Degrees of freedom in social bonds of crested macaque females.

Julie Duboscq [1,2,3,4*†], Christof Neumann [1,2,5,6**], Muhammad Agil [7], Dyah Perwitasari-Farajallah [8,9], Bernard Thierry [3,4], Antje Engelhardt [1,2***]

[1] Junior Research Group of Primate Sexual Selection, German Primate Center, Göttingen, Germany, [2] Courant Research Centre for the Evolution of Social Behaviour, Göttingen, Germany, [3] Université de Strasbourg, Institut Pluridisciplinaire Hubert Curien, Strasbourg, France, [4] Centre National de la Recherche Scientifique, Département Ecologie, Physiologie et Ethologie, Strasbourg, France, [5] Junior Research Group of Primate Kin Selection, Max-Planck-Institute for Evolutionary Anthropology, Leipzig, Germany, [6] Institute of Biology, Faculty of Bioscience, Pharmacy and Psychology, University of Leipzig, Leipzig, Germany, [7] Faculty of Veterinary Sciences, Bogor Agricultural University, Bogor, Indonesia, [8] Primate Research Center, Bogor Agricultural University, Bogor, Indonesia, [9] Faculty of Mathematics and Natural Sciences, Bogor Agricultural University, Bogor, Indonesia

* corresponding author: julie.a.m.duboscq@gmail.com

† present affiliation of Julie Duboscq: Kyoto University Wildlife Research Centre, 2-24 Tanaka-Sekiden-cho, Sakyo, Kyoto, Japan 606-8203.

** present affiliation of Christof Neumann: Université de Neuchâtel, Institute of Biology, Department of Comparative Cognition, Neuchâtel, Switzerland

***present affiliation of Antje Engelhardt: Liverpool John Moores University, School of Natural Sciences and Psychology, Liverpool, United Kingdom

Word count main text: 6351

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.

Degrees of freedom in social bonds of crested macaque females.

Julie Duboscq [1,2,3,4*†], Christof Neumann [1,2,5,6**], Muhammad Agil [7], Dyah Perwitasari-Farajallah [8,9], Bernard Thierry [3,4], Antje Engelhardt [1,2***]

[1] Junior Research Group of Primate Sexual Selection, German Primate Center, Göttingen, Germany, [2] Courant Research Centre for the Evolution of Social Behaviour, Göttingen, Germany, [3] Université de Strasbourg, Institut Pluridisciplinaire Hubert Curien, Strasbourg, France, [4] Centre National de la Recherche Scientifique, Département Ecologie, Physiologie et Ethologie, Strasbourg, France, [5] Junior Research Group of Primate Kin Selection, Max-Planck-Institute for Evolutionary Anthropology, Leipzig, Germany, [6] Institute of Biology, Faculty of Bioscience, Pharmacy and Psychology, University of Leipzig, Leipzig, Germany, [7] Faculty of Veterinary Sciences, Bogor Agricultural University, Bogor, Indonesia, [8] Primate Research Center, Bogor Agricultural University, Bogor, Indonesia, [9] Faculty of Mathematics and Natural Sciences, Bogor Agricultural University, Bogor, Indonesia

* corresponding author: julie.a.m.duboscq@gmail.com

[†] present affiliation of Julie Duboscq: Kyoto University Wildlife Research Centre, 2-24 Tanaka-Sekiden-cho, Sakyo, Kyoto, Japan 606-8203.

** present affiliation of Christof Neumann: Université de Neuchâtel, Institute of Biology, Department of Comparative Cognition, Neuchâtel, Switzerland

***present affiliation of Antje Engelhardt: Liverpool John Moores University, School of Natural Sciences and Psychology, Liverpool, United Kingdom

Word count main text: 6351

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.

Keywords

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

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 (feral horses (*Equus caballus)*, Cameron, Setsaas, & Linklater, 2009; bottlenose dolphins (*Tursiops sp.*) Frère et al., 2010; talapoin monkeys (*Miopethicus talapoin*), Keverne, Martensz, & Tuite, 1989; Barbary macaques (*Macaca sylvanus*), McFarland & Majolo, 2013; Young, Majolo, Heistermann, Schülke, & Ostner, 2014; chacma baboons (*Papio cynocephalus ursinus*), Silk et al., 2009, 2010; humans (*Homo sapiens*), Uchino 2006). For individuals, the value of social bonds is also related to the direct or indirect benefits they may obtain from daily social exchanges (primate males: Ostner & Schülke, 2014; mammalian females: Silk, 2007a), e.g. reciprocation of social grooming, reduction of aggression, increased coalitionary support during conflicts, or better access to food resources (ravens (*Corvus corax*), Fraser & Bugnyar, 2011; baboons (*P. ursinus*), King, Clark, & Cowlishaw, 2011; spotted hyenas (*Crocuta crocuta*), Smith, Memenis, & Holekamp, 2007), which ultimately may impact their fitness and well-being.

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 relatedness, dominance status, personality, reproductive state or energetic needs are more likely to form strong and enduring social bonds than others (yellow-bellied marmots (*Marmota flaviventris*): Armitage & Schwartz, 2000; chacma baboons: Barrett & Henzi, 2001; giraffes (*Giraffa camelopardalis*), Carter, Seddon, Frère, Carter, & Goldizen, 2013; mountain goats (*Oreamnos americanus*), Godde, Côté, & Réale, 2015; rhesus macaques (*M. mulatta*), de Waal &

Lutrell, 1986; ring-tailed coatis (*Nasua nasua*), 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 (primates: Schino, 2007; hyenas: Smith et al., 2010).

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 affect measures of fitness, health or well-being, e.g. preferred associates (Frère et al., 2011) or top three partners (Silk et al., 2006a). However, animals may have a variety of options for regulating the consequences of bonds. First, the predictability and equitability of an individual’s social relationships may be as important as their strength (e.g. the sheer amount of research on cooperation and reciprocity: Nowak, 2006; Trivers, 1971, 2006). In addition, “weak” bonds, as opposed to “strong” bonds, within a social network may also be important. For example, weak bonds contribute to stabilising the overall network in *Escherichia coli* (Csermely, 2004). In humans, although a few strong bonds are individually more influential, more numerous weak bonds enhance the propagation of novel information (Bakshy, Rosenn, Marlow, & Adamic, 2012). Finally, it has been shown that variance in bond strength is actually more predictive of fitness than strength itself (longevity in rock hyraxes (*Procavia capensis*), Barocas, Ilany, Koren, Kam, & Geffen, 2011; pup production in degus (*Octodon degus*), 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.

It has also 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, 2001, 2006). For instance, female chacma baboons did not sustain constant differentiated relationships with other females across time but changed cyclically between “brief associations”, “casual acquaintances” and “constant companionships” according to food availability (i.e. between food-abundant and food-scarce periods) (Henzi, Lusseau, Weingrill, van

Schaik & Barrett, 2009). In addition, 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). Therefore, individuals may 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. Although this seems rather straightforward in animal societies that display flexibility in their social structure (i.e. group membership and group size regularly changing, 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, of hyenas or African elephants (Barrett & Henzi, 2001; Ilani, Booms, & Holekamp, 2015; Sick et al., 2014).

Macaques (genus *Macaca*) are an ideal candidate for the investigation of variation in social strategies. Although the different macaque species share the same social organisation (philopatric females organised in stable matrilineal dominance hierarchies), 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; Thierry, 2013). Such social variation can be expected to influence the structure and function of social bonds (Thierry, 1990; Butovskaya, 2004). Specifically, when power asymmetries are pronounced and the degree of nepotism is high, as in less tolerant species, individuals' options regarding who to interact with and how are limited. These constraints may lead to individuals having a relatively low number of strong, predictable and equitable partnerships within a social group. In contrast, when social rules are more relaxed, i.e. 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 develop a greater diversity and number of social bonds (Thierry, 1990; Butovskaya, 2004; Cooper & Bernstein 2008; Duboscq et al., 2013). Thus, the degrees of freedom that individuals have in their relationships within their group can 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 (Thierry, 1990; Butovskaya, 2004).

