical degree of relatedness 0.5 (mean \pm SD = 0.51 ± 0.12 , N = 60 mother-infant pairs). DML
243 between adult females ranged between 0 and 0.72 with a median of 0.05 (median_{PB} = 0.05, range_{PB} =
244 0 – 0.53; median_{RI} = 0.05, range_{RI} = 0 – 0.72).

245 Age difference: We assessed the age category (young, middle-aged or old) females belonged
246 to based on their reproductive history (e.g. number of dependent infants or cycling status) known
247 since 2006, the shape of their nipples (e.g. short or long), the presence of physical injuries and their
248 general appearance. Based on these categories, we then scored dyads as belonging to the same or to
249 different age classes.

250

251 *Bond characteristics*

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

$$255 \quad CSI_{ij} = \left[\left(\frac{G_{ij}}{G} \right) + \left(\frac{P_{ij}}{P} \right) + \left(\frac{P_{posij}}{P_{pos}} \right) \right] / 3,$$

256 where G_{ij} is the grooming rate (duration of grooming given and received in minutes per hour of
 257 dyadic observation time) between individual i and j and G is the mean grooming rate across all dyads
 258 in the group; P_{ij} is the rate of close proximity (number of instances females were within one body-
 259 length of each other per hour of dyadic observation time) between individual i and j and P the mean
 260 proximity rate for all dyads in the group and P_{posij} is the rate of positive outcome upon approach
 261 (number of close proximity approaches followed by affiliation per hour of dyadic observation time)
 262 between individual i and j and P_{pos} the mean rate of positive outcome upon approach for all dyads in
 263 the group. A CSI above the average of all dyads in the group (equal to 1) indicates a strong bond (Silk
 264 et al., 2006b).

265 Bond temporal variation (hereafter predictability) was assessed over three periods of six
 266 months each. We calculated the CSI again for each dyad for each period, then computed the
 267 coefficient of variation (CV, standard deviation divided by the mean) over the three CSIs for each
 268 dyad (Majolo, Ventura, & Schino, 2010). The higher the CV, the lower the predictability of CSI
 269 values across the three periods, i.e. the more CSI values varied across the three periods. Note that, in
 270 this way, even weak but stable bonds will be considered predictable.

271 Bond equitability represents how balanced social exchanges are within a dyad (Silk et al.,
 272 2013). The Equitability Index (EI) was calculated as a composite symmetry index (Silk et al., 2013),
 273 computed from symmetry indices of the behaviours composing the CSI and was calculated as:

$$274 \quad EI_{ij} = \left[\left(1 - \left| \frac{G_{ij} - G_{ji}}{G_{ij} + G_{ji}} \right| \right) + \left(1 - \left| \frac{P_{ij} - P_{ji}}{P_{ij} + P_{ji}} \right| \right) + \left(1 - \left| \frac{P_{posij} - P_{posji}}{P_{posij} + P_{posji}} \right| \right) \right] / 3,$$

275 where G is grooming duration, P the rate of being in close proximity, P_{pos} the rate of positive outcome
 276 upon approach, and i and j the individuals in the dyad. An index of 1 indicates perfect equitability
 277 between the two individuals in the dyad, while 0 indicates that one individual alone was responsible

278 for all grooming and proximity interactions. Note that this index takes into account the directionality
279 of interactions.

280

281 *Fitness-related behaviours*

282 We defined coalitionary support as a focal female intervening aggressively or peacefully in
283 support of another female or receiving such an intervention herself during an aggressive interaction
284 with another individual (Petit & Thierry, 1994; Duboscq et al., 2014). We calculated the frequency of
285 support as the number of support instances over the total number of aggressive interactions each
286 member of the dyad was separately involved in (Duboscq et al., 2014). Due to the low frequency of
287 occurrences, for subsequent analyses we transformed this variable into a binary variable, i.e. the
288 behaviour did or did not occur within the dyad (Duboscq et al., 2014). We calculated the frequency of
289 feeding in proximity as the number of point samples spent feeding while other females were within 5-
290 body-length proximity, controlling for overall dyadic proximity and observation time. Hourly
291 frequencies of aggression were taken from Duboscq and colleagues (2013).

292

293 Statistical analyses

294

295 *Structure of social bonds*

296 We first tested for correlations between the three bond characteristics to assess their
297 relationships with each other and to test the prediction that stronger bonds would be more predictable
298 and equitable than weaker bonds. We built symmetric matrices of the CSI scores, the CVs and the EIs
299 before running a Quadratic Assignment Permutation (QAP) procedure with 1,000 permutations
300 between those matrices two-by-two (function qaptest in the sna package; Butts, 2008). We then built
301 three (generalised) linear mixed models (GLMM, Bolker et al., 2008), one for each of the social bond
302 components as response variables, including relatedness (DML), absolute Elo-rating difference (Elo#)
303 and age difference (age#, as a categorical variable, close/distant) as predictors and member 1 and
304 member 2 of the dyad and group as random effects.

305

306 *Function of social bonds*

307 We built three models to investigate the value of social bonds, with the occurrence of
308 coalitionary support, feeding-in-proximity rate and aggression rate as response variables and bond
309 strength (CSI), predictability (CV), equitability (EI), as well as relatedness (DML), absolute Elo-
310 rating difference (Elo#) and age difference (age#) as predictors and member 1 and member 2 of the
311 dyad and group as random effects.

312 All analyses were done in R version 3.2.1 (R Development Core Team, 2015). We
313 implemented GLMMs with a Gaussian (and Maximum Likelihood) or binomial error structure using
314 the function “lmer” from the package “lme4” (v. 1.1-11, Bates, Maechler, Bolker, & Walker, 2015).
315 We transformed numerical variables whenever necessary (log, square-root or fourth root) and
316 standardised all numeric variables to a mean of 0 and a standard deviation of 1 for optimal fitting and
317 the subsequent interpretation or comparison of model estimates. For all models, we checked a variety
318 of assumptions and diagnostics (normally distributed and homogeneous residuals, variance inflation
319 factors < 2 , Cooks’ distance, dfbetas; Field, Miles, & Field, 2012). No obvious violation of
320 assumptions was detected. We tested the final full model (including all fixed and random effects)
321 against an informed null model, i.e. including only the intercept, control factors (absolute Elo
322 difference, DML, and age difference) and random factors, using likelihood ratio tests (LRT). We used
323 95% confidence intervals to assess whether a predictor significantly contributed to explaining the
324 response variable (interval excluding 0). For clarity, detailed results from the models are given in
325 Tables A1 to A3 in the Appendix.

