Animal Behaviour 123 (2017) 411–426

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Degrees of freedom in social bonds of crested macaque females

Julie Duboscq [a, b, c, d, *], Christof Neumann [a, b, e, f, 1], Muhammad Agil [g], Dyah Perwitasari-Farajallah [h, i], Bernard Thierry [c, d], Antje Engelhardt [a, b, 2]

[a] Junior Research Group of Primate Sexual Selection, German Primate Center, Göttingen, Germany
[b] Courant Research Centre for the Evolution of Social Behaviour, Göttingen, Germany
[c] Université de Strasbourg, Institut Pluridisciplinaire Hubert Curien, Strasbourg, France
[d] Centre National de la Recherche Scientifique, Département Ecologie, Physiologie et Ethologie, Strasbourg, France
[e] Junior Research Group of Primate Kin Selection, Max-Planck-Institute for Evolutionary Anthropology, Leipzig, Germany
[f] Institute of Biology, Faculty of Bioscience, Pharmacy and Psychology, University of Leipzig, Leipzig, Germany
[g] Faculty of Veterinary Sciences, Bogor Agricultural University, Bogor, Indonesia
[h] Primate Research Center, Bogor Agricultural University, Bogor, Indonesia
[i] Faculty of Mathematics and Natural Sciences, Bogor Agricultural University, Bogor, Indonesia

ARTICLE INFO

Article history:
Received 5 July 2016
Initial acceptance 29 July 2016
Final acceptance 18 October 2016
Available online 18 December 2016
MS. number: 16-00594R

Keywords:
behavioural strategy
equitability
predictability
primates
social bonds
social dynamics
strength

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

Social bonds are positive social relationships among pairs of individuals of the same group (Silk, 2007a; Silk, Cheney, & Seyfarth, 2013). 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 wellbeing compared to others (Cameron, Setsaas, & Linklater, 2009; Frère et al., 2010; McFarland & Majolo, 2013; Silk et al., 2010, 2009; Uchino, 2006; Young, Majolo, Heistermann, Schülke, & Ostner, 2014). For individuals, the value of social bonds is also related to the direct or indirect benefits they may

* Correspondence and present address: J. Duboscq, Kyoto University Wildlife Research Centre, 2-24 Tanaka-Sekiden-cho, Sakyo, Kyoto 606-8203, Japan.
E-mail address: julie.a.m.duboscq@gmail.com (J. Duboscq).
[1] Present address: Université de Neuchâtel, Institute of Biology, Department of Comparative Cognition, Neuchâtel, Switzerland.
[2] Present address: Liverpool John Moores University, School of Natural Sciences and Psychology, Liverpool, U.K.

http://dx.doi.org/10.1016/j.anbehav.2016.11.010
0003-3472/

obtain from daily social exchanges, e.g. in reconciliation after conflicts (e.g. Fraser & Bugnyar, 2011), or for better access to food resources (e.g. Smith, Memenis, & Holekamp, 2007), which ultimately may impact their fitness and wellbeing (Ostner & Schülke, 2014; Silk, 2007a).

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 certain bonds. In many animal societies, individuals that are similar in terms of genetic relatedness, dominance status, personality, reproductive state or energetic needs are more likely to form strong and enduring social bonds than others (Armitage & Schwartz, 2000; Carter, Seddon, Frère, Carter, & Goldizen, 2013; Godde, Côté, & Réale, 2015; Hirsch, Stanton, & Maldonado, 2012; Seyfarth et al., 2014). 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 nonrelative may be more valuable (Schino, 2007; Smith et al., 2010). Similarly, pregnant or early lactating female chacma baboons, *Papio ursinus*, were less likely to become involved in coalitions and, thus, were not reliable cooperation partners for both kin and nonkin (Barrett & Henzi, 2001).

Research on the benefits of social bonds among same-sex adult group members has so far mostly considered how bond characteristics at the extreme positive end of the spectrum, e.g. preferred associates (Frère et al., 2010) or top three partners (Silk, Altmann, & Alberts, 2006a), affect measures of fitness, health or wellbeing. However, animals may have a variety of options for regulating the consequences of bonds. First, establishing and maintaining predictable and/or equitable bonds may bring as many, if not more, benefits as having strong bonds (e.g. the sheer amount of research on cooperation and reciprocity: Nowak, 2006; Trivers, 1971, 2006). In addition, 'weak' bonds within a social network may be as important as 'strong' bonds, inasmuch as weak bonds contribute to stabilizing the overall network or to enhancing the propagation of information or innovation (Bakshy, Rosenn, Marlow, & Adamic, 2012; Granovetter, 1973). Finally, it has been shown that variance in bond strength rather than absolute strength itself predicts fitness (e.g. Barocas, Ilany, Koren, Kam, & Geffen, 2011; Wey, Burger, Ebensperger, & Hayes, 2013). Studies integrating the different dimensions of social bonds simultaneously and on a continuous scale are therefore indispensable for deepening our understanding of the link between sociality and fitness.

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

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

In this study, we aimed to investigate these degrees of freedom and the interplay between the structure and the value of social bonds in wild female crested macaques, *Macaca nigra*, which express a tolerant social style (Duboscq et al., 2013; Petit, Abegg, & Thierry, 1997). Crested macaques live in a relatively predictable and safe ecological environment (low predation risk and abundant food year-round; O'Brien & Kinnaird, 1997) while facing dynamic social conditions, e.g. male migration and hierarchical changes, which are a potential source of social instability in the group (Marty, Hodges, Agil, & Engelhardt, 2015; Neumann, 2013). Females reproduce year-round (Kerhoas et al., 2014), which is another potential source of fluctuation in the amount of time and attention females can devote to their female social partners (Barrett & Henzi, 2001; Bardi, Shimizu, Fujita, Borgognini Tarli, & Huffman, 2001; Brent, MacLarnon, Platt, & Semple, 2013; D'Amato, Troisi, Scucchi, & Fuccillo, 1982). Previous studies on the same population showed that female crested macaques form highly diverse affiliative social networks (Duboscq et al., 2013). In one study, the strength of female–female social bonds was positively linked to predator deterrence, suggesting that strong bonds play a role in enhancing survival (Micheletta et al., 2012). In another, bond strength did not affect the occurrence and frequency of reconciliation, an important conflict management strategy (Duboscq, Agil, Engelhardt, & Thierry, 2014). Nevertheless, 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 females to express many degrees of social freedom in their choice of social partners and the patterning of their social bonds.

Specifically, since macaques form stable, matrilineal, hierarchical societies, kin and adjacently ranked dyads are expected to form the strongest, most predictable and most equitable bonds (Silk, 2007b). However, given the tolerant social style of crested macaques and their expected great degrees of social freedom, we hypothesized that these dyad characteristics would not predict social bond characteristics. To test this hypothesis and to quantify the structure of bonds, we analysed the relationship between three measures of dyadic similarities (relatedness, similarity in age and dominance rank) and three social bond characteristics, namely strength, predictability and equitability. Furthermore, under the

hypothesis that social bond characteristics are linked to fitness in a positive predictable way (Silk, 2007a, 2007b), variation in these characteristics is expected to substantially explain the occurrence or frequency of behaviours directly or indirectly linked to fitness benefits, such as a reduction in aggression, increased probability of 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 hypothesized that the characteristics of social bonds would not predict the occurrence of these fitness-related behaviours. To test this hypothesis and to establish the value of bonds, we tested the extent to which each social bond characteristic influenced coalitionary support, feeding-in-proximity and aggression. By taking a more integrated perspective of social bonds in a species with a tolerant social style, we address the concept of individuals' degrees of social freedom within their stable network of social relationships (Butovskaya, 2004; Thierry, 1990).

METHODS

Ethical Note

This research adheres to all legal requirements and guidelines of the German and Indonesian governments and institutions (permit numbers 1240/FRP/SM/VI/2008 and SI-101/Set-3/2008) and to the ASAB/ABS (2012) guidelines for the Treatment of Animals in Behavioural Research and Teaching. No trapping or tagging was done as this is a wild population of critically endangered animals. The study animals were fully habituated to human observers at least 1 year before the start of data collection. Habituation consisted of following the group silently each day and for the entire day wearing a project-specific T-shirt until observers could approach any individual to within 5 m without it reacting. All adult monkeys could be individually identified based on physical characteristics alone (scars and old injuries (e.g. a limp), facial features, body shape, etc.). Binoculars were used to ensure accuracy in identification and data collection. All observers followed the same rules: no more than five observers were assigned to a group on a given day; no observers were to approach the monkeys to within 2 m; no observers were to interact with the animals in any way; and no observers were to disturb the natural behaviour of the subjects in any way. Furthermore, observers showing signs of sickness were not allowed in the forest until they produced a medical note certifying they were clear of infection, and all waste produced during observation was either buried or brought back to camp.