In this study, we aim to investigate these degrees of freedom and the interplay between the structure and the value of social bonds in wild female crested macaques (*M. nigra*), which express a tolerant social style (Petit, Abegg, & Thierry, 1997; Duboscq et al., 2013). The study population of crested macaques lives 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 (Neumann, 2013; Marty, Hodges, Agil, & Engelhardt, in press). 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 (D'Amato, Troisi, Scucchi, & Fuccillo, 1982; Bardi, Shimizu, Fujita, Borgognini Tarli, & Huffman, 2001; Barrett & Henzi, 2001; Brent, MacLarnon, Platt, & Semple, 2013). 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 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.

Specifically, since macaques form stable matrilineal hierarchical societies (Cords, 2012), kin and adjacently-ranked dyads are expected to form the strongest, most predictable and equitable bonds (Silk, 2007b). However, given the tolerant social style of crested macaques and their expected great degrees of social freedom, we made the hypothesis that these dyad characteristics would not predict social bond strength, equitability and predictability. To test this prediction and to establish the structure of bonds, we analysed the relationship between three measures of dyadic similarities (degree of relatedness, proximity 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 explain a substantial amount of variation in 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 made the hypothesis that the characteristics of social bonds will 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 (Thierry, 1990; Butovskaya, 2004).

Methods

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 biology of crested macaques that started in 2006. We studied two groups, "PB" and "R1", comprised of ca. 60 and 80 individuals respectively. The monkeys were fully habituated to human observers and all adults could be individually identified based on physical characteristics.

JD and two field assistants collected behavioural data between October 2008 and May 2010 on all adult females (15 – 18 in PB, 21 – 24 in R1) using focal animal sampling (Martin & Bateson, 1993) (interobserver reliability: Cohen's kappa = 0.69–0.90, correlation coefficients between behavioural variables = 0.79 – 0.98). We collected 30 minute-point-sample observations for activity (foraging, feeding, socialising, resting, and travelling). Every second minute, we also noted the identity of neighbours in three proximity categories: in body contact, within one body-length, and within five body-lengths. We recorded focal social events continuously, including the start and end time of interactions, the sequence of all behaviours, as well as the identity and behaviours of all social partners. This study included a total of 2,480 hours of focal data focusing on 35 females that were present during the entire study period (median_{PB} = 68 hours per female, range_{PB}: 65 – 78, N_{PB} = 14; median_{R1} = 66 hours per female, range_{R1}: 59 – 71, N_{R1} = 21). Behavioural interactions were expressed as duration (e.g. social grooming) or frequency (e.g. approach) per focal and per dyadic (sum of two focals') observation time over the whole study period (i.e. 19 months).

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

Dyad characteristics

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

Kinship: DNA was extracted from 100–150 mg of faeces with the GEN-IAL® All-tissue DNA extraction kit following the manufacturer's instructions. We amplified 12 short-tandem repeats (or microsatellites - 10 tetranucleotide loci and 2 dinucleotide loci), proven to be informative in humans and other primates (see Appendix). We used a two-step multiplex chain polymerase reaction (PCR) approach (Arandjelovic et al., 2009). In the first step, all loci were amplified in a single reaction in an Eppendorf® Master Gradient machine following cycles of denaturation, annealing and elongation (see Appendix). We followed multiplex PCRs with singleplex PCRs, using the same protocol but for each primer separately (see Appendix). Singleplex PCR products were then sequenced in an ABI 3130xL sequencer. Allele sizes were finally read into PeakScanner (Applied Biosystems®). Given that we had several samples per individual, allele sizes were considered definitive when at least two different samples of the same individual produced the same results in at least four amplifications for heterozygotes and six for homozygotes (multi-tubes approach, Taberlet et al., 1996). Consensus genotypes were found for a median of 12 loci (range = 6 – 12) and processed using COANCESTRY® software, which provides two likelihood methods and five moment estimators of relatedness (Wang, 2011). We chose the dyadic maximum likelihood (DML) estimator of Milligan (2003) because it 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 assessed 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), the presence of physical injuries and their general appearance. 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 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. A CSI above the average of all dyads in the group (equal to 1) indicates a strong bond (Silk et al., 2006b).

Bond temporal variation (hereafter predictability) was assessed over three periods of six months each. 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). The higher the CV, the lower the predictability of CSI values 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:

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

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 or peacefully in support of another female or receiving such an intervention herself during an aggressive interaction with another individual (Petit & Thierry, 1994; Duboscq et al., 2014). 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 a Quadratic Assignment Permutation (QAP) procedure with 1,000 permutations between those matrices two-by-two (function qaptest in the sna package; Butts, 2008). We then built three (generalised) linear mixed models (GLMM, Bolker et al., 2008), one for each of the social bond components as response variables, including relatedness (DML), absolute Elo-rating difference (Elo#) and age difference (age#, as a categorical variable, close/distant) as predictors and member 1 and member 2 of the dyad and group as random effects.

Function of social bonds

We built three 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 well as relatedness (DML), absolute Elo-rating difference (Elo#) and age difference (age#) as predictors and member 1 and member 2 of the dyad and group as random effects.

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” 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 optimal fitting and the subsequent interpretation or comparison of model estimates. For all models, we checked a variety of assumptions and diagnostics (normally distributed and homogeneous residuals, variance inflation factors < 2, Cooks’ distance, dfbetas; Field, Miles, & Field, 2012). No obvious violation of assumptions was detected. We tested the final full model (including all fixed and random effects) against an informed null model, i.e. including only the intercept, control factors (absolute Elo difference, DML, and age difference) and random factors, using likelihood ratio tests (LRT). We used 95% confidence intervals to assess whether a predictor significantly contributed to explaining the response variable (interval excluding 0). For clarity, detailed results from the models are given in Tables A1 to A3 in the Appendix.

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 a random 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 costumed simulation proceeded in four steps: 1/ add an error 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 10,000 simulations, depending on the response variable, which indicates relatively robust results. Detailed results of these simulations are given in Table A3 of the 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), indicating that in both groups, most bonds had average strength (mean equal to one in each group). The distribution of CSI scores, giving an assessment of how skewed dyadic affiliative behaviours are, was not right-skewed (Figure 1) as is typical in other species, indicating that females established and maintained affiliative relationships with numerous female partners. 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 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.

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

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

All three characteristics were positively correlated in both groups (QAP tests, PB: N = 105: strength-predictability: rho = 0.59, p = 0.001; strength-equitability: rho = 0.91, $p < 0.001$; predictability-equitability: rho = 0.95, $p < 0.001$; R1: N = 210: strength-predictability: rho = 0.76, p = 0.001; strength-equitability: rho = 0.85, $p < 0.001$; predictability-equitability: rho = 0.65, $p < 0.001$), 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: $\text{LRT}_{\text{full-null}}$: $\chi^2 = 39.45$, d.f. = 3, $p < 0.001$; $\beta \pm \text{SE}$ [95% CI] = -0.33 ± 0.06 [-0.45 – -0.20]; 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]; 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 A1; Figure 2). None of the tested bond characteristics were related to the relatedness and age difference of the dyads (Table A1).