326

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

328 Microsatellite-based relatedness estimators have been deemed unreliable for accurately
329 measuring genetic relatedness in populations without pedigree information (Csilléry et al., 2006; van
330 Horn, Altmann, & Alberts, 2008). We tackled this issue by using the approach suggested by Tinsley
331 Johnson and colleagues (2014) of controlling for measurement error in relatedness estimates by
332 running models repeatedly with a random amount of error added to the observed relatedness value of
333 a given dyad. In our data, the maximum observed difference between the estimated relatedness

334 (DML) and the true theoretical relatedness ($r = 0.5$) of all 60 known mother-infant pairs was 0.41. We
335 therefore introduced an error taken from a random uniform distribution of numbers between -0.41 and
336 +0.41, which we feel is conservative as 95% of the DML values for known mother-infant pairs were
337 within 0.25 of the pairs' true relatedness ($r = 0.5$). Our costumed simulation proceeded in four steps:
338 1/ add an error between -0.41 and +0.41 to the DML index of all female-female dyads in the dataset,
339 2/ run the models again with the modified DML index, 3/ perform a likelihood ratio test between the
340 full model with modified DML and a reduced model excluding modified DML and 4/ determine the
341 number of simulations in which the significance of the effect of the modified DML index on the
342 response variable was different from the tests with the original models with the original data. The
343 DML index was not a significant predictor of the response variable in 96% to 100% of the 10,000
344 simulations, depending on the response variable, which indicates relatively robust results. Detailed
345 results of these simulations are given in Table A3 of the Appendix.

346

347 **Results**

348

349 The structure of social bonds

350

351 CSI scores ranged from 0.05 to 3.54 in the R1 group and from 0.16 to 4.99 in the PB group,
352 with a median of 0.89 and 0.88 respectively (Figure 1), indicating that in both groups, most bonds had
353 average strength (mean equal to one in each group). The distribution of CSI scores, giving an
354 assessment of how skewed dyadic affiliative behaviours are, was not right-skewed (Figure 1) as is
355 typical in other species, indicating that females established and maintained affiliative relationships
356 with numerous female partners. 45.7% (96/210 in R1) and 40% (42/105 in PB) of female dyads had a
357 CSI score above the average of the group (i.e., above 1) and the CSI score of the top 10% of dyads
358 was 2.34 in both groups (Figure 1). Females had a median of 9 (range 2–13) above-average (CSI > 1)
359 relationships in R1 and 6 (range 2–11) in PB.

360 The mean coefficient of variation (R1 = 0.66 ± 0.01 SD, PB = 0.70 ± 0.14 SD) indicated
361 moderate to low bond strength predictability across the three 6-months periods (Figure 2). 94% of all

362 females had at least one recurring partner over at least two periods amongst their three top partners
363 and 47% of all females had at least one recurring partner over all three periods amongst their top three
364 partners but no female had the same three recurring top partners across all three periods (Figure 2).

365 Bond equitability was overall relatively moderate ($\text{mean}_{R1} = 0.22 \pm 0.47 \text{ SD}$, $\text{mean}_{PB} = 0.27 \pm$
366 0.13 SD), indicating relatively balanced social exchanges amongst the two members of a dyad.

367 All three characteristics were positively correlated in both groups (QAP tests, PB: $N = 105$:
368 strength-predictability: $\rho = 0.59$, $p = 0.001$; strength-equitability: $\rho = 0.91$, $p < 0.001$;
369 predictability-equitability: $\rho = 0.95$, $p < 0.001$; R1: $N = 210$: strength-predictability: $\rho = 0.76$, $p =$
370 0.001 ; strength-equitability: $\rho = 0.85$, $p < 0.001$; predictability-equitability: $\rho = 0.65$, $p < 0.001$),
371 indicating that stronger bonds were more equitable but less predictable over time than weaker bonds
372 and that more predictable bonds were less equitable than less predictable ones.

373 Female dyads with smaller dominance differences had significantly stronger, more
374 predictable and more equitable social bonds than those with greater dominance differences (strength:
375 $\text{LRT}_{\text{full-null}}: \chi^2 = 39.45$, d.f. = 3, $p < 0.001$; $\beta \pm \text{SE}$ [95% CI] = -0.33 ± 0.06 [$-0.45 - -0.20$];
376 predictability: $\text{LRT}_{\text{full-null}}: \chi^2 = 8.53$, d.f. = 3, $p = 0.036$; $\beta \pm \text{SE} = 0.11 \pm 0.06$ [$0.00 - 0.19$];
377 equitability: $\text{LRT}_{\text{full-null}}: \chi^2 = 21.32$, d.f. = 3, $p < 0.001$; $\beta \pm \text{SE} = -0.25 \pm 0.06$ [$-0.37 - -0.13$]; Table
378 A1; Figure 2). None of the tested bond characteristics were related to the relatedness and age
379 difference of the dyads (Table A1).

380

381 The value of social bonds

382

383 Rates of support between adult females were low; we recorded a total of 206 coalitionary
384 events (48 peaceful interventions, 158 aggressive ones) in the two groups over a total of 3,208
385 aggressive interactions. A female was found to be feeding in the proximity of another female around
386 once in every ten times she was found in proximity with that female (median = 0.11, range = 0.00 –
387 0.39, feeding scan per proximity scan). Females engaged in aggressive interactions with each other
388 about once every two hours (for details see Duboscq and colleagues (2013)).