Behavioural Data Collection and Analysis

Field site, study animals and data collection

Crested macaques are critically endangered and endemic to the island of Sulawesi, Indonesia (Sugardjito et al., 1989). The study population inhabits the Tangkoko Reserve, North Sulawesi (1°33′N, 125°10′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', composed of ca. 60 and 80 individuals, respectively.

J.D. 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 min point sample observations for activity (foraging (searching for and manipulating food), feeding (putting food to mouth and chewing), socializing (being involved in social interactions including aggression), resting (staying immobile, eyes closed) and travelling (moving in a decided direction)). 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 (based on the maximum average body length of a female crested macaque, 55 cm, Zinner et al., 2013). 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 2480 h of focal data focusing on the 35 females that were continuously present during the entire study period ($\text{median}_{PB} = 68$ h per female, range_{PB} 65–78, $N_{PB} = 14$; $\text{median}_{R1} = 66$ h per female, range_{R1} 59–71, $N_{R1} = 21$). By doing so, we deliberately focused on general patterns and a stable core of individuals to make our study comparable to others. Behavioural interactions were expressed as duration (e.g. social grooming) or frequency (e.g. approach) per focal individual and per dyad (sum of two focal individuals) observation time over the whole study period (i.e. 19 months).

Additionally, for genetic relatedness determination, 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, 2014), 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 (i.e. one individual approaches another one without any threatening 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 ad libitum and during focal observations. At the beginning of the observation period, each group member 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-rating (hereafter termed Elo 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 (GEN-IAL GmbH, Troisdorf, Germany). We amplified 12 short-tandem repeats (or microsatellites; 10 tetranucleotide loci and two 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, Foster City, CA,

U.S.A.). 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 (multitubes 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 ($\text{median}_{PB} = 0.05$, range_{PB} 0.53; $\text{median}_{R1} = 0.05$, range_{R1} 0–0.72).

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

Bond characteristics

The strength of dyadic social bonds was quantified with the composite sociality index or CSI (Silk, Altmann, & Alberts, 2006b). It is built from matrices of dyadic social interactions and was calculated as follows:

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

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

Bond temporal variation (hereafter predictability) was assessed over three periods of 6 months each. Sampling efforts (i.e. observation time) per individual in each period were very similar. Six months is the maximum number of months after which all dyads were seen in proximity at least once, thus characterizing relatively accurate and robust matrices of interactions. We calculated the CSI again for each dyad for each period, then computed the coefficient of variation (CV, standard deviation divided by the mean) over the three CSIs for each dyad (Majolo, Ventura, & Schino, 2010). For statistical analysis, we multiplied the CV by −1 so that the lower (i.e. the more negative) the CV, the lower the predictability of the relationship across the three periods, i.e. the more CSI values varied across the three periods. 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:

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

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. This index takes into account the directionality of interactions.

Fitness-related behaviours

We defined coalitionary support as a focal female intervening aggressively (e.g. by threatening or chasing away one of the opponents) or peacefully (e.g. by embracing or lipsmacking at one of the opponents) in support of another female or receiving such an intervention herself during an aggressive interaction with another individual (Duboscq et al., 2014; Petit & Thierry, 1994). We calculated the frequency of support as the number of support instances over the total number of aggressive interactions in which each member of the dyad was separately involved (Duboscq et al., 2014). Owing 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 five body lengths, controlling for overall dyadic proximity and observation time. Hourly frequencies of aggression were taken from Duboscq et al. (2013).

Statistical Analyses

Structure of social bonds

We first tested for correlations between the three bond characteristics to assess their relationships with each other and to test the prediction that stronger bonds would be more predictable and equitable than weaker bonds. We built symmetric matrices of the CSI scores, the CVs and the EIs before running matrix correlations in MatMan v1.1 (de Vries, Netto, & Hanegraaf, 1993) with 1000 permutations between these matrices two-by-two. We then built three (generalized) linear mixed models (GLMM, Bolker et al., 2008), one for each social bond characteristic as response variable, and including relatedness (DML), absolute Elo-rating difference (Elo difference) and age difference (as a categorical variable same/different) as test predictors and member 1 and member 2 of the dyad (i.e. female identities randomly assigned to either variable) independently nested in group as random effects. We ran simulations in which female ID was randomly assigned to either member 1 or member 2; model parameters were recalculated and compared to the original results. This showed that this random assignment did not affect our conclusions (see Tables A1–A3, Figs A1–A3 in the Appendix).

Function of social bonds

We built three more models to investigate the value of social bonds, with the occurrence of coalitionary support, feeding-in-proximity rate and aggression rate as response variables and bond strength (CSI), predictability (CV) and equitability (EI) as test

predictors. In these models, we included as control predictors (predictors included in the null model) relatedness (DML), absolute Elo-rating difference (Elo difference) and age difference, and member 1 and member 2 of the dyad (i.e. female identities randomly assigned to either variable) independently nested in group as random effects (see Tables A4–A6, Figs A4–A6 in the Appendix for simulations identical to those described in the previous section).

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

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

Microsatellite-based relatedness estimators have been deemed unreliable for accurately measuring genetic relatedness in populations without pedigree information (Csilléry et al., 2006; van Horn, Altmann, & Alberts, 2008). We tackled this issue by using the approach suggested by Tinsley Johnson, Snyder-Mackler, Beehner, and Bergman (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 mother–infant pairs was 0.41. We therefore introduced an error taken from a 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 pair's true relatedness ($r = 0.5$). Our custom simulation proceeded in four steps: (1) add an error from a uniform distribution between −0.41 and +0.41 to the DML index of all female–female dyads in the data set; (2) run the models again with the modified DML index; (3) perform an LRT 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 96–100% of the 1000 simulations, depending on the response variable, which indicates that our results are relatively robust against errors in relatedness estimations (Table A7, Appendix).

RESULTS

The Structure of Social Bonds

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

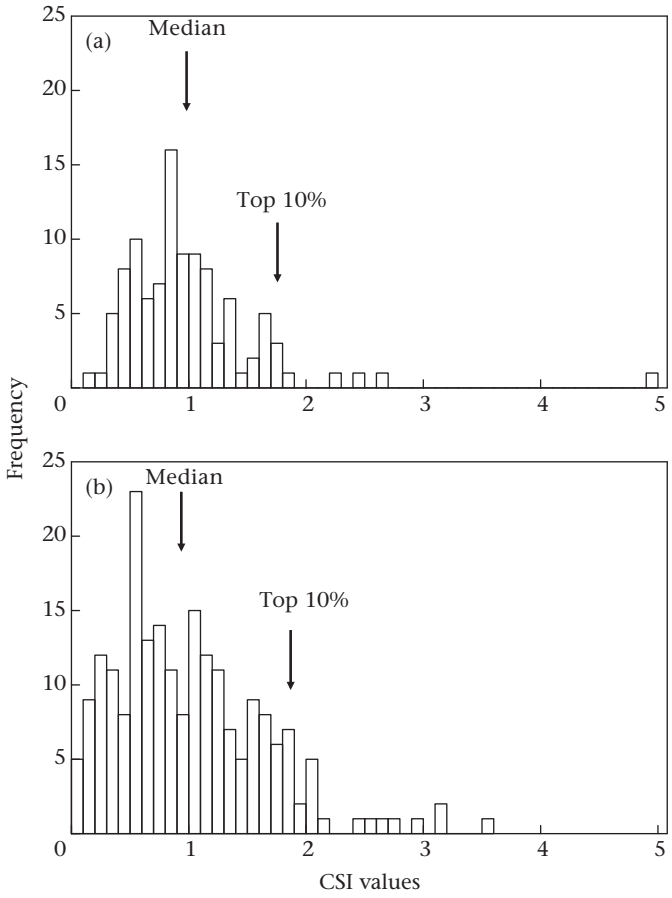

Figure 1. Distribution of overall CSI scores of female–female dyads in the two study groups, (a) PB and (b) R1. The arrows indicate the median and the limit of 10% of the strongest CSI scores. The fact that the distribution is only moderately skewed to the right (i.e. towards 0) indicates how average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

The mean coefficient of variation indicated moderate to low bond strength predictability across the three 6-month periods (mean $CV_{R1} = 0.66 \pm 0.01$ SD, mean $CV_{PB} = 0.70 \pm 0.14$ SD; Fig. 2). Ninety-four per cent of all females had at least one recurring partner over at least two periods among their top three partners and 47% of all females had at least one recurring partner over all three periods among their top three partners, but no female had the same three recurring top partners across all three periods (Fig. 2).