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 components ($LRT_{full-null}$: $\chi^2 = 1.86$, d.f. = 3, $p = 0.603$; Table A2; Figure 3). In contrast, dyads that had stronger and less predictable bonds fed more often in proximity than others ($LRT_{full-null}$: $\chi^2 = 11.15$, d.f. = 3, $p = 0.011$; strength: β ± SE [95% CI] = 0.16 ± 0.06 [0.03 - 0.28]; predictability: β ± SE [95% CI] = 0.20 ± 0.07 [0.04 - 0.35]; Table A2; 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 ($LRT_{full-null}$: $\chi^2 = 23.54$, d.f. = 3, $p < 0.001$; strength: β ± SE [95% CI] = 0.25 ± 0.06 [0.12 - 0.37]; equitability: β ± SE [95% CI] = -0.20 ± 0.05 [-0.33 - -0.10]; Table A2; Figure 3).

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 1 and moderately left-skewed 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 positively related 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 (baboons: Smith, Albers, & Altmann, 2003; hyenas: Wahaj et al., 2004; rhesus macaques: 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., in press), 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. 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).

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

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

The most consistent finding in our study was the effect of dominance rank differences, i.e. strong, predictable and equitable bonds were more likely to be formed by dyads with small differences in dominance rank. In female primates and hyenas, the maintenance of these bonds has been linked to competition for social partners, as females struggle for access to the highest-ranking females and end up socialising most with affiliates of adjacent ranks due to competitive exclusion (Seyfarth, 1977). However, because in the study population power asymmetries between females were relatively moderate, counter-aggression frequent and affiliative and proximity networks quite diverse (Duboscq et al., 2013), we argue that social competition was low and competitive exclusion was ineffective so this hypothesis does not provide a satisfying explanation for our results. Social bond formation and maintenance may instead involve the reciprocal exchange of social commodities if adjacently-ranked partners were generally more similar – in terms of personality, energetic needs or 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 (Noë & Hammerstein, 1994; Barrett & Henzi, 2006), 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 symmetry and predictability, rather than strength, of social bonds influenced the occurrence of conflict management behaviour. 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 with lactation or oestrous). Third, the negative relationship between equitability and aggression rate could indicate that less equitable dyads often need to negotiate their relationship through engaging in mild aggression. 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 (Thierry, 1990; Butovskaya, 2004). Nevertheless, females also seem to specifically rely on certain partners, with whom they have strong, predictable or equitable bonds, in specific contexts or in especially challenging situations (Duboscq et al., 2014; 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 (Petit, Desportes, & Thierry, 1992; McComb & Semple, 2005; Hare, Melis, Woods, Hasting, & Wrangham, 2007; 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 way. 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. 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.

Acknowledgments

This article is dedicated to Ugiek and Antri. We gratefully acknowledge the permission of the Indonesian State Ministry of Research and Technology (RISTEK), the Directorate General of Forest Protection and Nature Conservation (PHKA) in Jakarta and the Department for the Conservation of Natural Resources (BKSDA) in Manado, particularly Pak Untung and Pak Yunus, to conduct this research in the Tangkoko-Batuangus Nature Reserve. We thank all the members of the Macaca Nigra Project for their support in the field, and especially Dwi Yandhi Febryianti and Jérôme Micheletta for their help with data collection.

Compliance with ethical standards

Funding: This study was funded by the Volkswagen Foundation (funding initiative Evolutionary Biology, grant I/84 200) and Primate Conservation Inc. (grant PCI 757) to JD and by a grant from the German Research Council (EN 916/2) to AE.

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

Ethical approval: This research adheres to all legal requirements and guidelines of the German and Indonesian governments and institutions, and to the ASAB/ASB guidelines for the treatment of animals in behavioural research and teaching.

References

Albers, P. C. H., & de Vries, H. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour, 61*, 489–495. doi: 10.1006/anbe.2000.1571

Arandjelovic, M., Guschanski, K., Schubert, G., Harris, T. R., Thalmann, O., Siedel, H., & Vigilant, L. (2009) Two-step multiplex polymerase chain reaction improves the speed and accuracy of genotyping using DNA from noninvasive and museum samples. *Molecular Ecology Resources, 9*, 28–36. doi: 10.1111/j.1755-0998.2008.02387.x

Armitage, K. B., & Schwartz, O. A. (2000). Social enhancement of fitness in yellow-bellied marmots. *Proceedings of the National Academy of Science, 97*, 12149–12152. doi:10.1073/pnas.200196097

Aureli, F., Fraser, O. N., Schaffner, C. M., & Schino, G. (2012). The regulation of social relationships. In: J. C. Mitani, J. Call, P. M. Kappeler, R. Palombit, & J. Silk (Eds.) *The evolution of primate societies* (pp. 531–551). Chicago, U.S.A.: The University of Chicago Press.

Barocas, A., Ilany, A., Koren, L., Kam, M., & Geffen, E. (2011). Variance in centrality within rock hyrax social networks predicts adult longevity. *PLoS ONE, 6*, 1–8. doi:10.1371/journal.pone.0022375

Bakshy, E., Rosenn, I., Marlow, C., & Adamic, L. (2012). The role of social networks in information diffusion. In *Proceedings of the 21st international conference on World Wide Web* (pp. 519–528). New York: ACM. doi:10.1145/2187836.2187907

Bardi, M., Shimizu, K., Fujita, S., Borgognini Tarli, S. M., & Huffman, M. (2001). Social behavior and hormonal correlates during the perinatal period in Japanese macaques. *Hormones & Behavior, 39*, 239–246. doi: 10.1006/hbeh.2001.1651

Barrett, L., & Henzi, P. (2001). Constraints on relationship formation among female primates. *Behaviour, 139*, 263–289. doi:10.1163/156853902760102672.

Barrett, L., & Henzi, P. (2006). Monkeys, market and minds: biological markets and primate sociality. In: P. M. Kappeler & C. P. van Schaik (Eds.) *Cooperation in Primates and Humans: Mechanisms and Evolution* (pp. 209-232). Berlin, Germany: Springer.

Bates, D. M., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*, 1-48. doi:10.18637/jss.v067.i01.

Blumstein, D. T. (2013). Yellow-bellied marmots: insights from an emergent view of sociality. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*, 20120349. doi:10.1098/rstb.2012.0349

Bolker, B., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2008) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution, 24*, 127–135. doi: 10.1016/j.tree.2008.10.008

Brent, L. J. N., MacLarnon, A. M., Platt, M. L., & Semple, S. (2013). Seasonal changes in the structure of rhesus macaque social networks. *Behavioral Ecology and Sociobiology, 67*, 349–359. doi: 10.1007/s00265-012-1455-8

Butovskaya, M. L. (2004). Social space and degrees of freedom. In: B. Thierry, M. Singh, & W. Kaumanns (Eds.) *Macaque societies, a model for the study of social organisation* (pp. 182–185). Cambridge, U.K.: Cambridge University Press.

Butts, C. T. (2008). Social Network Analysis with sna. *Journal of Statistical Software, 24*, 1–51.

Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences, 106*, 13850–13853. doi:10.1073/pnas.0900639106

Carter, K. D., Seddon, J., Frère, C., Carter, J. K., & Goldizen, A. W. (2013). Fission-fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. *Animal Behaviour, 85*, 385-394. doi:10.1016/j.anbehav.2012.11.011

Chapais, B. (2006). Kinship, competence and cooperation in primates. In: P. M. Kappeler, & C. P. van Schaik (Eds.) *Cooperation in primates and humans: mechanisms and evolution* (pp. 47-64). Berlin: Springer.

Chapais, B. (2004). How kinship generates dominance structures: a comparative perspective. In B. Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque Societies* (pp. 186–204). Cambridge, U.K.: Cambridge University Press.