389 Coalitionary support was not explained by any of the tested bond components ($LRT_{full-null}: \chi^2$
390 $= 1.86$, d.f. = 3, $p = 0.603$; Table A2; Figure 3). In contrast, dyads that had stronger and less
391 predictable bonds fed more often in proximity than others ($LRT_{full-null}: \chi^2 = 11.15$, d.f. = 3, $p = 0.011$;
392 strength: $\beta \pm SE$ [95% CI] = 0.16 ± 0.06 [0.03 - 0.28]; predictability: $\beta \pm SE$ [95% CI] = 0.20 ± 0.07
393 [0.04 - 0.35]; Table A2; Figure 3). Finally, dyads that had stronger bonds were more frequently
394 aggressive towards each other, while those with more equitable bonds fought less often than others
395 ($LRT_{full-null}: \chi^2 = 23.54$, d.f. = 3, $p < 0.001$; strength: $\beta \pm SE$ [95% CI] = 0.25 ± 0.06 [0.12 - 0.37];
396 equitability: $\beta \pm SE$ [95% CI] = -0.20 ± 0.05 [-0.33 - -0.10]; Table A2; Figure 3).

397

398 Discussion

399

400 Social bonds in the studied female crested macaques showed contrasting patterns in their
401 structure and value compared to other species with nepotistic hierarchical societies for which
402 comparable data are available. Bonds were mostly of average strength (i.e. median strength close to 1
403 and moderately left-skewed distribution), relatively equitable but only moderately enduring over the
404 19 months of the study. Social bonds were stronger, more predictable and more equitable amongst
405 females close in dominance status than others, but not amongst kin or age peers. The three
406 components of social bonds were positively related but had differential effects on the three fitness-
407 related behaviours investigated. Thus, our predictions that dyad characteristics have little influence on
408 social bond components and that these components have relatively weak effects on fitness-related
409 behaviours were mostly fulfilled, showing the extent to which the studied females can express great
410 degrees of freedom within their established network of relationships.

411 We observed a relatively weak influence of kinship on female social relationships; compared
412 with less related females, more related females did not form significantly stronger, more predictable
413 or equitable bonds, revealing a weakly nepotistic society. Several factors may contribute to the
414 observed weak nepotism. First and foremost, the fact that we could not distinguish matriline, due to
415 the lack of a pedigree, and could not differentiate maternal from paternal relatives may have hidden
416 kinship effects on behaviour. In several mammals, paternal relatives interact with each other

417 substantially more often than with non-kin but also substantially less often than with maternal kin
418 (baboons: Smith, Albers, & Altmann, 2003; hyenas: Wahaj et al., 2004; rhesus macaques: Wenzel et
419 al. 2013). Male reproductive skew and group tenure influence the proportion of paternal relatives in a
420 group (Widdig 2013); high male reproductive skew and short male tenure, which is a characteristic of
421 this population of crested macaques (Higham et al., 2012; Marty et al., in press), can lead to a
422 relatively high proportion of paternal relatives. These conditions have been hypothesised to be a
423 strong driver for high social tolerance amongst female macaques (Schülke & Ostner, 2008). Indeed, a
424 weak kin bias amongst numerous paternal relatives may blur a strong kin bias between fewer maternal
425 relatives. A hint to that effect is the relatively consistent positive influence of small dominance
426 differences (most likely maternal rather than paternal relatives) on social behaviour. Another related
427 factor is the use of a continuous measure of kinship which may have obscured any distinction between
428 kin categories (e.g. mother-daughter, sister-sister) that may be of greater significance for individuals
429 (Kapsalis & Berman, 1996).

430 Notwithstanding these limitations, these results indicate that an overall weak kin bias in social
431 relationships constitutes a shared characteristic of tolerant societies, such as Barbary (*M. sylvanus*)
432 and Tonkean macaques (*M. tonkeana*), which contrasts with more despotic species of macaques and
433 other primates such as baboons (Paul, 2006; Thierry, 2007; Cords, 2012). This finding is also
434 consistent with predictions from the primate socioecological model (Sterck, Watts, & van Schaik,
435 1997); a weakly nepotistic hierarchy may indeed stem from the low profitability of kin support when
436 rank-related fitness benefits are not pronounced because direct competition for food is relatively low
437 (Chapais, 2004). The study population indeed lives in a felid-predator-free, food-abundant
438 environment (O'Brien & Kinnaird, 1997). Higher-ranking females appear to reproduce better than
439 low-ranking females, but this pattern varies with demographic and ecological conditions (Kerhoas et
440 al., 2014). The observed weak nepotistic pattern is common in other animal societies with high
441 cooperation levels and even more flexible social structures (e.g., chimpanzees: Langergraber, Mitani,
442 & Vigilant, 2007; meerkats: Clutton-Brock, 2009; hyenas: East & Hofer, 2010; raccoons: Hirsch,
443 Prange, Hauver, & Gehrt, 2013), which suggests great potential for relatively high degrees of freedom
444 in social relationships in the crested macaques too.

445 Overall, female-female bond strength did not show the typical left-skewed distribution of
446 more despotic primate species (at least those for which similar data are available: Assamese macaque
447 (*M. assamensis*) males: Kalbitz, Ostner, & Schülke, 2016; chacma baboon females: Silk et al., 2006b;
448 Barbary macaque males: Young, Majolo, Schülke, & Ostner, 2014), indicating that female crested
449 macaques formed mostly average-strength bonds and very few strong bonds. This pattern is strikingly
450 different from the typical few strong-many weak bonds pattern found in the above mentioned species
451 and confirms the propensity of female crested macaques to form diverse and large affiliative networks
452 (Duboscq et al., 2013). Furthermore, bond strength and equitability were negatively related to
453 predictability, such that stronger and more equitable bonds were less predictable than weaker and less
454 equitable bonds. This result indicates the limited endurance of strong bonds compared to average or
455 weak bonds, which also contrasts with findings in other species in which strong bonds appeared very
456 stable over time (e.g., Kalbitz et al., 2016; Mitani, 2009; Silk et al., 2006a; Young et al., 2014). The
457 temporal variation found in bond strength suggests that preferred associations of female crested
458 macaques are of an opportunistic nature. This is likely to be related to varying social contexts that we
459 did not address in our current study, such as the presence or absence of dependent infants (variable
460 throughout the year), social instability due to demographic changes (e.g. frequent male migration) or
461 changes in environmental conditions (e.g. massive seasonal fruiting of fig trees), all of which have
462 been shown to modulate relationships between group members (birds and mammals: Wrangham &
463 Rubenstein, 1986; baboons: Barrett & Henzi, 2001; Henzi et al., 2009; hyenas: East & Hofer, 2010).