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

All three characteristics were correlated in both groups (Mantel tests: PB: $N = 105$ dyads: strength–predictability: Pearson's $r = -0.50$, $Z = 27.7$, $P < 0.001$; strength–equitability: Pearson's $r = 0.80$, $Z = 77.6$, $P < 0.001$; predictability–equitability: Pearson's $r = -0.71$, $Z = 20.7$, $P < 0.001$; R1: $N = 210$ dyads: strength–predictability: Pearson's $r = -0.55$, $Z = 133.6$, $P = 0.001$;

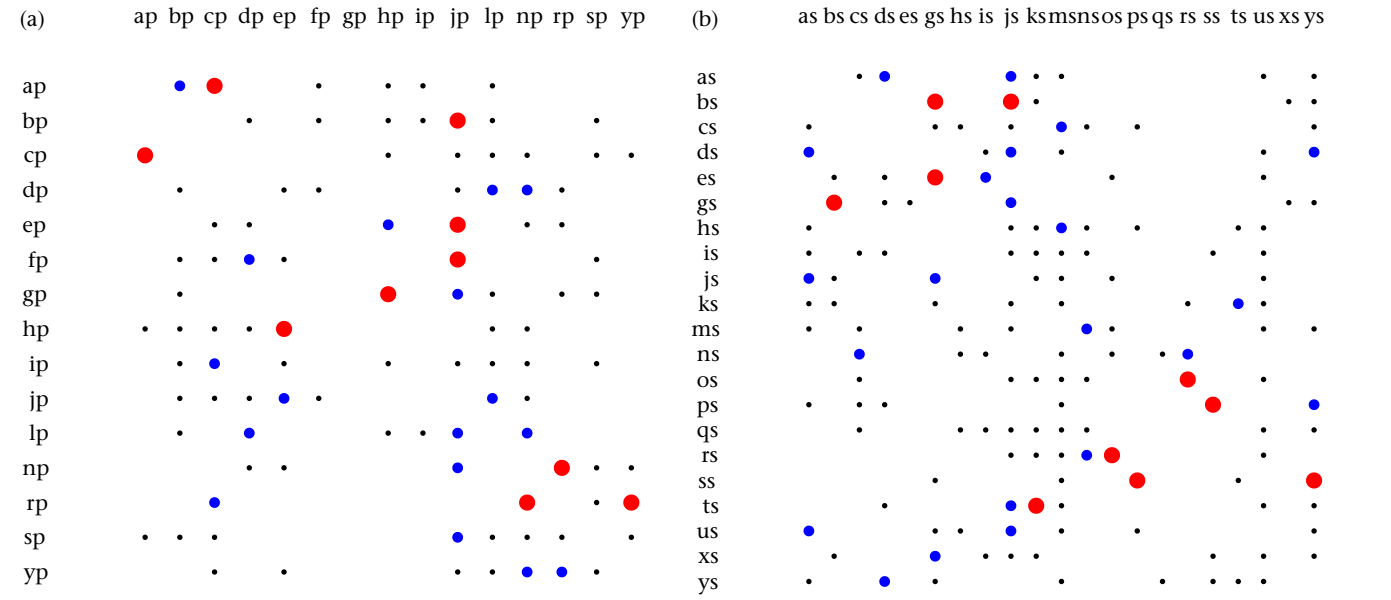

Figure 2. Variation in CSI scores of female–female dyads in the two study groups, (a) PB and (b) R1, across three 6-month periods. Row and column labels represent female identities. A circle denotes that the female in the column was among the top three partners of the female in the row at least once (small black), twice (medium blue) or three times (big red) across the three periods. The presence of few red circles but many black circles illustrates how bond strength changes across periods and lacks predictability.

strength–equitability: Pearson's $r = 0.79$, $Z = 143.0$, $P < 0.001$; predictability–equitability: Pearson's $r = -0.72$, $Z = 85.6$, $P < 0.001$), indicating that stronger bonds were more equitable but less predictable over time than weaker bonds and that more predictable bonds were less equitable than less predictable ones.

Female dyads with smaller dominance differences had significantly stronger, more predictable and more equitable social bonds than those with greater dominance differences (Table 1, Fig. 3). None of the tested bond characteristics were significantly related to the relatedness and age difference of the dyads (Table 1, Fig. 3).

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 3208 aggressive interactions. A female was found to be feeding in the proximity of another female around once in every 10 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 2 h (for details see Duboscq et al., 2013).

Coalitionary support was not explained by any of the tested bond characteristics (Table 2, Fig. 3). In contrast, dyads that had stronger and less predictable bonds fed more often in proximity than others (Table 2, Fig. 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 (Table 2, Fig. 4).

DISCUSSION

Social bonds in the studied female crested macaques showed contrasting patterns in their structure and value compared to other species with nepotistic hierarchical societies for which comparable data are available. Bonds were mostly of average strength (i.e. median strength close to the mean, 1, and relatively symmetric distribution), relatively equitable but only moderately enduring over the 19 months of the study. Social bonds were stronger, more predictable and more equitable among females close in dominance status than others, but not among kin or age peers. The three components of social bonds were correlated but had differential effects on the three fitness-related behaviours investigated. Thus, our predictions that dyad characteristics have little influence on social bond components and that these components have relatively weak effects on fitness-related behaviours were mostly fulfilled, showing the extent to which the studied females can express many