Clutton-Brock, T. H. (2009). Cooperation between non-kin in animal societies. *Nature, 462*, 51–57. doi:10.1038/nature08366

Cooper, M. A., & Bernstein, I. S. (2008) Evaluating dominance styles in Assamese and rhesus macaques. *International Journal of Primatology, 29,* 225–243. doi:10.1007/s10764-008-9236-y

Cords, M. (2012). The behavior, ecology and social evolution of cercopithecine monkeys. In: J. C. Mitani, J. Call, P. M. Kappeler, R. Palombit, & J. Silk (Eds.) *The evolution of primate societies* (pp. 91–112). Chicago, U.S.A.: The University of Chicago Press.

Csilléry, K., Johnson, T., Beraldi, D., Clutton-Brock, T. H., Coltman, D., Hansson, B., Spong, G., & Pemberton, J. M. (2006) Performance of marker-based relatedness estimators in natural populations of outbred vertebrates. *Genetics, 173*, 2091–2101.

Csermely, P. (2004). Strong links are important, but weak links stabilize them. *Trends in Biochemical Sciences*, *29,* 331–334. doi:10.1016/j.tibs.2004.05.004

D’Amato, F. R., Troisi, A., Scucchi, S., & Fuccillo, R. (1982) Mating season influence on allogrooming in a confined group of Japanese macaques: a quantitative analysis. *Primates, 23,* 220–232. doi: 10.1093/beheco/aru099

Duboscq, J., Agil, M., Engelhardt, A., & Thierry, B. (2014). The function of post-conflict interactions: new prospects from the study of a tolerant species of primate. *Animal Behaviour, 87,* 107–120. doi:10.1016/j.anbehav/2013-10-1018

Duboscq, J., Micheletta, J., Agil, M., Hodges, K., Thierry, B., & Engelhardt, A. (2013). Social tolerance in wild female crested macaques, *Macaca nigra*, in Tangkoko-Batuangus Nature Reserve, Sulawesi, Indonesia. *American Journal of Primatology, 75*, 361–375. doi:10.1002/ajp.22114

Duboscq, J., Neumann, C., Perwitasari-Farajallah, D., & Engelhardt, A. 2008. Daytime birth of a baby crested black macaque (*Macaca nigra*) in the wild." *Behavioural processes*, *79*, 81-84. doi:10.1016/j.beproc.2008.04.010

East, M. L., & Hofer, H. (2010) Social environments, social tactics and their fitness consequences in complex mammalian societies. In: T. Székely T, A. J. Moore, J. Komdeur (Eds) *Social Behaviour: Genes, Ecology and Evolution* (pp. 360-391). Cambridge, U.K.: Cambridge University Press.

Field, A., Miles, J., & Field, Z. (2012). *Discovering statistics using R*. London, U.K.: SAGE Publications Ltd.

Fraser, O. N., & Bugnyar, T. (2011) Ravens reconcile after aggressive conflicts with valuable partners. *PLoS ONE, 6,* e18118–e18118. doi:10.1371/journal.pone.0018118

Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L., & Sherwin, W. B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the National Academy of Sciences*, *107,* 19949–19954. doi:10.1073/pnas.1007997107

Godde, S., Côté, S. D., & Réale, D. (2015). Female mountain goats, *Oreamnos americanus*, associate according to kinship and reproductive status. *Animal Behaviour, 108*, 101–107. doi:10.1016/j.anbehav.2015.07.005

Hare, B., Melis, A. P., Woods, V., Hasting, S., & Wrangham, R. W. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology, 17*, 619–623. doi:10.1016/j.cub.2007.02.040

Hemelrijk, C. K. (1999). An individual-orientated model of the emergence of despotic and egalitarian societies. *Proceedings of the Royal Society B: Biological Sciences, 266,* 361–369. doi:10.1098/rspb.1999.0646

Henzi, S. P., Lusseau, D., Weingrill, T., van Schaik, C. P., & Barrett, L. (2009). Cyclicity in the structure of female baboon social networks. Behavioral Ecology and Sociobiology, 63, 1015–1021. doi:10.1007/s00265-009-0720-y

Hirsch, B. T., Prange, S., Hauver, S. A., & Gehrt, S. D. (2013) Genetic relatedness does not predict racoon social network structure. *Animal Behaviour, 85,* 463–470. doi:10.1016/j.anbehav.2012.12.011

Hirsch, B. T., Stanton, M. A., Maldonado, J. E. (2012). Kinship shapes affiliative social networks but not aggression in ring-tailed coatis. *PLoS ONE, 7,* e37301. doi:10.1371/journal.pone.0037301

Ilany, A., Booms, A. S., & Holekamp, K. E. (2015). Topological effects of network structure on long-term social network dynamics in a wild mammal. *Ecology Letters,* 687–695. doi:10.1111/ele.12447

Kalbitz, J., Ostner, J., & Schülke, O. (2016). Strong, equitable and long-term social bonds in the dispersing sex in Assamese macaques. *Animal Behaviour, 113,* 13-22. doi:10.1016/j.anbehav.2015.11.005

Kapsalis, E., & Berman, C. M. (1996). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) I. Criteria for kinship. *Behaviour, 133*, 1209–1234. doi:10.1163/156853996X00387

Kerhoas, D., Mundry, R., Perwitasari-Farajallah, D., Agil, M., Widdig, A. & Engelhardt, A. (2014). Social and ecological factors influencing offspring survival in wild macaques. *Behavioral Ecology, 25*, 1164–1172. doi:10.1093/beheco/aru099

Keverne, E. B., Martensz, N. D., & Tuite, B. (1989) Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology, 14,* 155–161. doi:10.1016/0306-4530(89)90065-6

King, A. J., Clark, F. E., & Cowlishaw, G. (2011) The dining etiquette of desert baboons: the roles of social bonds, kinship, and dominance in co-feeding networks. *American Journal of Primatology, 73,* 1–7. doi:10.1002/ajp.20918

Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Science, 104,* 7786–7790. doi:10.1073/pnas.0611449104

Majolo, B., Ventura, R., & Schino, G. (2010). Assymetry and dimensions of relationships quality in the Japanese macaque (*Macaca fuscata yakui*). International Journal of Primatology, 31, 736–750. doi:10.1007/s10764-010-9424-4

Martin, P., & Bateson, P. (1993). *Measuring Behaviour - An Introductory Guide* (2nd ed). Cambridge, U.K.: Cambridge University Press.

Marty, P. R., Hodges, K., Agil, M., & Engelhardt, A. (in press). Alpha male replacements and delayed dispersal in crested macaques (*Macaca nigra*). *American Journal of Primatology*. doi: 10.1002/ajp.22448

McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters*, *1*, 381–385. doi: 10.1098/rsbl.2005.0366

Micheletta, J., Waller, B. M., Panggur, M. R., Neumann, C., Duboscq, J., Agil, M., & Engelhardt, A. (2012). Social bonds affect anti-predator behaviour in a tolerant species of macaques, *Macaca nigra*. *Proceedings of the Royal Society B: Biological Sciences, 279,* 4042–4050. doi: 10.1098/rspb.2012.1470

Milligan, B. (2003). Maximum-likelihood estimation of relatedness. *Genetics, 163*, 1153–1167.

Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour, 77*, 633–640. doi:10.1016/j.anbehav.2008.11.021

Neumann, C., & Kulik, L. (2013). EloRating: Animal dominance hierarchies by Elo Rating. http://CRAN.R-project.org/package=EloRating

Neumann, C. (2013). Achievement and maintenance of dominance in male crested macaques (*Macaca nigra*) (Doctoral thesis). Leipzig, Germany: University of Leipzig.