464 The most consistent finding in our study was the effect of dominance rank differences, i.e.
465 strong, predictable and equitable bonds were more likely to be formed by dyads with small
466 differences in dominance rank. In female primates and hyenas, the maintenance of these bonds has
467 been linked to competition for social partners, as females struggle for access to the highest-ranking
468 females and end up socialising most with affiliates of adjacent ranks due to competitive exclusion
469 (Seyfarth, 1977). However, because in the study population power asymmetries between females were
470 relatively moderate, counter-aggression frequent and affiliative and proximity networks quite diverse
471 (Duboscq et al., 2013), we argue that social competition was low and competitive exclusion was
472 ineffective so this hypothesis does not provide a satisfying explanation for our results. Social bond

473 formation and maintenance may instead involve the reciprocal exchange of social commodities if
474 adjacently-ranked partners were generally more similar – in terms of personality, energetic needs or
475 reproductive state – or competent partners in cooperation (Chapais, 2006; Schino & Aureli, 2009).
476 These reciprocal exchanges could be highly dynamic and opportunistic in a biological market
477 susceptible to environmental and social conditions (Noë & Hammerstein, 1994; Barrett & Henzi,
478 2006), thereby generating a potential source of variation in the endurance of social bonds too.

479 The potential opportunistic nature of these social bonds seems also apparent in the analyses of
480 their potential adaptive value. Previous studies on the same population showed somewhat contrasting
481 results. The strength of social bonds was related to anti-predator responses, indicating their
482 importance in threatening situations (Micheletta et al., 2012). However, the symmetry and
483 predictability, rather than strength, of social bonds influenced the occurrence of conflict management
484 behaviour. Furthermore, the occurrence of reconciliation – an important mechanism of social
485 cohesion – appears to function as appeasement, a short-term tactic, rather than to repair relationships,
486 a more long-term strategy (Duboscq et al., 2014). In the current study, variance in bond characteristics
487 helped only to a certain extent to explain variation in three additional fitness-related behaviours. First,
488 more strongly bonded females fed more often in proximity but also fought more often with each other
489 than females with weaker bonds. This indicates that more strongly bonded dyads may be more
490 resilient to disruptions of their bond (by aggression) over food than less strongly bonded dyads
491 (Aureli, Fraser, Schaffner, & Schino, 2012). Second, this is consistent with the finding that partners
492 with less predictable bonds also fed more often in proximity, as stronger bonds tended to be less
493 predictable. The link between bond predictability and co-feeding frequency suggests either that
494 partners with enduring relationships avoid endangering the stability of their relationship over feeding
495 competition, or that the endurance of bonds is affected by another factor that we have not considered,
496 for example female energetic needs (perhaps in relation with lactation or oestrous). Third, the
497 negative relationship between equitability and aggression rate could indicate that less equitable dyads
498 often need to negotiate their relationship through engaging in mild aggression. This could be the case
499 if one partner gets frustrated to be at the lesser end of the social exchange, especially since less
500 equitable bonds also tended to be weaker in strength. These results stress the need to consider more

501 than one dimension of social bonds simultaneously in order to get a more integrative picture of how
502 animals balance the costs and benefits of social bonds. Experiments involving cooperative tasks could
503 help disentangle the respective weight of bond characteristics in social decision-making in terms of
504 partner choice, coalition formation, trust or punishment.

505 Overall, it appears that the female crested macaques under study generally form a dynamic
506 number and large diversity of good average partners, rather than a tight network of enduring strong
507 ones, perhaps similar to what has been suggested for males of the same species (Neumann, 2013;
508 Neumann, Agil, Widdig, & Engelhardt, 2013). As such, females seem able to express great degrees of
509 social freedom with regards to their dominance and kin relationships (Thierry, 1990; Butovskaya,
510 2004). Nevertheless, females also seem to specifically rely on certain partners, with whom they have
511 strong, predictable or equitable bonds, in specific contexts or in especially challenging situations
512 (Duboscq et al., 2014; Micheletta et al., 2012). This “many-good-friends” strategy can be costly
513 temporally and energetically, but it can also bring a wide range of benefits, including enhanced
514 negotiation skills, improved collective decision-making, and facilitated cooperation in joint-action
515 problems (Petit, Desportes, & Thierry, 1992; McComb & Semple, 2005; Hare, Melis, Woods,
516 Hasting, & Wrangham, 2007; Sueur & Petit, 2008; Thierry et al., 2008).

517 The contrast between the stability of the social structure of macaques, in general, and the
518 degrees of freedom shown by female crested macaques, in particular, in establishing and maintaining
519 relationships leads to questions about the temporal dynamics of social bonds and the short- and long-
520 term reciprocity of social exchanges within stable societies. It highlights the need to consider more
521 carefully the whole network of bonds, weak and strong, in a more integrated way. More importantly,
522 fitness-related behaviours, like coalitionary support, are presumably based on long-term alliances.
523 Thus, to what extent patterns in so-called strategic behaviours can actually resist the magnitude of
524 changes in social bonds is currently not clear. Investigating this question could help to determine how
525 dynamic societies actually are and whether species or population differences in dynamics exist.
526 Fluctuations in social networks are indeed pervasive in species with flexible (Schradin, 2013) or
527 seasonal sociality (Blumstein, 2013; Brent et al., 2013; Prange, Gehrt, & Hauver, 2011). Whether our
528 findings reflect a pattern more common than previously thought or are typical for this study

529 population remains to be investigated and requires comparative studies. This is of tremendous
530 importance to better understand the social components of fitness and the mechanisms linking sociality
531 to fitness.

532

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534

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542

543 **Compliance with ethical standards**

544

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552

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839

840 **Figure legends**

841

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

847

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

854

855 **Figure 3:** Effect of dominance difference (left panels), relatedness (middle panels) and age difference
856 (right panels) on bond strength (top panels), bond predictability (middle panels), and bond equitability
857 (bottom panels). The straight full line represents the estimate variation as predicted by the model, the
858 dotted lines are the associated lower and upper 95% confidence intervals of the estimate, the grey
859 points are the original data points transformed and scaled as in the statistical model.