Table 1
Dyad characteristics and social bond components

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

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

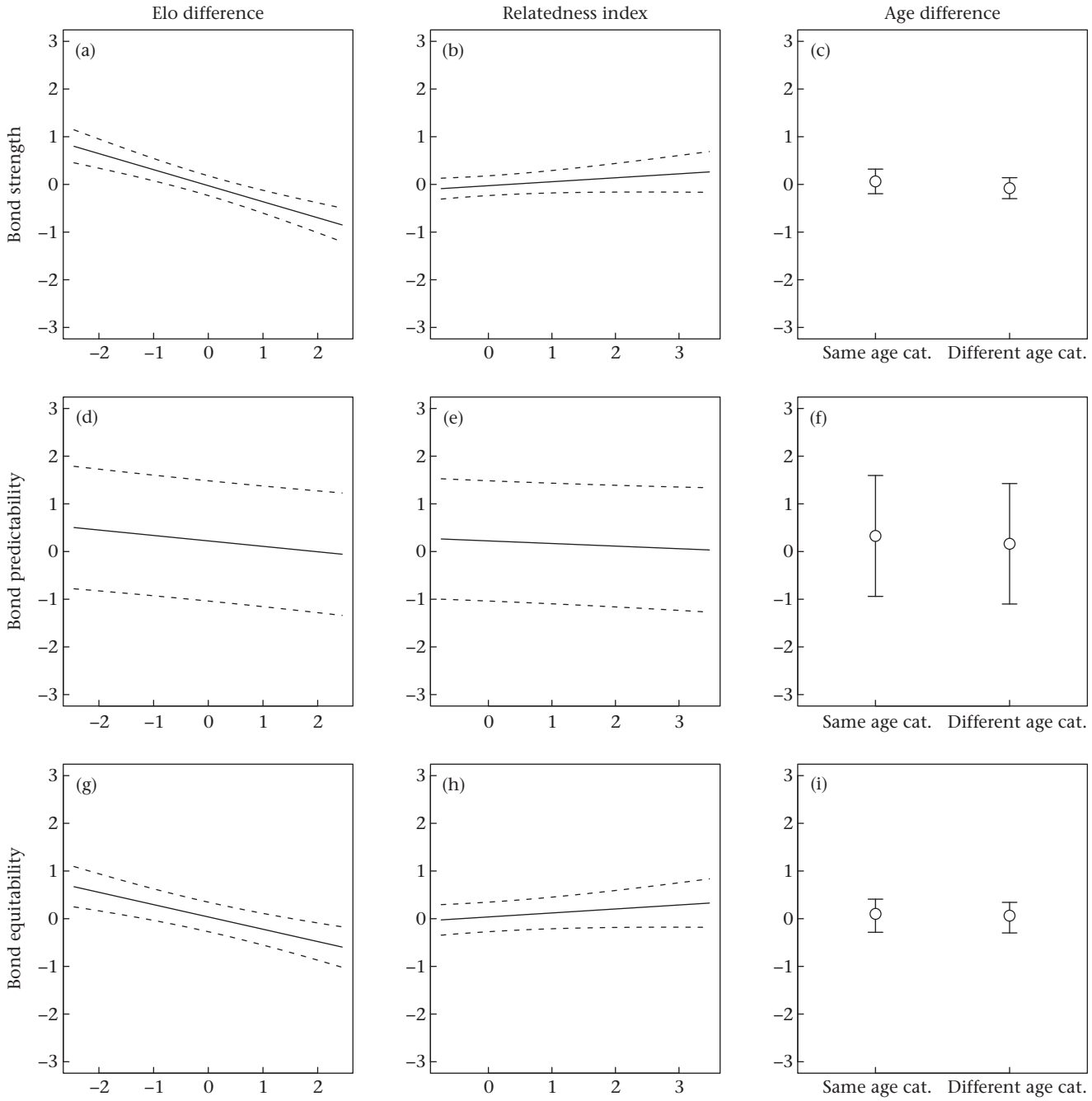

Figure 3. Effect of (a, d, g) Elo difference (from left to right = smaller to greater difference), (b, e, h) relatedness (from left to right = smaller to greater difference) and (c, f, i) age difference on (a, b, c) bond strength (from bottom up = weak to strong scores), (d, e, f) bond predictability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

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, owing 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 nonkin but also substantially less often than with maternal kin (Smith, Alberts, & Altmann, 2003; Wahaj et al., 2004; Wenzel, Ostner, & Schülke, 2013). Male reproductive skew and group tenure influence the proportion of paternal relatives in a group (Widdig, 2013); high male reproductive skew and short male tenure, which is a characteristic of this population of crested macaques (Higham et al., 2012; Marty et al., 2015), can lead to a relatively high proportion of paternal relatives. These conditions have been hypothesized to be a strong driver for high social tolerance among female macaques (Schülke & Ostner, 2008). Indeed, a weak kin bias among numerous

Table 2
Bond components and fitness-related benefits

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

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

paternal relatives may blur a strong kin bias between fewer maternal relatives. A hint to that effect is the relatively consistent positive influence of small dominance differences (most likely maternal rather than paternal relatives) on social behaviour whereas age difference had little to no effect (peers are more likely to be paternal than maternal relatives). Another related factor is the use of a continuous measure of kinship, which may have obscured any distinction between kin categories (e.g. mother–daughter, sister–sister) that may be of greater significance for individuals (Kapsalis & Berman, 1996).

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 macaques, *Macaca sylvanus*, and Tonkean macaques, *Macaca tonkeana*, which contrasts with more despotic species of macaques and other primates such as baboons (Cords, 2012; Paul, 2006; Thierry, 2007). 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. meerkats, *Suricata suricatta*: Clutton-Brock, 2009; hyaenas, *Crocuta crocuta*: East & Hofer, 2010; racoons, *Procyon lotor*: Hirsch, Prange, Hauver, & Gehrt, 2013; chimpanzees, *Pan troglodytes*: Langergraber, Mitani, & Vigilant, 2007), which suggests considerable potential for relatively large degrees of freedom in social relationships in the crested macaques too.

Overall, female–female bond strength did not show the typical asymmetrical distribution of more despotic primate species (at least those for which similar data are available: Assamese macaque, *Macaca 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 bonds of median strength (close to the average of the group which is by definition equal to 1), some weak and some strong bonds, and very few very 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. Although the actual number of strongest and weakest bonds a female has may remain constant, the identity of those partners and the absolute values of CSI vary considerably. 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 (Barrett & Henzi, 2001; East & Hofer, 2010; Henzi et al., 2009; Wrangham & Rubenstein, 1986). Investigating the effect of these sociodemographic events on bond formation and maintenance will be a fruitful endeavour in understanding better social dynamics. Furthermore, we advocate using continuous social indices instead of categories based on arbitrary cutoff points that are typically reported, such as three top partners versus remaining partners. Until evidence accumulates that these cutoffs are meaningful to individuals, we think it is prudent to move away from categorizations of social bonds into classes and to take the full breadth of the network of social relationships into account to fully comprehend the extent of social dynamics (see for example Young, 2016).

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 status. In female primates and hyaenas, 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 socializing 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 very 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 (Barrett & Henzi, 2006;

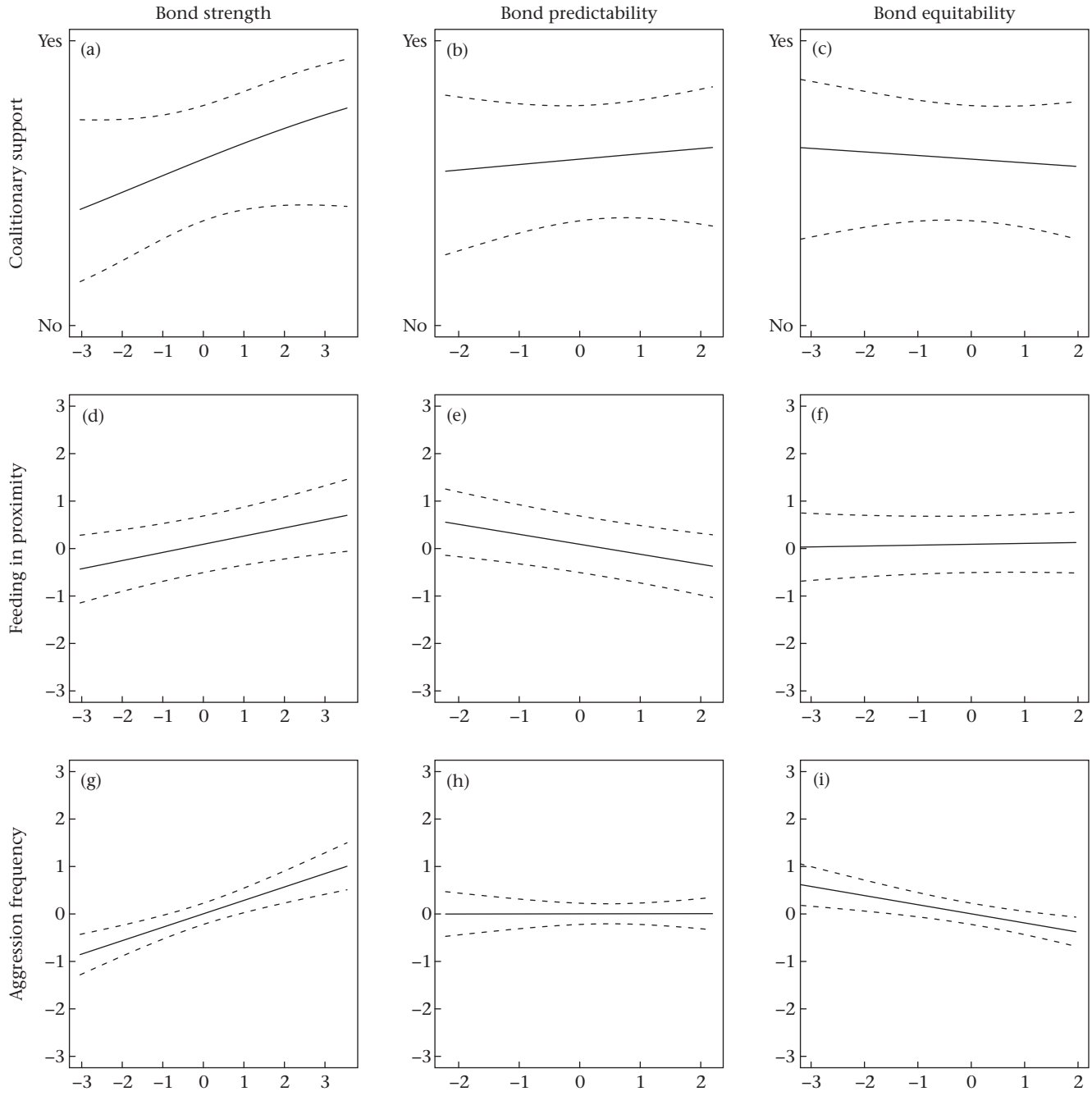

Figure 4. Effect of (a, d, g) bond strength (from bottom up = weak to strong scores), (b, e, h) bond predictability (from bottom up = low to high predictability) and (c, f, i) bond equitability (from bottom up = from low to high equitability) on (a, b, c) coalitionary support, (d, e, f) feeding in proximity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

Noë & Hammerstein, 1994), thereby generating a potential source of variation in the endurance of social bonds too.