Neumann, C., Agil, M., Widdig, A., & Engelhardt, A. (2013). Personality of wild male crested macaques (*Macaca nigra*). *PLoS ONE, 8,* e69383. *doi:10.1371/.* doi: 10.1371/journal.pone.0069383

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A., & Engelhardt, A. (2011) Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour, 82,* 911–921. doi: 10.1016/j.anbehav.2011.07.016

Newberry, R., & Swanson, J (2001) Breaking Social Bonds. In L. J. Keeling, & H. W. Gonyou (Eds.), *Social Bonds in Farm Animals* (pp. 307–331). Oxon, U.K.: CABI Publishing.

Noë R., & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, *35*, 1–11. doi:10.1007/BF00167053

Nowak, M. A. (2006). Five Rules for the Evolution of Cooperation. *Science*, *314*, 1560–1563. doi:10.1126/science.1133755

Nsubuga, A. M., Robbins, M. M., Roeder, A. D., Morin, P., Boesch, C., & Vigilant, L. (2004) Factors affecting the amount of genomic DNA extracted from ape faeces and the identification of an improved sample storage method. *Molecular Ecology, 13*, 2089–2094. doi: 10.1111/j.1365-294X.2004.02207.x

O'Brien, T. G., & Kinnaird, M. F. (1997). Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology, 18,* 321–351. doi: 10.1023/A:1026330332061

Ostner, J., & Schülke, O. (2014). The evolution of social bonds in primate males. *Behaviour,* 151, 871–906. doi: 10.1163/1568539X-00003191

Paul, A. (2006). Kinship and behaviour in Barbary macaques. In: J.K. Hodges, & J. Cortes (Eds) *The Barbary macaques: Biology, Management and Conservation* (pp. 47 - 61). Nottingham, U.K.: Nottingham University Press.

Petit, O., Abegg, C., & Thierry, B. (1997). A comparative study of aggression and conciliation in three cercopithecine monkeys (*Macaca fuscata*, *Macaca nigra*, *Papio papio*). *Behaviour, 134,* 415–432. doi: 10.1163/156853997X00610

Petit, O., Desportes, C., & Thierry, B (1992). Differential probability of "coproduction" in two species of macaques (*Macaca tonkeana*, *M. mulatta*). *Ethology, 90,* 107–120. doi: 0.1111/j.1439-0310.1992.tb00825.x

Petit, O., & Thierry, B. (1994). Aggressive and peaceful interventions in conflicts in Tonkean macaques. *Animal Behaviour, 48,* 1427–1436. doi:10.1006/anbe.1994.1378

Prange, S., Gehrt, S. D., & Hauver, S. (2011). Frequency and duration of contacts between free-ranging raccoons: uncovering a hidden social system. *Journal of Mammalogy*, *92*, 1331–1342. doi:10.1644/10-MAMM-A-416.1

R Development Core Team (2015) R: A language and environment for statistical computing, version 3.2.1.

Schino, G. (2007). Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, *18,* 115–120. doi: 10.1093/beheco/arl045

Schino, G., & Aureli, F. (2009). Reciprocal altruism in primates: partner choice, cognition, and emotions. *Advances in the Study of Behavior, 39,* 45–69. doi: 10.1016/S0065-3454(09)39002-6

Schradin, C. (2013) Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Philosophical Transactions of the Royal Society B: Biological Science, 368,* 20120346. doi: 10.1098/rstb.2012.0346

Schülke, O., & Ostner, J. (2008). Male reproductive skew, paternal relatedness, and female social relationships. *American Journal of Primatology, 70,* 695–698. doi: 10.1002/ajp.20546

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology, 65,* 671–698. doi:10.1016/0022-5193(77)90015-7

Seyfarth, R. M., Silk, J. B., & Cheney, D. L. (2014). Social bonds in female baboons: the interaction between personality, kinship and rank. *Animal Behaviour, 87,* 23–29. doi:10.1016/j.anbehav.2013.10.008

Sick, C., Carter, A. J., Marshall, H. H., Knapp, L. A., Dabelsteen, T., & Cowlishaw, G. (2014). Evidence for varying social strategies across the day in chacma baboons. *Biology Letters*, 10, 20140249. doi:10.1098/rsbl.2014.0249

Silk, J. B., Cheney, D. L., & Seyfarth, R. M. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology, 22,* 213–225. doi:10.1002/evan.21367

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., et al. (2010). Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. *Current Biology, 20,* 1359–1361. doi:10.1016/j.cub.2010.05.067

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., et al. (2009). The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences*, *276,* 3099–3104. doi:10.1098/rspb.2009.0681

Silk, J. B. (2007a). The adaptive value of sociality in mammalian groups. *Philosophical Transaction of the Royal Society B: Biological Sciences, 362*, 539–559. doi: 10.1098/rstb.2006.1994.

Silk, J. B. (2007b). Social components of fitness in primate groups. *Science, 317*, 1347–1351. doi: 10.1126/science.1140734

Silk, J. B., Altmann, J., & Alberts, S. C. (2006a). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology, 61,* 197–204. doi: 10.1007/s00265-006-0250-9

Silk J. B., Altmann J., Alberts S. C. (2006b). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobioly, 61,* 183–195. doi: 10.1007/s00265-006-0249-2

Smith, J. E., van Horn, R. C., Powning, K. S., Cole, A. R., Graham, K. E., Memenis, S. K., Holekamp, K. E. (2010). Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology, 21*, 284–303. doi:10.1093/beheco/arp181

Smith, J. E., Memenis, S. K., Holekamp, K. E. (2007). Rank-related partner choice in the fission-fusion society of the spotted hyena (*Crocuta crocuta*). *Behavioral Ecology and Sociobiology, 61,* 753–765. doi: 10.1007/s00265-006-0305-y

Smith, K. L., Alberts, S. C., & Altmann, J. (2003). Wild female baboons bias their social behaviour towards paternal half-sisters. *Proceedings of the Royal Society B: Biological Science, 270*, 503–510. doi: 10.1098/rspb.2002.2277

Sterck, E. H. M., Watts, D. P., van Schaik C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology, 41*, 291–309. doi:10.1007/s002650050390

Sueur, C., & Petit, O. (2008). Shared or unshared consensus decision in macaques? *Behavioral Processes, 78*, 84–92. doi: 10.1016/j.beproc.2008.01.004

Sugardjito, J., Southwick, C. H., Supriatna, J., Kohlhaas, A., Baker, S. C., Erwin, J., Froehlich, J., & Lerche, N. (1989). Population survey of macaques in northern Sulawesi. *American Journal of Primatology, 18*, 285–301. doi: 10.1002/ajp.1350180403

Taberlet, P., Griffin, S., Goossens, B., Questiau, S., Manceau, V., Escaravage, N., Waits, L. P., Bouvet, J. (1996) Reliable genotyping of samples with very low DNA quantities using PCR. *Nucleic Acids Research, 24,* 3189–3194. doi:10.1093/nar/24.16.3189

Thierry, B. (2013). Identifying constraints in the evolution of primate societies. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368,* 20120342. doi:10.1098/rstb.2012.0342

Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C., & De Waal, F. B. M. (2008). A comparative study of conflict resolution in macaques: insights into the nature of trait covariation. *Animal Behaviour, 75,* 847–860. doi: 10.1016/j.anbehav.2007.07.006

Thierry, B. (2007). Unity in diversity: lessons from macaque societies. *Evolutionary Anthropology, 16*, 224–238. doi: 10.1002/evan.20147