860

861 **Figure 4:** Effect of bond strength (left panels), bond predictability (middle panels), and bond
862 equitability (right panels) on coalitionary support (top panels), feeding in proximity frequency (middle
863 panels), and aggression frequency (bottom panels). The straight full line represents the estimate
864 variation as predicted by the model, the dotted lines are the associated lower and upper 95%
865 confidence intervals of the estimate, the grey points are the original data points transformed and
866 scaled as in the statistical model.

Degrees of freedom in social bonds of crested macaque females.

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Highlights

Most bonds were of average strength, of moderate endurance and balanced

Close-ranked females had stronger, more predictable and equitable bonds than others

Bond characteristics and fitness-related behaviours were linked in complex ways

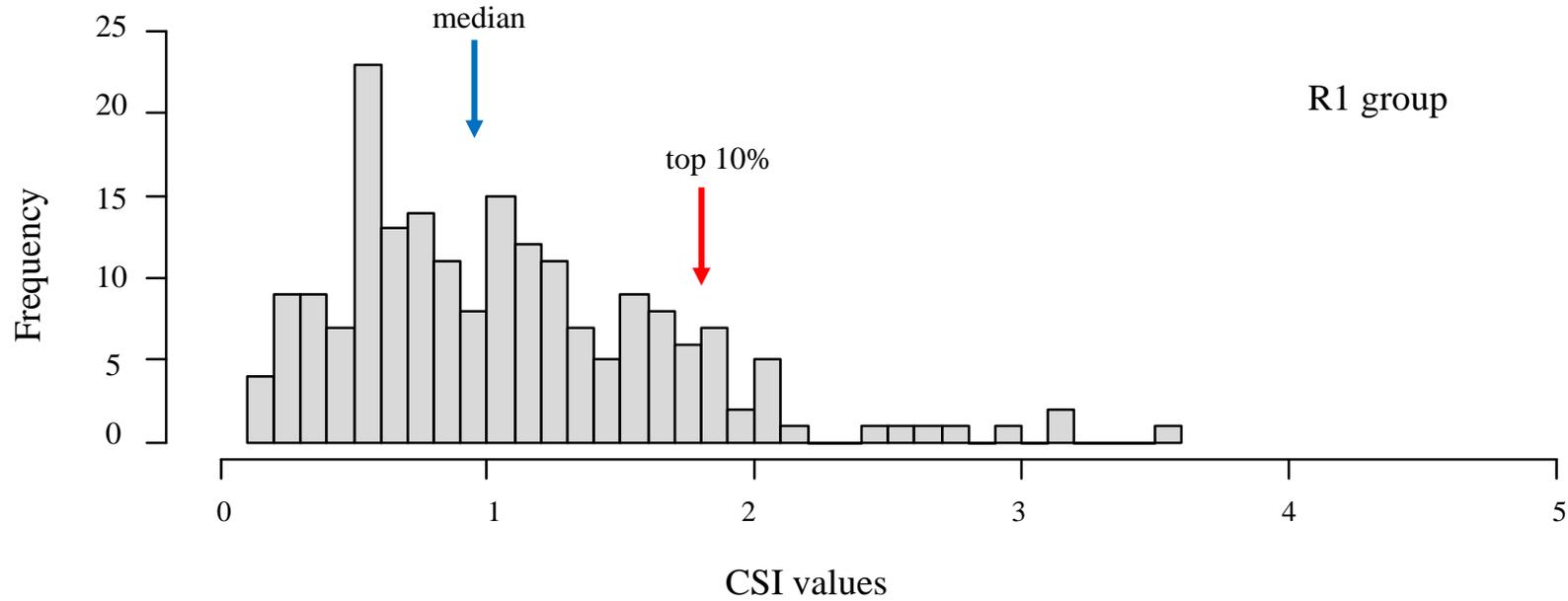
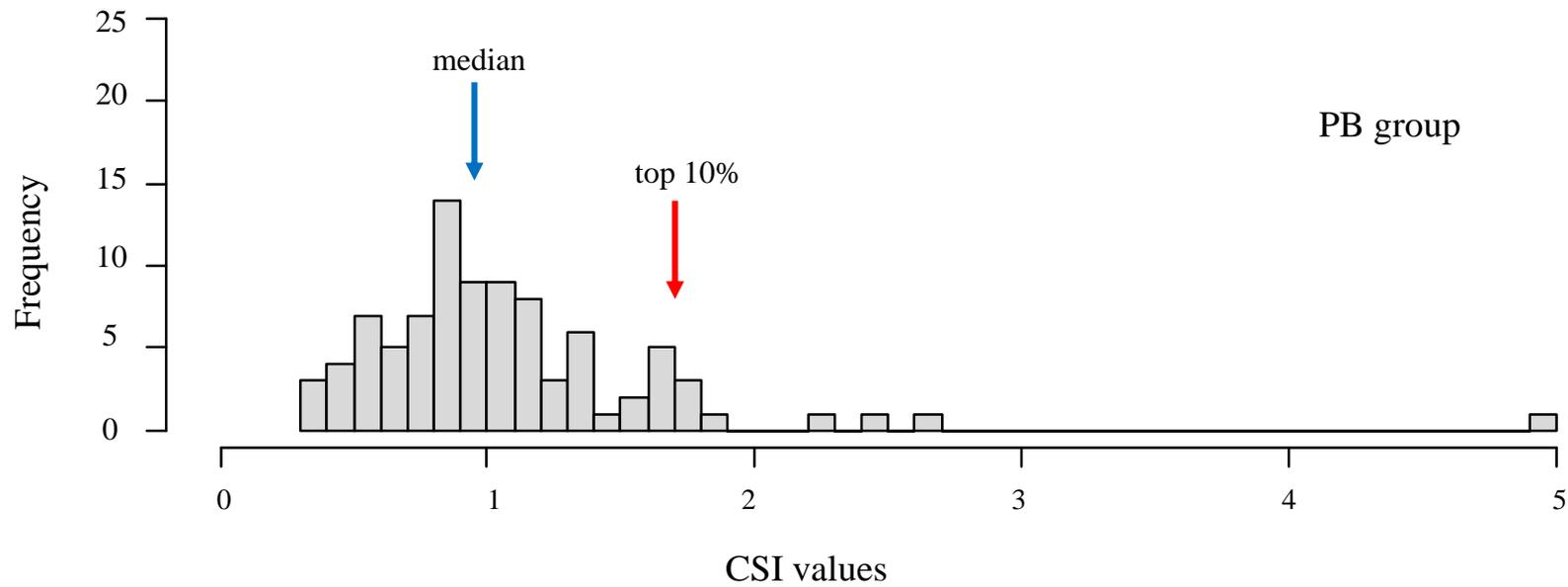
Tolerant females can express great degrees of freedom in their social relationships