The potential opportunistic nature of these social bonds also seems apparent in the analyses of their potential adaptive value. Previous studies on the same population showed somewhat contrasting results. The strength of social bonds was related to anti-predator responses, indicating their importance in threatening situations (Micheletta et al., 2012). However, the equitability and predictability, rather than strength, of social bonds influenced the occurrence of conflict management behaviour (Duboscq et al., 2014). Furthermore, the occurrence of reconciliation, an important mechanism of social cohesion, appears to function as appeasement, a short-term tactic, rather than to repair relationships, a more long-term strategy (Duboscq et al., 2014). In the current study, variance in bond characteristics helped only to a certain extent to explain variation in three additional fitness-related behaviours. First, more strongly bonded females fed more often in proximity but also fought more often with each other than females with weaker bonds. This indicates that more strongly bonded dyads may be more resilient to disruptions of their bond (by aggression) over food than less strongly bonded dyads (Aureli, Fraser, Schaffner, & Schino, 2012). Second, this is consistent with the finding that partners with less predictable bonds also fed more often in proximity, as stronger bonds tended to be less predictable.

The link between bond predictability and co-feeding frequency suggests either that partners with enduring relationships avoid endangering the stability of their relationship over feeding competition, or that the endurance of bonds is affected by another factor that we have not considered, for example female energetic needs (perhaps in relation to reproductive state). Third, the negative relationship between equitability and aggression rate could indicate that less equitable dyads often need to negotiate their relationship through engaging in agonistic interactions, which are often mild in this species (Duboscq et al., 2013). This could be the case if one partner gets frustrated to be at the lesser end of the social exchange, especially since less equitable bonds also tended to be weaker in strength. These results stress the need to consider more than one dimension of social bonds simultaneously 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 that suggested for males of the same species (Neumann, 2013; Neumann, Agil, Widdig, & Engelhardt, 2013). As such, females seem able to express large degrees of social freedom with regard to their dominance and kin relationships (Butovskaya, 2004; Thierry, 1990). Nevertheless, females also seem to specifically rely on certain partners, with whom they have strong, predictable or equitable bonds, in specific contexts (post-conflict interactions, Duboscq et al., 2014) or in especially challenging situations (predator deterrence, Micheletta et al., 2012). This 'many-good-friends' strategy can be costly temporally and energetically, but it can also bring a wide range of benefits, including enhanced negotiation skills, improved collective decision making, and facilitated cooperation in joint-action problems (Hare, Melis, Woods, Hasting, & Wrangham, 2007; McComb & Semple, 2005; Petit, Desportes, & Thierry, 1992; Sueur & Petit, 2008; Thierry et al., 2008).

The contrast between the stability of the social structure of macaques, in general, and the degrees of freedom shown by female crested macaques, in particular, in establishing and maintaining relationships leads to questions about the temporal dynamics of social bonds and the short- and long-term reciprocity of social exchanges within stable societies. It highlights the need to consider more carefully the whole network of bonds, weak and strong, in a more integrated continuous way as advocated by Granovetter (1973). More importantly, fitness-related behaviours, like coalitionary support, are presumably based on long-term alliances. Thus, to what extent patterns in so-called strategic behaviours can resist the magnitude of changes in social bonds is currently not clear. It is possible that females with stronger, more equitable, more predictable bonds or more numerous such partners benefit from a better extrinsic support network than others (Harcourt 1989; Silk, 2007a, 2007b). This extrinsic power may not be 'observable' as such because it often translates into conflict prevention or avoidance. Investigating this question could help to determine how dynamic societies actually are and whether species or population differences in dynamics exist. Fluctuations in social networks are indeed pervasive in species with flexible (Schradin, 2013) or seasonal sociality (Blumstein, 2013; Brent et al., 2013; Prange, Gehrt, & Hauver, 2011). Whether our findings reflect a pattern more common than previously thought or are typical for this study population remains to be investigated and requires comparative studies. This is of tremendous importance to better understand the social components of fitness and the mechanisms linking sociality to fitness.

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. This study was funded by the Volkswagen Foundation (funding initiative Evolutionary Biology, grant I/84 200) and Primate Conservation Inc. (grant PCI 757) to J.D. and by a grant from the German Research Council (EN 916/2) to A.E. All authors declare they have no conflict of interest of any kind.

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. http://dx.doi.org/10.1006/anbe.2000.1571.

Arandjelovic, M., Guschanski, K., Schubert, G., Harris, T. R., Thalmann, O., Siedel, H., et al. (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. http://dx.doi.org/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 Sciences of the United States of America, 97*, 12149–12152. http://dx.doi.org/10.1073/pnas.200196097.

ASAB/ABS. (2012). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour, 83*, 301–309. http://dx.doi.org/10.1016/j.anbehav.2011.10.031.

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, IL: The University of Chicago Press.

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, NY: ACM. http://dx.doi.org/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. http://dx.doi.org/10.1006/hbeh.2001.1651.

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. http://dx.doi.org/10.1371/journal.pone.0022375.

Barrett, L., & Henzi, P. (2001). Constraints on relationship formation among female primates. *Behaviour, 139*, 263–289. http://dx.doi.org/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. http://dx.doi.org/10.18637/jss.v067.i01.

Bayes, M., Smith, K., Alberts, S., Altmann, J., & Bruford, M. (2000). Testing the reliability of microsatellite typing from faecal DNA in the savannah baboon. *Conservation Genetics, 1*, 173–176. http://dx.doi.org/10.1023/A:1026595324974.

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. http://dx.doi.org/10.1098/rstb.2012.0349.

Bolker, B., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., et al. (2008). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology and Evolution, 24*, 127–135. http://dx.doi.org/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. http://dx.doi.org/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.

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 of the United States of America, 106*, 13850–13853. http://dx.doi.org/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. http://dx.doi.org/10.1016/j.anbehav.2012.11.011.

Chapais, B. (2004). How kinship generates dominance structures: A comparative perspective. In B. Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque societies, a model for the study of social organisation* (pp. 186–204). Cambridge, U.K.: Cambridge University Press.

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, Germany: Springer.

Clutton-Brock, T. H. (2009). Cooperation between non-kin in animal societies. *Nature, 462*, 51–57. http://dx.doi.org/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. http://dx.doi.org/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, IL: The University of Chicago Press.

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

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. http://dx.doi.org/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. http://dx.doi.org/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. http://dx.doi.org/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. *Behavioral Processes, 79*, 81–84. http://dx.doi.org/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, 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.

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

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 of the United States of America, 107*, 19949–19954. http://dx.doi.org/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. http://dx.doi.org/10.1016/j.anbehav.2015.07.005.

Granovetter, M. (1973). The strength of weak ties. *American Journal of Sociology, 78*, 1360–1380. http://dx.doi.org/10.1086/225469.

Harcourt, A. H. (1989). Social influences on competitive ability: Alliances and their consequences. In V. Stanen, & R. A. Foley (Eds.), *Comparative socioecology: The behavioural ecology of humans and other mammals* (pp. 223–242). Oxford, U.K.: Blackwell.

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. http://dx.doi.org/10.1016/j.cub.2007.02.040.

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. http://dx.doi.org/10.1007/s00265-009-0720-y.

Higham, J. P., Heistermann, M., Saggau, C., Agil, M., Perwitasari-Farajallah, D., & Engelhardt, A. (2012). Sexual signalling in female crested macaques and the evolution of primate fertility signals. *BMC Evolutionary Biology, 12*, 89. http://dx.doi.org/10.1186/1471-2148-12-89.

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. http://dx.doi.org/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. http://dx.doi.org/10.1371/journal.pone.0037301.

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. http://dx.doi.org/10.1016/j.anbehav.2007.08.027.

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. http://dx.doi.org/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. http://dx.doi.org/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. http://dx.doi.org/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. http://dx.doi.org/10.1093/beheco/aru099.

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 Sciences of the United States of America, 104*, 7786–7790. http://dx.doi.org/10.1073/pnas.0611449104.

Majolo, B., Ventura, R., & Schino, G. (2010). Asymmetry and dimensions of relationships quality in the Japanese macaque (*Macaca fuscata yakui*). *International Journal of Primatology, 31*, 736–750. http://dx.doi.org/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. (2015). Alpha male replacements and delayed dispersal in crested macaques (*Macaca nigra*). *American Journal of Primatology*. http://dx.doi.org/10.1002/ajp.22448.

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

McFarland, R., & Majolo, B. (2013). Coping with the cold: Predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biology Letters, 9*, 20130428. http://dx.doi.org/10.1098/rsbl.2013.0428.