Thierry, B., Bynum, E. L., Baker, S. C., Kinnaird, M. F., Matsumura, S., Muroyama, Y., et al. (2000). The social repertoire of Sulawesi macaques. *Primate Research*, *16*, 203–226. doi:10.2354/psj.16.203

Thierry, B. (1990). Feedback loop between kinship and dominance: the macaque model. *Journal of Theoretical Biology*. *145,* 511–522. doi:10.1016/S0022-5193(05)80485-0

Tinsley Johnson, E., Snyder-Mackler, N., Beehner, J. C., & Bergman, T. J. (2014) Kinship and dominance rank influence the strength of social bonds in female geladas (*Theropithecus gelada*). *International Journal of Primatology, 35,* 288–304. doi: 10.1007/s10764-013-9733-5

Uchino, B. N. (2006). Social Support and Health: A Review of Physiological Processes Potentially Underlying Links to Disease Outcomes. *Journal of Behavioral Medicine*, *29*, 377–387. doi:10.1007/s10865-006-9056-5

van Horn, R. C., Altmann, J., & Alberts, S. C. (2008). Can’t get there from here: inferring kinship from pairwise genetic relatedness. *Animal Behaviour, 75*, 1173–1180. doi:10.1016/j.anbehav.2007.08.027

van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In: V. Standen, & R. A. Foley (Eds) *Comparative Socioecology: The Behavioural Ecology of Humans and other Mammals* (pp. 195-218). Oxford, U.K.: Blackwell Scientific Publications.

Ventura R, Majolo B, Koyama NF, et al (2006) Reciprocation and interchange in wild Japanese macaques: grooming, co-feeding, and agonistic support. Am J Primatol 68:1138–1149. doi:10.1002/ajp.20314

Wahaj, S. A., van Horn, R. C., van Horn, T. L., Dreyer, R., Hilgris, R., Schwarz, J., Holekamp, K. E. (2004). Kin discrimination in the spotted hyena (*Crocuta crocuta*): nepotism among siblings. *Behavioral Ecology and Sociobiology, 56*, 237–247. doi: 10.1007/s00265-004-0783-8

Wang, J. (2011). COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. *Molecular Ecology Resources, 11*, 141–145. doi: 10.1111/j.1755-0998.2010.02885.x

Wenzel, S., Ostner, J., & Schülke, O. (2013). Paternal relatedness predicts the strength of social bonds among female rhesus macaques. *PLoS ONE, 8*, e59789–e59789. doi: 10.1371/journal.pone.0059789

Wey, T. W., Burger, J. R., Ebensperger, L. A., & Hayes, L. D. (2013). Reproductive correlates of social network variation in plurally breeding degus (*Octodon degus*). *Animal Behaviour*, *85*, 1407–1414. doi:10.1016/j.anbehav.2013.03.035

Whitehead, H. (2008). *Analysing animal societies: quantitative methods for vertebrates social analysis*. Chicago, U.S.A.: The University of Chicago Press.

Widdig, A. (2013) The impact of male reproductive skew on kin structure and sociality in multi-male groups: Altmann (1979) revisited. *Evolutionary Anthropology, 22,* 239–250. doi: 10.1002/evan.21366

Wrangham, R. W., & Rubenstein, D. I. (1986) Social evolution in birds and mammals. In: D. I. Rubenstein, & Wrangham R. W. (Eds) *Ecological Aspects of Social Evolution - Birds and Mammals* (pp. 452–470). Princeton, USA: Princeton University Press.

Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2014). Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. *Proceedings of the National Academy of Science, 111*, 195–200. doi:10.1073/pnas.1411450111

Young, C., Majolo, B., Schülke, O., & Ostner, J. (2014). Male social bonds and rank predict supporter selection in cooperative aggression in wild Barbary macaques. *Animal Behaviour*, *95*, 23–32. doi:10.1016/j.anbehav.2014.06.007

Figure legends

Figure 1: Distribution of overall CSI scores of female-female dyads in the two study groups, up PB and down R1. The blue arrow indicates the median and the red arrow 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.

Figure 2: Variation in CSI scores of female-female dyads in the two study groups, left PB and right 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 grey), twice (medium blue) or three times (big red) across the three periods. The presence of few red circles but many grey dots illustrate how bond strength changes across periods and lacks of predictability.

Figure 3: Effect of dominance difference (left panels), relatedness (middle panels) and age difference (right panels) on bond strength (top panels), bond predictability (middle panels), and bond equitability (bottom panels). 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 grey points are the original data points transformed and scaled as in the statistical model.

Figure 4: Effect of bond strength (left panels), bond predictability (middle panels), and bond equitability (right panels) on coalitionary support (top panels), feeding in proximity frequency (middle panels), and aggression frequency (bottom panels). 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 grey points are the original data points transformed and scaled as in the statistical model.

Degrees of freedom in social bonds of crested macaque females.

Julie Duboscq [1,2,3,4*†], Christof Neumann [1,2,5,6**], Muhammad Agil [7], Dyah Perwitasari-Farajallah [8,9], Bernard Thierry [3,4], Antje Engelhardt [1,2***]

[1] Junior Research Group of Primate Sexual Selection, German Primate Center, Göttingen, Germany, [2] Courant Research Centre for the Evolution of Social Behaviour, Göttingen, Germany, [3] Université de Strasbourg, Institut Pluridisciplinaire Hubert Curien, Strasbourg, France, [4] Centre National de la Recherche Scientifique, Département Ecologie, Physiologie et Ethologie, Strasbourg, France, [5] Junior Research Group of Primate Kin Selection, Max-Planck-Institute for Evolutionary Anthropology, Leipzig, Germany, [6] Institute of Biology, Faculty of Bioscience, Pharmacy and Psychology, University of Leipzig, Leipzig, Germany, [7] Faculty of Veterinary Sciences, Bogor Agricultural University, Bogor, Indonesia, [8] Primate Research Center, Bogor Agricultural University, Bogor, Indonesia, [9] Faculty of Mathematics and Natural Sciences, Bogor Agricultural University, Bogor, Indonesia