These patterns are under-appreciated in stable nepotistic hierarchical societies

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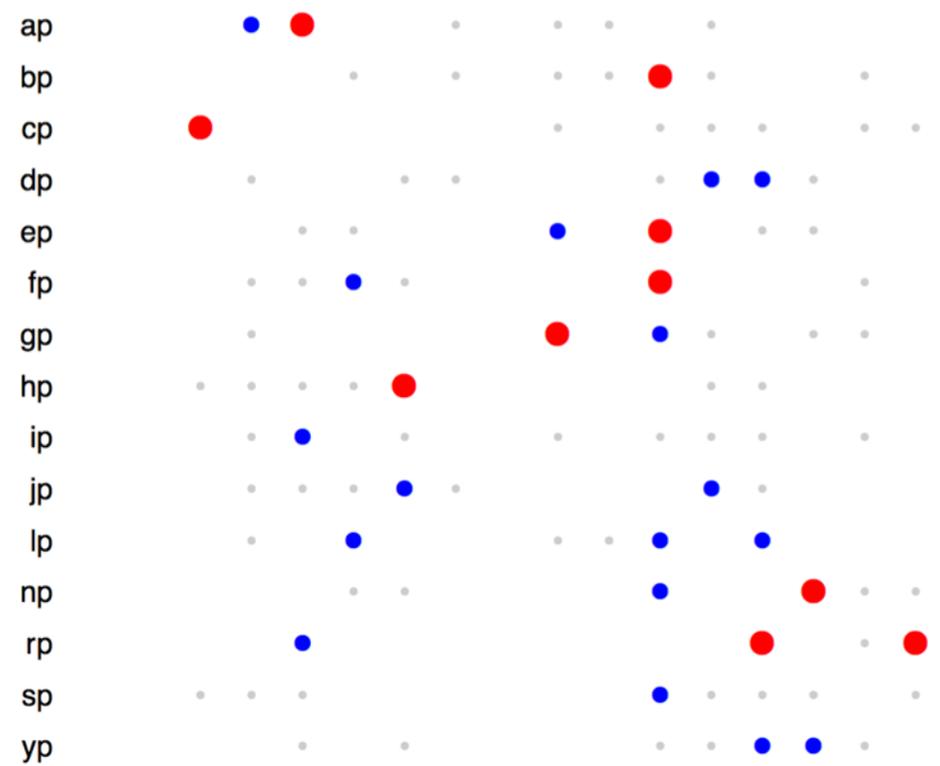
Figure