Micheletta, J., Waller, B. M., Panggur, M. R., Neumann, C., Duboscq, J., Agil, M., et al. (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. http://dx.doi.org/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. http://dx.doi.org/10.1016/j.anbehav.2008.11.021.

Morin, P. A., Chambers, K. E., Boesch, C., & Vigilant, L. (2001). Quantitative polymerase chain reaction analysis of DNA from non-invasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). *Molecular Ecology, 10*, 1835–1844. http://dx.doi.org/10.1046/j.0962-1083.2001.01308.x.

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. http://dx.doi.org/10.1371/journal.pone.0069383.

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

Neumann, C., & Kulik, L. (2014). *EloRating: Animal dominance hierarchies by Elo rating*. http://CRAN.R-project.org/package=EloRating.

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. http://dx.doi.org/10.1007/BF00167053.

Nowak, M. A. (2006). Five rules for the evolution of cooperation. *Science, 314*, 1560–1563. http://dx.doi.org/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. http://dx.doi.org/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. http://dx.doi.org/10.1023/A:1026330332061.

Ostner, J., & Schülke, O. (2014). The evolution of social bonds in primate males. *Behaviour, 151*, 871–906. http://dx.doi.org/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. http://dx.doi.org/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. http://dx.doi.org/10.1111/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. http://dx.doi.org/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. http://dx.doi.org/10.1644/10-MAMM-A-416.1.

R Development Core Team. (2015). *R: A language and environment for statistical computing, version 3.2.1*. Vienna, Austria: R Foundation for Statistical Computing.

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.

Schino, G. (2007). Grooming and agonistic support: A meta-analysis of primate reciprocal altruism. *Behavioral Ecology, 18*, 115–120. http://dx.doi.org/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. http://dx.doi.org/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. http://dx.doi.org/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. http://dx.doi.org/10.1002/ajp.20546.

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology, 65*, 671–698. http://dx.doi.org/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. http://dx.doi.org/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. http://dx.doi.org/10.1098/rsbl.2014.0249.

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

Silk, J. B. (2007b). Social components of fitness in primate groups. *Science, 317*, 1347–1351. http://dx.doi.org/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. http://dx.doi.org/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 Sociobiology, 61*, 183–195. http://dx.doi.org/10.1007/s00265-006-0249-2.

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. http://dx.doi.org/10.1098/rspb.2009.0681.

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. http://dx.doi.org/10.1016/j.cub.2010.05.067.

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

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. http://dx.doi.org/10.1098/rspb.2002.2277.

Smith, J. E., van Horn, R. C., Powning, K. S., Cole, A. R., Graham, K. E., Memenis, S. K., et al. (2010). Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology, 21*, 284–303. http://dx.doi.org/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. http://dx.doi.org/10.1007/s00265-006-0305-y.

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. http://dx.doi.org/10.1007/s002650050390.

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

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

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

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

Thierry, B. (2004). Social epigenesis. In B. Thierry, M. Singh, & W. Kaumanns (Eds.), *Macaque Societies, a model for the study of social organization* (pp. 267–290). Cambridge, U.K.: Cambridge University Press.

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

Thierry, B. (2013). Identifying constraints in the evolution of primate societies. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*, 20120342. http://dx.doi.org/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. http://dx.doi.org/10.1016/j.anbehav.2007.07.006.

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. http://dx.doi.org/10.2354/psj.16.203.

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. http://dx.doi.org/10.1007/s10764-013-9733-5.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology, 46*, 35–57. http://www.jstor.org/stable/2822435.

Trivers, R. L. (2006). Reciprocal altruism: 30 years later. In P. M. Kappeler, & C. P. van Schaik (Eds.), *Cooperation in primates and humans* (pp. 67–83). New York, NY: Springer.

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. http://dx.doi.org/10.1007/s10865-006-9056-5.

de Vries, H., Netto, W. J., & Hanegraaf, P. L. H. (1993). Matman: A program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour, 125*, 157–175. http://dx.doi.org/10.1163/156853993X00218.

Wahaj, S. A., van Horn, R. C., van Horn, T. L., Dreyer, R., Hilgris, R., Schwarz, J., et al. (2004). Kin discrimination in the spotted hyena (*Crocuta crocuta*): Nepotism among siblings. *Behavioral Ecology and Sociobiology, 56*, 237–247. http://dx.doi.org/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. http://dx.doi.org/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*. http://dx.doi.org/10.1371/journal.pone.0059789. e59789– e59789.

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. http://dx.doi.org/10.1016/j.anbehav.2013.03.035.

Whitehead, H. (2008). *Analysing animal societies: quantitative methods for vertebrates social analysis*. Chicago, IL: 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. http://dx.doi.org/10.1002/evan.21366.

Wrangham, R. W., & Rubenstein, D. I. (1986). Social evolution in birds and mammals. In D. I. Rubenstein, & R. W. Wrangham (Eds.), *Ecological aspects of social evolution—Birds and mammals* (pp. 452–470). Princeton, NJ: Princeton University Press.

Young, M. E. (2016). The problem with categorical thinking by psychologists. *Behavioural Processes, 123*, 43–53. http://dx.doi.org/10.1016/j.beproc.2015.09.009.

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 Sciences of the United States of America, 111*, 195–200. http://dx.doi.org/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. http://dx.doi.org/10.1016/j.anbehav.2014.06.007.

Zhang, Y.-W., Morin, P. A., Ryder, O. A., & Zhang, Y.-P. (2001). A set of human tri-and tetra-nucleotide microsatellite loci useful for population analyses in gorillas (*Gorilla gorilla gorilla*) and orangutans (*Pongo pygmaeus*). *Conservation Genetics, 2*, 391–395. http://dx.doi.org/10.1023/A:1012594626095.

Zinner, D., Fickenscher, G., Roos, C., Anandam, M. V., Bennett, E. L., Davenport, T. R. B., et al. (2013). Family Cercopithecidae (old world monkeys). In R. A. Mittermeier, A. B. Rylands, & D. E. Wilson (Eds.), *Handbook of the mammals of the world Vol 3 Primates*. Barcelona, Spain: Lynx Edicion.

APPENDIX

Complete DNA analysis protocol

We first measured DNA purity by absorbance of a subset of our samples to verify that extraction had been successful and that samples were of good enough quality (Morin, Chambers, Boesch, & Vigilant, 2001). We amplified 12 short-tandem repeats (or microsatellites), 10 tetranucleotide loci and two dinucleotide loci, proven to be informative in humans and other primates (* or + indicates primers that have been modified specifically for *Macaca fascicularis* or *M. nigra*, respectively: D1s548, D3s1768*, D5s1457, D6s493^{+}, D6s501^{+}, D7s2204, D10s1432, D11s925, D12s67^{+}, D13s765*, D14s255^{+}, D18s536; e.g. Bayes, Smith, Alberts, Altmann, & Bruford, 2000; Zhang, Morin, Ryder, & Zhang, 2001). We used a two-step multiplex chain polymerase reaction (PCR) approach (Arandjelovic et al., 2009). In a first step, all loci were amplified in a single reaction with 4 μl of DNA extract (diluted 1:25–1:50) for each 20 μl of reaction product, 2 μl H_2O, 2 μl QIAGEN enzyme buffer (25 mM Tris–HCl pH 8.0, 35 mM KCl, 0.1 mM EDTA, 1 mM DTT, 50% glycerol, 0.5% Tween 20, 0.5% Igepal CA-630 and stabilizers), 1 μl dNTPs 0.5 mM, 0.8 μl bovine serum albumin (BSA) 20 mg/ml, 0.4 μl MgCl 25 mM, 0.4 μl of each primer unlabelled forward and reverse, 0.2 μl QIAGEN Hot Master Taq 5 U/μl) in an Eppendorf Master Gradient machine.