* corresponding author: julie.a.m.duboscq@gmail.com

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

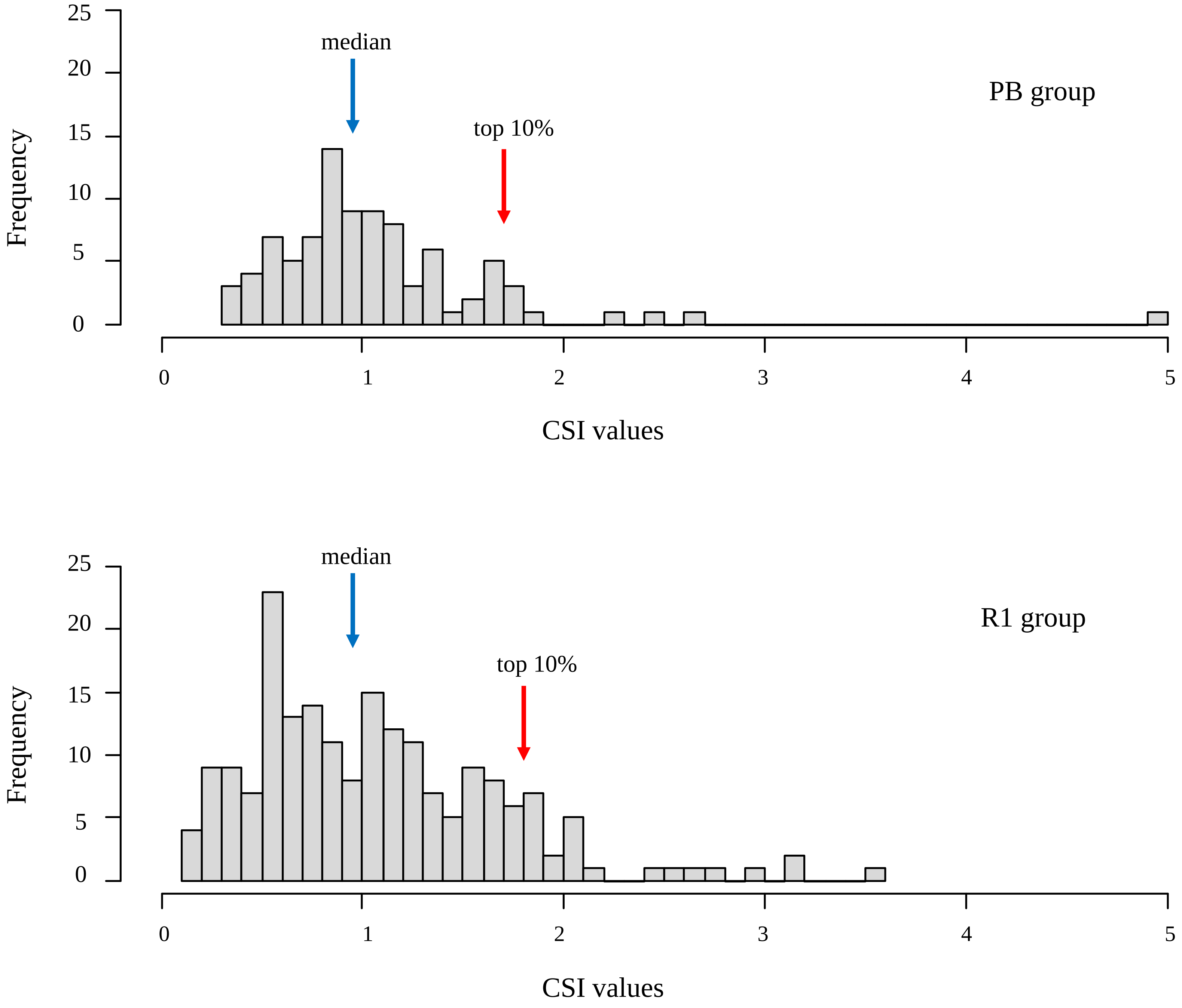
Tolerant females can express great degrees of freedom in their social relationships

These patterns are under-appreciated in stable nepotistic hierarchical societies

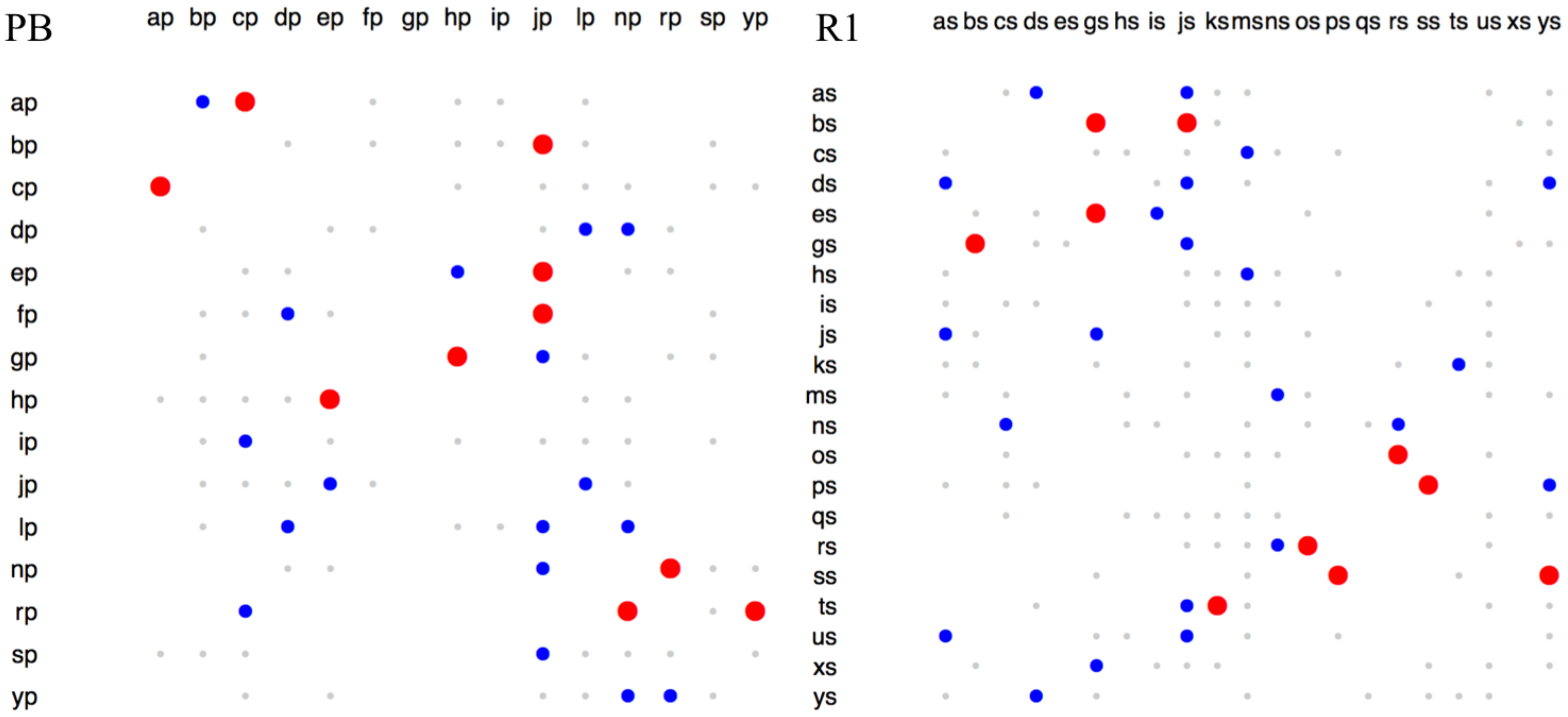
Acknowledgments

This article is dedicated to Ugiek and Antri. We gratefully acknowledge the permission of the Indonesian State Ministry of Research and Technology (RISTEK), the Directorate General of Forest Protection and Nature Conservation (PHKA) in Jakarta and the Department for the Conservation of Natural Resources (BKSDA) in Manado, particularly Pak Untung and Pak Yunus, to conduct this research in the Tangkoko-Batuangus Nature Reserve. We thank all the members of the Macaca Nigra Project for their support in the field, and especially Dwi Yandhi Febryianti and Jérôme Micheletta for their help with data collection.