Figure

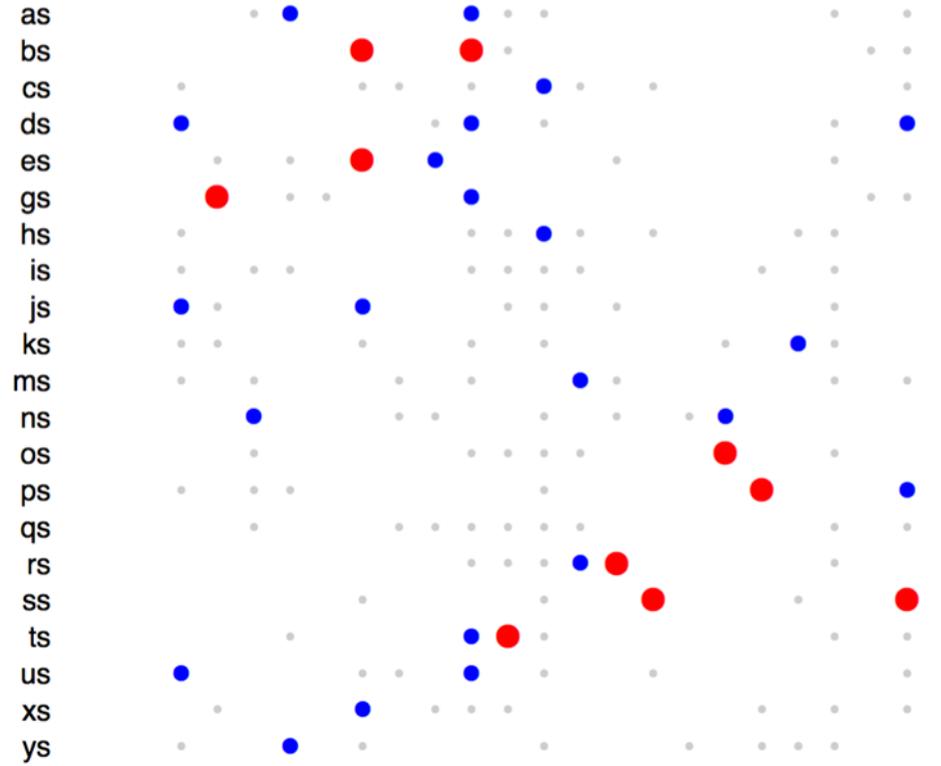
PB

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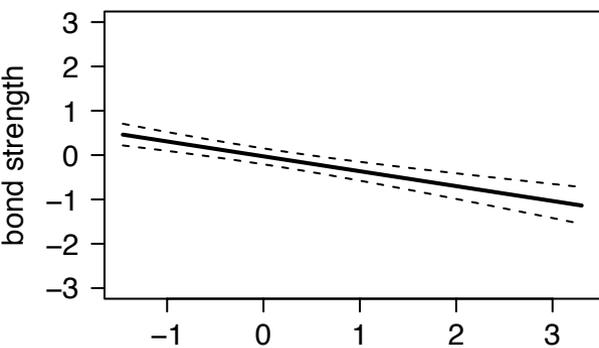
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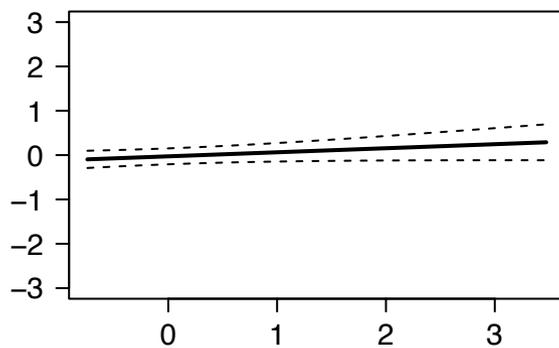


Figure

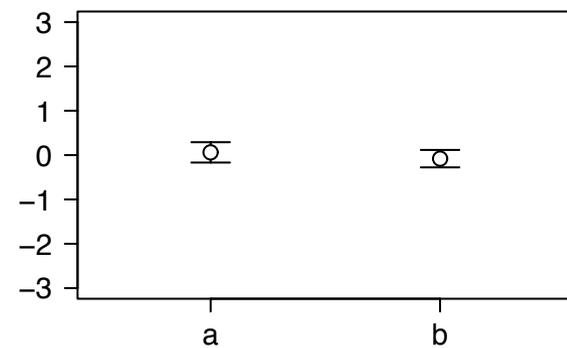
dominance difference



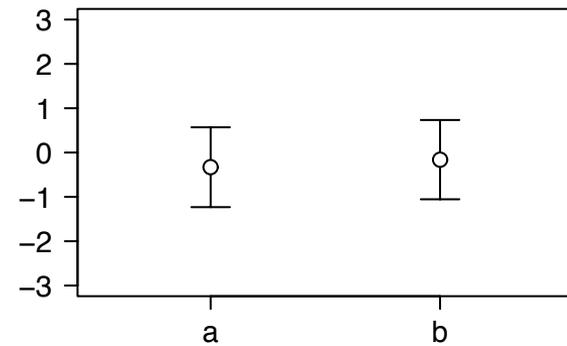
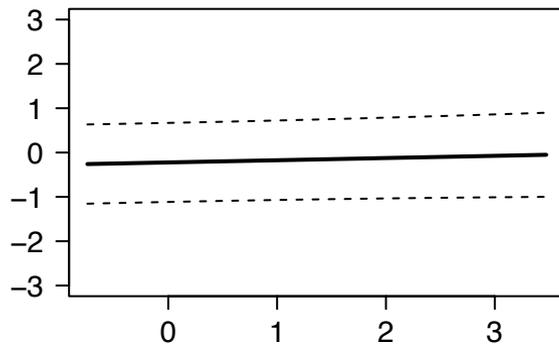
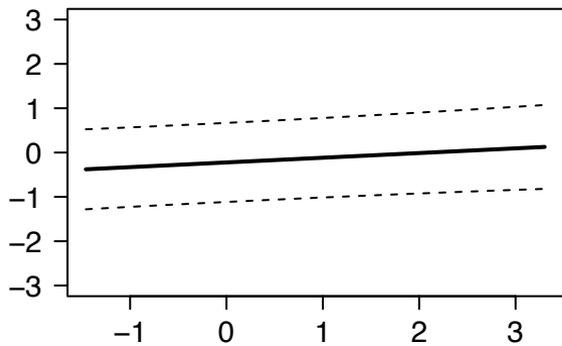
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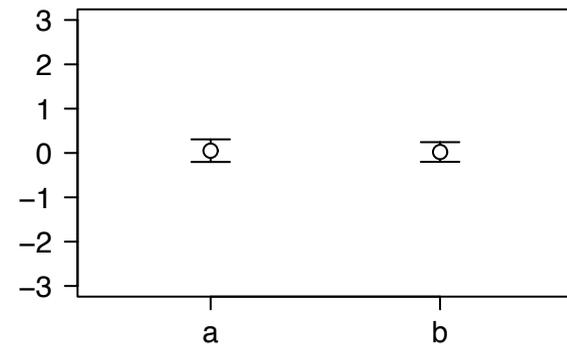
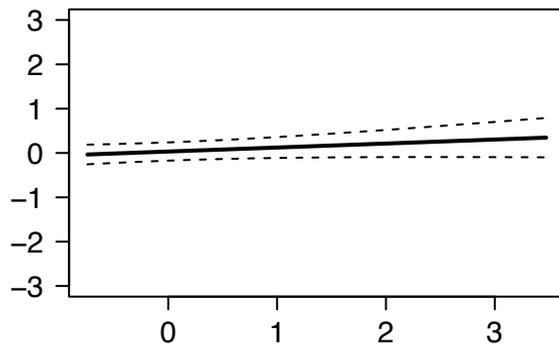
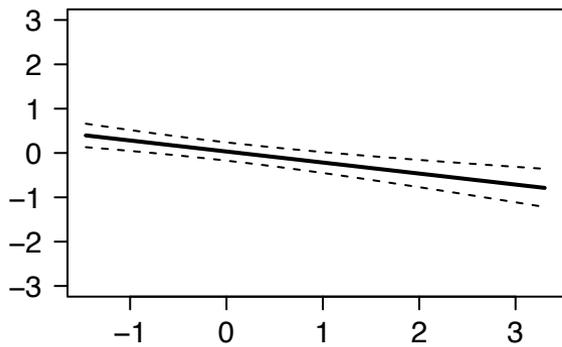
age difference