We started with 2 min of denaturation at 94 °C, then ran 30 cycles of 20 s of denaturation at 94 °C, 30 s of annealing at 54 °C, 30 s of elongation at 70 °C and ended with 10 min of final elongation at 70 °C. We followed multiplex PCR by singleplex PCRs, following the same protocol but with each primer separated and different annealing temperatures specific to each primer. We included 1 μl of multiplex PCR product and 19 μl of reaction product (14 μl H_2O, 2 μl QIAGEN enzyme buffer (25 mM Tris–HCl pH 8.0, 35 mM KCl, 0.1 mM EDTA, 1 mM DTT, 50% glycerol, 0.5% Tween 20, 0.5% Igepal CA-630 and stabilizers), 1 μl dNTPs 0.5 mM, 0.8 μl BSA 20 mg/ml, 0.5 μl of specific fluorescently labelled (HEX or FAM) primer forward and reverse, 0.2 μl QIAGEN Hot Master Taq 5 U/μl). For primers D3s1768, D6s501 and D12s67, we also added 0.4 μl MgCl 25 mM for better results, and consequently lowered the quantity of H_20 by the same amount. Singleplex PCR products were then prepared for sequencing by diluting PCR products between 1:25 and 1:100, and mixing 1.5 μl of diluted product into 14 μl of HiDye Formamide buffer mixed with a size standard (HD400 from Applied Biosystems, Foster City, CA, U.S.A.).

Model randomizations

In the following, we present results of a randomization procedure to assess the effects of assigning individuals to ID1 and ID2 in our mixed models. Specifically, for each model we assigned the two individuals of each dyad randomly to ID1 and ID2. This was done independently for each dyad. With this randomized data set, we refitted our models, extracted parameters and repeated this step 500 times for each of the six models.

For each of the six models, we calculated the following summary statistics across the 500 randomizations: (1) mean parameter estimates; (2) 90% and 10% percentiles of the parameter estimates; (3) mean standard errors of the parameter estimates; and (4) mean 95% confidence intervals.

Overall, the results from this procedure suggest that the assignment of individuals within dyads had no consequences as far as our conclusions are concerned and that our models were stable with regard to variation in our random effects structure.

Bond strength as function of Elo difference, DML and age difference

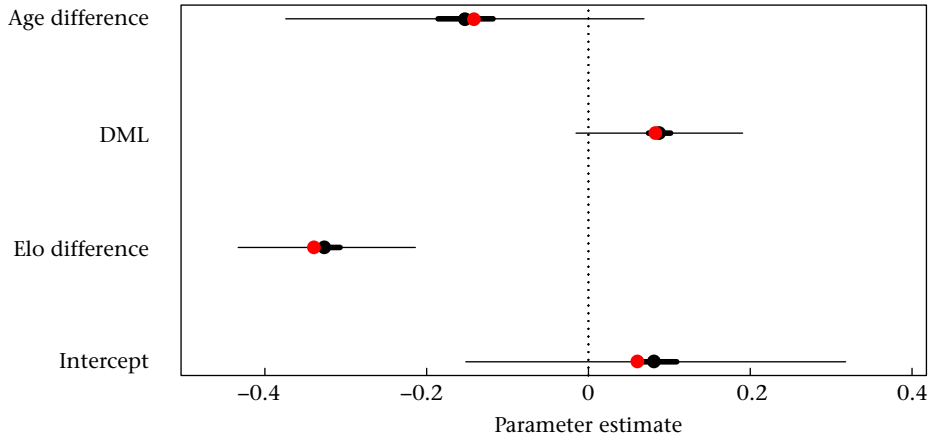

Figure A1. Graphical summary plot of bond strength model randomizations. Red circle: parameter estimate from original model; black circle: mean parameter estimate across randomized models; thick black line: 90% and 10% percentiles of parameter estimate across randomized models; thin black line: range between mean lower and upper bound of the 95% confidence interval.

Table A1
Summary of 500 randomizations of the bond strength model

	Mean β	β (10% and 90% percentile)	Mean SE	Mean CI_l	Mean CI_u
Intercept	0.08	0.06 to 0.11	0.12	−0.15	0.32
Elo difference	−0.32	−0.34 to −0.31	0.06	−0.43	−0.21
DML	0.09	0.07 to 0.10	0.05	−0.02	0.19
Age difference	−0.15	−0.19 to −0.12	0.11	−0.37	0.07

β is the estimated parameter, SE is the standard error, and CI_l and CI_u are the lower and upper bounds of the confidence intervals, respectively.

Bond predictability as function of Elo difference, DML and age difference

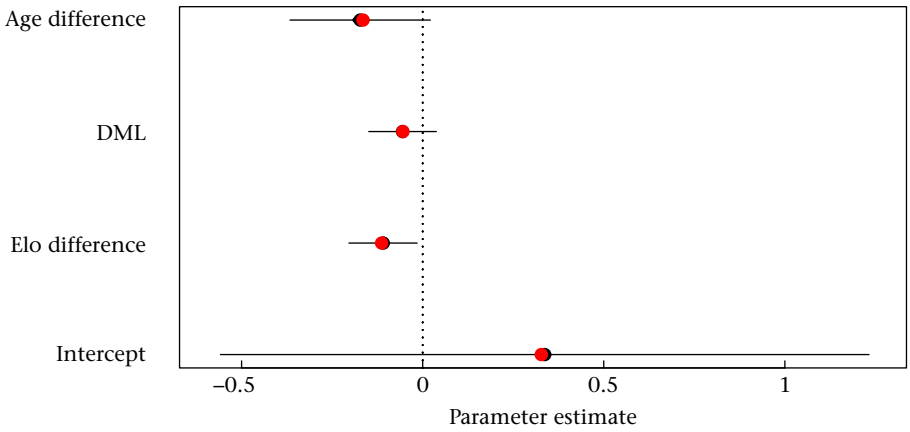

Figure A2. Graphical summary plot of bond predictability model randomizations. Red circle: parameter estimate from original model; black circle: mean parameter estimate across randomized models; thick black line: 90% and 10% percentiles of parameter estimate across randomized models; thin black line: range between mean lower and upper bound of the 95% confidence interval.

Table A2
Summary of 500 randomizations of the bond predictability model

	Mean β	β (10% and 90% percentile)	Mean SE	Mean CI_l	Mean CI_u
Intercept	0.34	0.32 to 0.35	0.46	−0.56	1.23
Elo difference	−0.11	−0.12 to −0.10	0.05	−0.20	−0.02
DML	−0.06	−0.06 to −0.05	0.05	−0.15	0.04
Age difference	−0.17	−0.19 to −0.15	0.10	−0.37	0.02

β is the estimated parameter, SE is the standard error, and CI_l and CI_u are the lower and upper bounds of the confidence intervals, respectively.

Bond equitability as function of Elo difference, DML and age difference

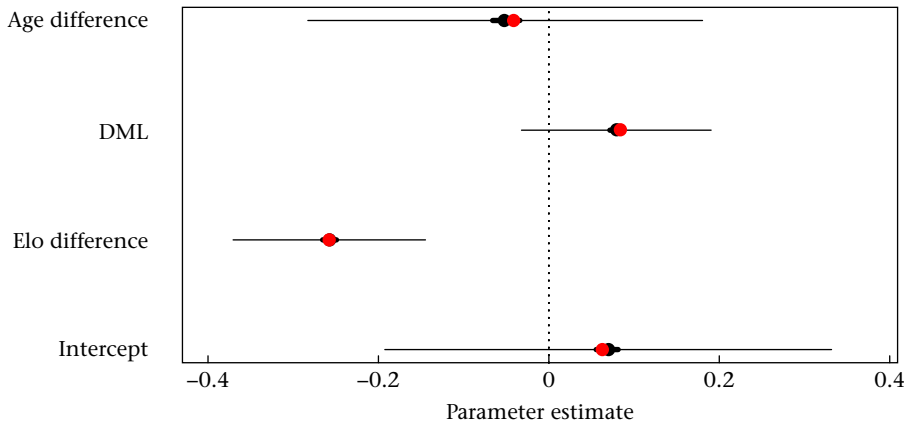

Figure A3. Graphical summary plot of bond equitability model randomizations. Red circle: parameter estimate from original model; black circle: mean parameter estimate across randomized models; thick black line: 90% and 10% percentiles of parameter estimate across randomized models; thin black line: range between mean lower and upper bound of the 95% confidence interval.

Table A3
Summary of 500 randomizations of the bond equitability model

	Mean β	β (10% and 90% percentile)	Mean SE	Mean CI_l	Mean CI_u
Intercept	0.07	0.06 to 0.08	0.13	−0.19	0.33
Elo difference	−0.26	−0.27 to −0.25	0.06	−0.37	−0.14
DML	0.08	0.07 to 0.09	0.06	−0.03	0.19
Age difference	−0.05	−0.07 to −0.03	0.12	−0.28	0.18

β is the estimated parameter, SE is the standard error, and CI_l and CI_u are the lower and upper bounds of the confidence intervals, respectively.