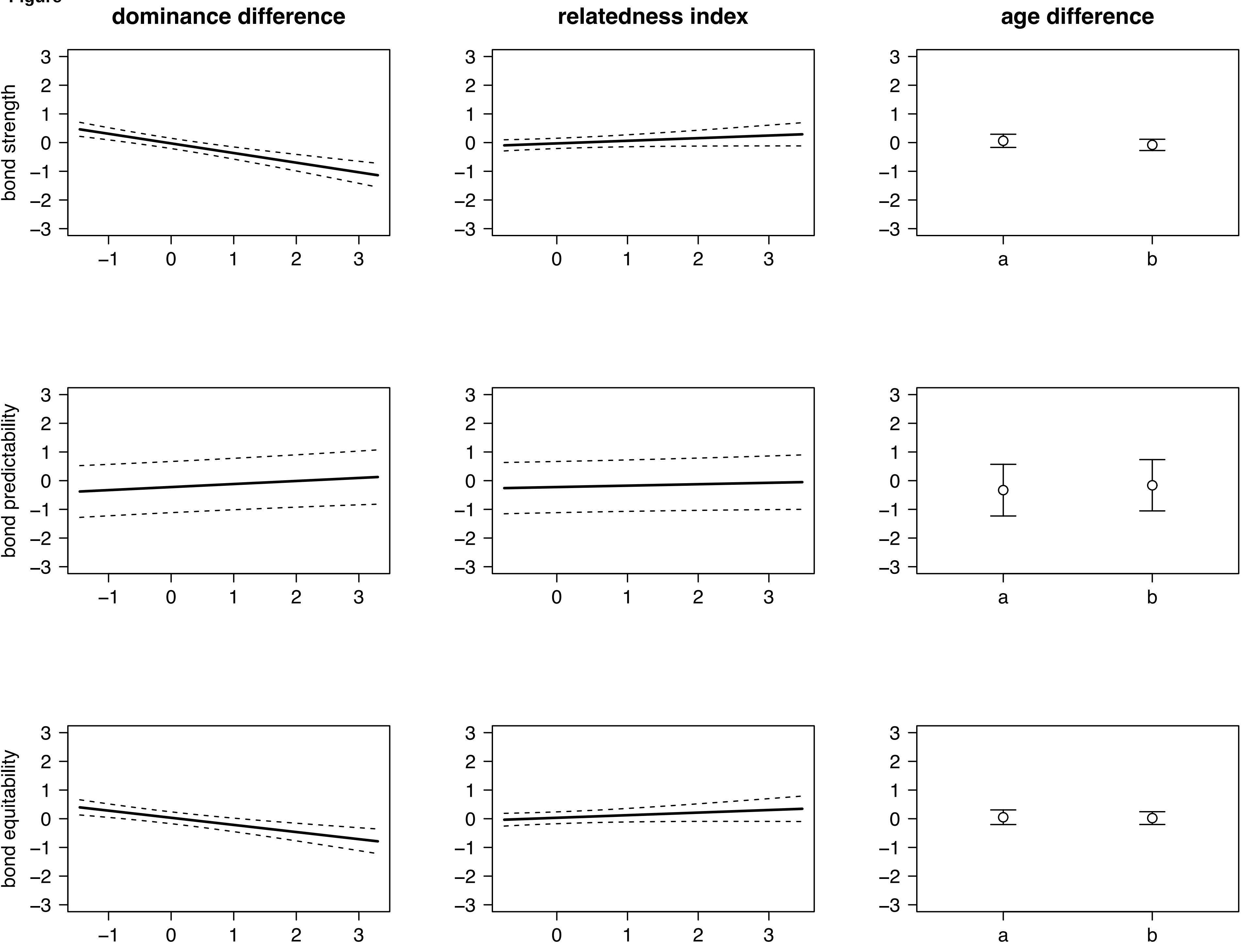
Figure


PB group
median
top 10%
Frequency
25
20
15
10
5
0
0
1
2
3
4
5
CSI values
R1 group
median
top 10%
Frequency
25
20
15
10
5
0
0
1
2
3
4
5
CSI values

Figure

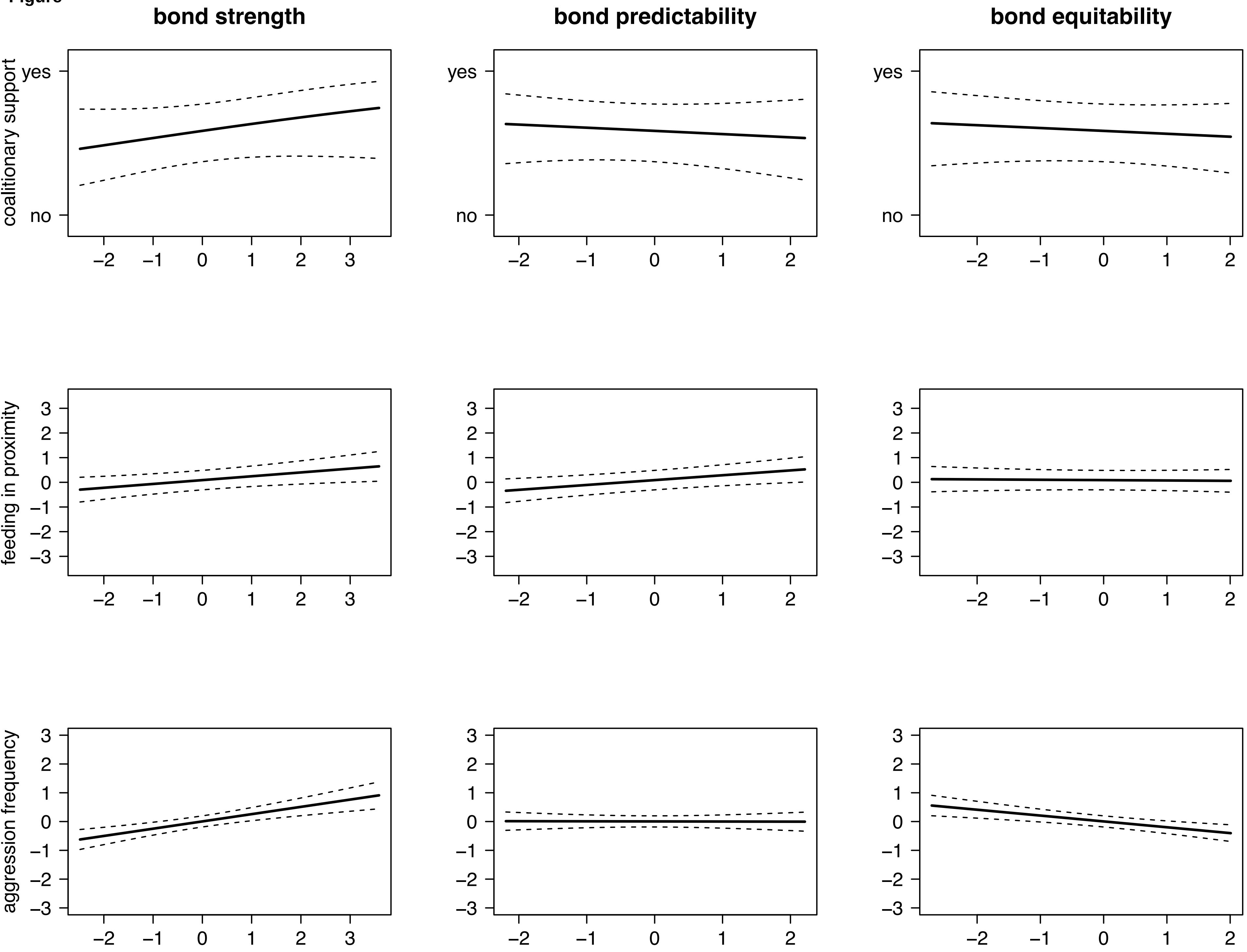

PB
ap bp cp dp ep fp gp hp ip jp lp np rp sp yp
ap
bp
cp
dp
ep
fp
gp
hp
ip
jp
lp
np
rp
sp
yp
R1
as bs cs ds es gs hs is js ks ms ns os ps qs rs ss ts us xs ys
as
bs
cs
ds
es
gs
hs
is
js
ks
ms
ns
os
ps
qs
rs
ss
ts
us
xs
ys

Figure



dominance difference
relatedness index
age difference
bond strength
bond predictability
bond equitability
3
2
1
0
−1
−2
−3
−1
0
1
2
3
a
b

Figure


bond strength
bond predictability
bond equitability
coalitionary support
yes
no
feeding in proximity
aggression frequency
−3
−2
−1
0
1
2
3