bond predictability

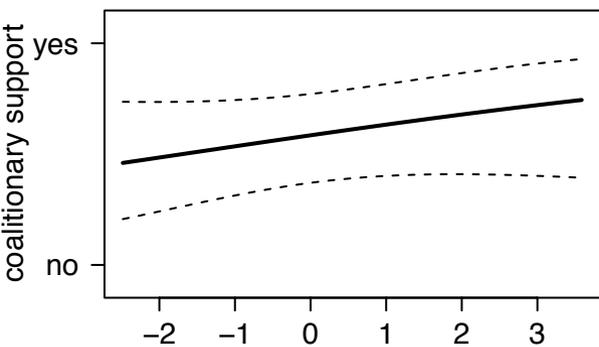


bond equitability

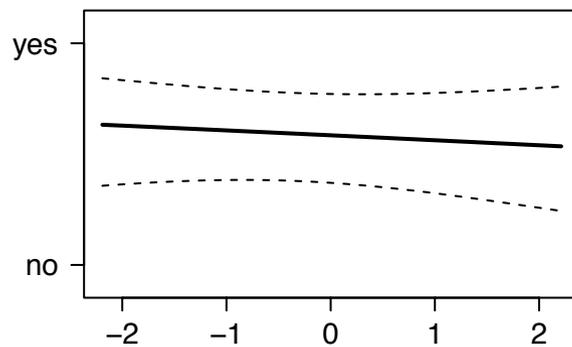


Figure

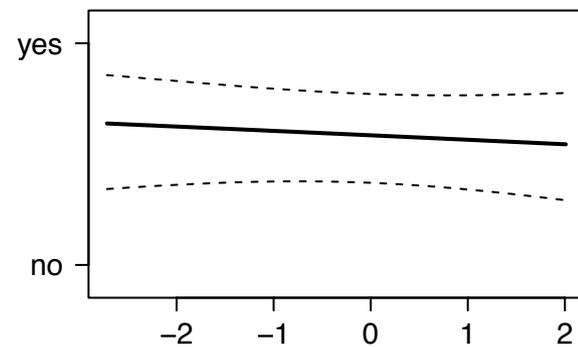
bond strength



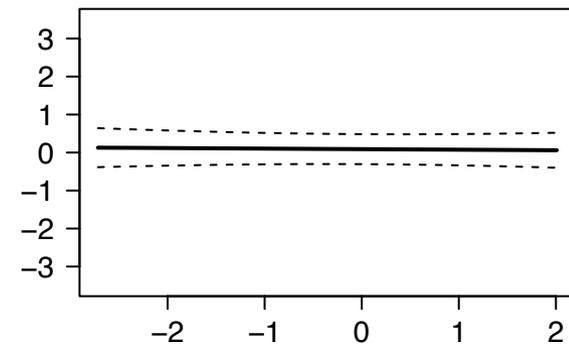
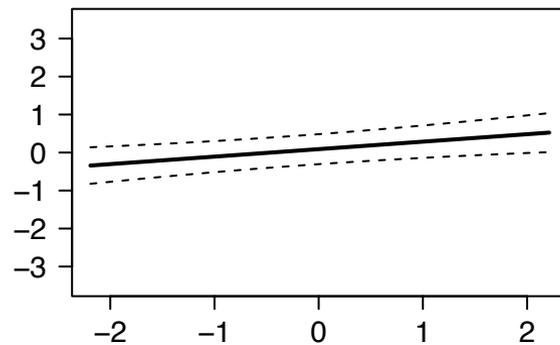
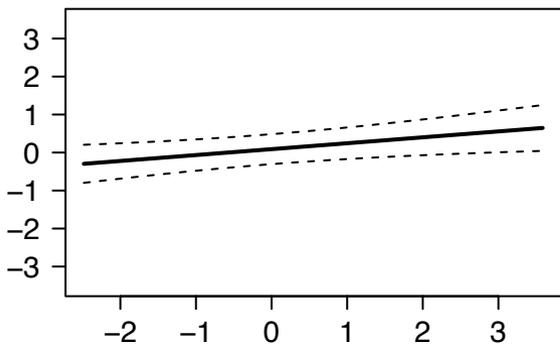
bond predictability



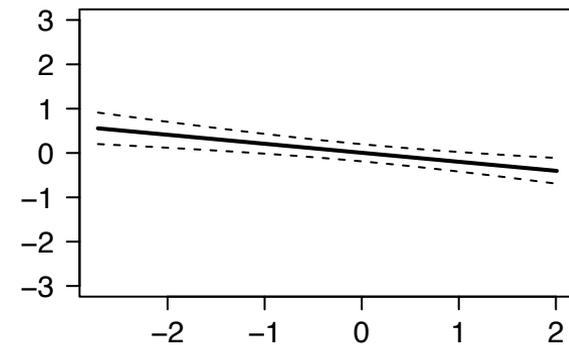
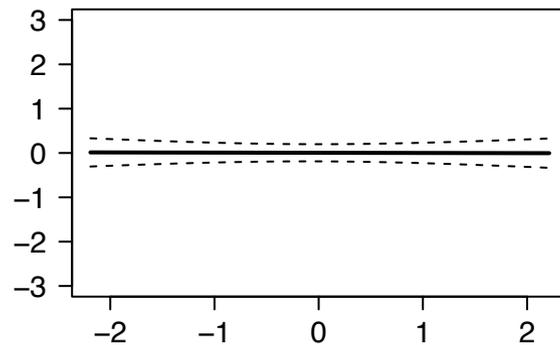
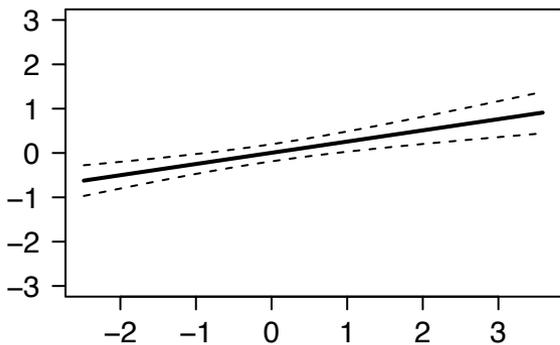
bond equitability



feeding in proximity



aggression frequency



Supplementary material for on-line publication only

[Click here to download Supplementary material for on-line publication only: social bonds_Duboscq et al_appendix_20160628.doc](#)