Coalitionary support as function of CSI, CV and EI

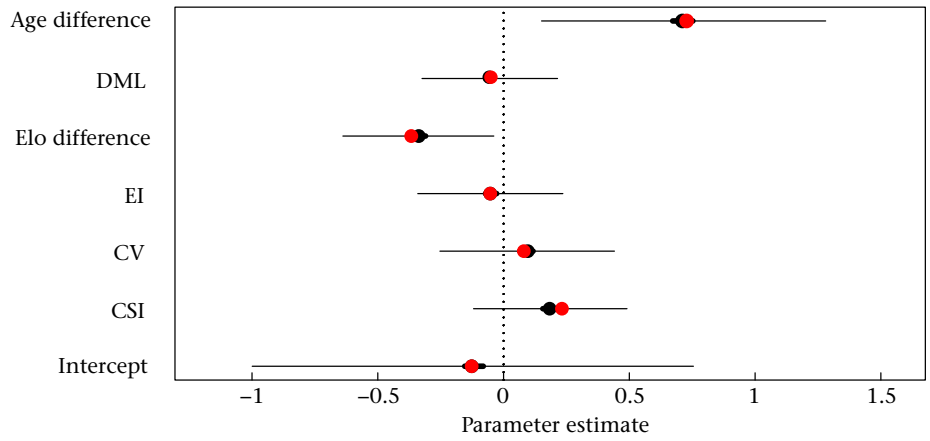

Figure A4. Graphical summary plot of coalitionary support model randomizations. Red circle: parameter estimate from original model; black circle: mean parameter estimate across randomized models; thick black line: 90% and 10% percentiles of parameter estimate across randomized models; thin black line: range between mean lower and upper bound of the 95% confidence interval.

Table A4
Summary of 500 randomizations of the coalitionary support model

	Mean β	β (10% and 90% percentile)	Mean SE	Mean CI_l	Mean CI_u
Intercept	−0.12	−0.15 to −0.08	0.45	−1.00	0.75
CSI	0.19	0.16 to 0.22	0.16	−0.12	0.49
CV	0.09	0.06 to 0.12	0.18	−0.25	0.44
EI	−0.05	−0.07 to −0.03	0.15	−0.34	0.24
Elo difference	−0.34	−0.37 to −0.31	0.15	−0.64	−0.04
DML	−0.05	−0.07 to −0.04	0.14	−0.32	0.21
Age difference	0.72	0.67 to 0.75	0.29	0.15	1.28

β is the estimated parameter, SE is the standard error, and CI_l and CI_u are the lower and upper bounds of the confidence intervals, respectively.

Feeding-in-proximity as function of CSI, CV and EI

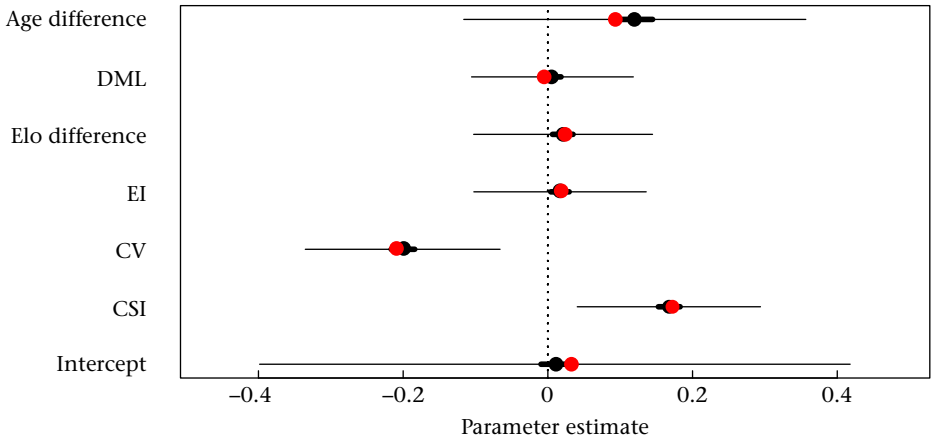

Figure A5. Graphical summary plot of feeding-in-proximity model randomizations. Red circle: parameter estimate from original model; black circle: mean parameter estimate across randomized models; thick black line: 90% and 10% percentiles of parameter estimate across randomized models; thin black line: range between mean lower and upper bound of the 95% confidence interval.

Table A5
Summary of 500 randomizations of the feeding-in-proximity model

	Mean β	β (10% and 90% percentile)	Mean SE	Mean CI_l	Mean CI_u
Intercept	0.01	−0.01 to −0.03	0.21	−0.40	0.42
CSI	0.17	0.15 to 0.18	0.06	0.04	0.29
CV	−0.20	−0.22 to −0.18	0.07	−0.34	−0.07
EI	0.02	0.00 to 0.03	0.06	−0.10	0.14
Elo difference	0.02	0.01 to 0.03	0.06	−0.10	0.14
DML	0.01	−0.01 to −0.02	0.06	−0.11	0.12
Age difference	0.12	0.09 to 0.14	0.12	−0.12	0.36

β is the estimated parameter, SE is the standard error, and CI_l and CI_u are the lower and upper bounds of the confidence intervals, respectively.

Aggression as function of CSI, CV and EI

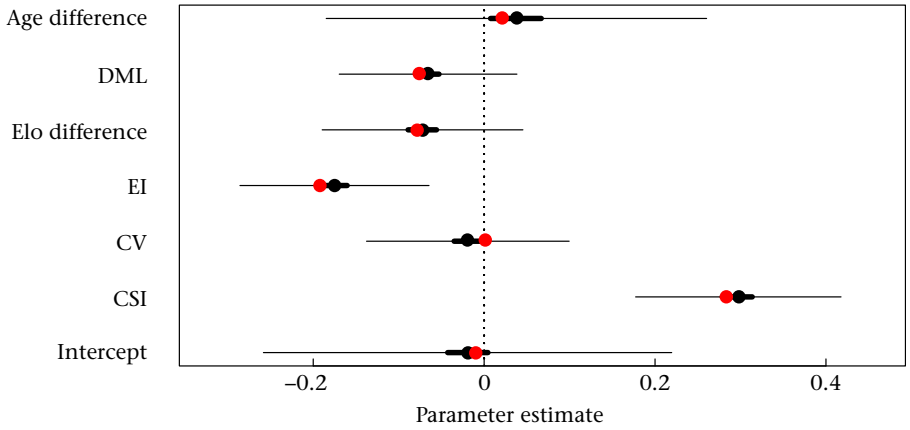

Figure A6. Graphical summary plot of aggression model randomizations. Red circle: parameter estimate from original model; black circle: mean parameter estimate across randomized models; thick black line: 90% and 10% percentiles of parameter estimate across randomized models; thin black line: range between mean lower and upper bound of the 95% confidence interval.

Table A6
Summary of 500 randomizations of the aggression model

	Mean β	β (10% and 90% percentile)	Mean SE	Mean CI_l	Mean CI_u
Intercept	−0.02	−0.04 to −0.00	0.12	−0.26	0.22
CSI	0.30	0.28 to 0.31	0.06	0.18	0.42
CV	−0.02	−0.04 to −0.00	0.06	−0.14	0.10
EI	−0.18	−0.19 to −0.16	0.06	−0.29	−0.06
Elo difference	−0.07	−0.09 to −0.06	0.06	−0.19	0.05
DML	−0.07	−0.08 to −0.05	0.05	−0.17	0.04
Age difference	0.04	0.01 to 0.07	0.11	−0.18	0.26

β is the estimated parameter, SE is the standard error, and CI_l and CI_u are the lower and upper bounds of the confidence intervals, respectively.

Introducing-error simulations

Table A7
Results of the introducing-error-simulations

Models	Original result (LRT)	No. of times LRT gives same result as original ($P>0.05$)	Minimum *P*	Maximum *P*	Median *P*
CSI	$\chi^2_1=2.46$, $P=0.116$	965	0.023	0.484	0.132
CV	$\chi^2_1=1.33$, $P=0.249$	1000	0.065	0.693	0.261
EI	$\chi^2_1=2.13$, $P=0.144$	986	0.018	0.483	0.153
Sup	$\chi^2_1=0.10$, $P=0.747$	1000	0.272	0.998	0.749
Feed	$\chi^2_1=0.00$, $P=0.954$	1000	0.385	1.000	0.865
Ag	$\chi^2_1=2.01$, $P=0.156$	993	0.020	0.518	0.169

Each model was run 1000 times. LRT = likelihood ratio test. CSI = bond strength model, CV = bond predictability model, EI = bond equitability model, Sup = coalitionary support model, Feed = feeding in proximity model, Ag = aggression model (see main text and Tables 1 and 2 in the main text).