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3 **Title:**

4 Personality homophily affects male social bonding in wild Assamese macaques (*Macaca*
5 *assamensis*)

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22

23 **ABSTRACT**

24 Animal social bonds are defined as stable, equitable and strong affiliative and cooperative
25 relationships similar to human friendships. Just as human friendships, social bonds are
26 thought to function as alliances that generate adaptive benefits via support in critical
27 situations. In humans, similarity in many sociodemographic, behavioural and intrapersonal
28 characteristics leads to trust and is predictive of friendships. Specifically, personality
29 homophily, that is the tendency of individuals to form social bonds with others who have a
30 similar personality, may increase predictability and facilitate trust and reciprocity among
31 partners with compatible behavioural tendencies. While evidence for social bonding in
32 nonhumans is accumulating, far less is known about its predictors. Here, personality
33 homophily effects on the formation and maintenance of social bonds are shown in twenty-four
34 wild male Assamese macaques (*Macaca assamensis*), at Phu Khieo Wildlife Sanctuary,
35 Thailand. Dyadic bond strength increased with increased similarity in the trait Connectedness
36 (i.e. frequent and diverse neighbours in 5m proximity and pronounced social tolerance, as
37 high rates of friendly approaches to and by others). To differentiate whether homophily
38 indeed predicted bond formation or whether bonded males' personalities became more similar
39 over time, we tested the stability of the connectedness traits in a subset of immigrating males
40 that had to form new bonds. Connectedness in these males remained stable suggesting that
41 males do not adapt their personality to their partner. Our results support the idea of a shared
42 evolutionary origin of homophily as a partner choice strategy in human and non-human
43 animals. The main selective advantage of personality similarity in animal social bonds may
44 result from a more reliable cooperation among individuals with similar cooperative
45 behavioural tendencies.

46 **Keywords:** personality, homophily, animal social bond, Assamese macaques, human
47 friendship, partner choice

48 INTRODUCTION

49 In mammals and birds, social bonds are defined as stable, equitable and strong affiliative
50 relationships similar to human friendships, and like friendships are thought to function as
51 alliances that generate adaptive benefits via support in critical situations (Brown & Brown,
52 2006; Cheney, 2011; Curry & Dunbar, 2013; DeScioli & Kurzban, 2009; Ostner & Schülke,
53 2014, 2018; Schino, 2007; Silk, 2007). Bond strength promotes coalition formation (e.g.,
54 Berghänel, Ostner, Schröder, & Schülke, 2011; Connor, Heithaus, & Barre, 2001; Gilby et al.,
55 2013; Perry, Barrett, & Manson, 2004; Watts, 2002; Young, Majolo, Schülke, & Ostner,
56 2014) and enhances cooperative success, possibly through increased trust in a bonded ally
57 (across a wide range of taxa in birds and mammals: Braun & Bugnyar, 2012; Engelmann &
58 Herrmann, 2016; Majolo et al., 2006; Marshall-Pescini, Schwarz, Kostelnik, Virányi, &
59 Range, 2017; Massen, Ritter, & Bugnyar, 2015; Molesti & Majolo, 2016; Olson & Spelke,
60 2008; Wood, Kim, & Li, 2016). In risky situations, when an individual has to choose with
61 whom to cooperate, social bonds spare situational judgement and cognitive effort of assessing
62 partner quality and honesty of signals, since they reduce uncertainty about the partner's
63 response (Cronin, 2012; Molesti & Majolo, 2016; Noë, 2006; Schino & Aureli, 2009).
64 According to standard evolutionary models, partner choice mechanisms are key to initiate and
65 maintain cooperative behaviours, and can lead to the formation of differentiated social
66 relationships from weak ties to social bonds in animal groups (Campennì & Schino, 2014;
67 Noë, 2006; Schino & Aureli, 2016).

68 Partner choice for the formation of social bonds may be guided by homophily, that is the
69 tendency of individuals to form ties with similar others (McPherson, Smith-Lovin, & Cook,
70 2001), as it may enhance predictability and trust in potential bond partner (Dunbar, 2018;
71 Massen & Koski, 2014; Weinstein & Capitanio, 2012). Animal and human social structure in
72 terms of spatial or socio-ecological associations partly results from assortment by age, sex,

73 kinship, body size, reproductive state, or genotype (e.g., Fowler, Settle, & Christakis, 2011;
74 Fu, Nowak, Christakis, & Fowler, 2012; McPherson et al., 2001).

75 Fitness-related advantages of choosing self-similar bond partners may arise from a shared
76 mode of communication and more efficient coordination and cooperation (Fu et al., 2012;
77 Noë, 2006). In theoretical models, homophily enhances the evolution of cooperation and
78 facilitates the spread of cooperation in human and nonhuman animal networks (Antal,
79 Ohtsuki, Wakeley, Taylor, & Nowak, 2009; Chiang & Takahashi, 2011; Nowak, Tarnita &
80 Antal, 2010; Riolo, Cohen, & Axelrod, 2001; Rivera, Soderstrom, & Uzzi, 2010; Voelkl &
81 Kasper, 2009).

82 In humans, similarity in many sociodemographic, behavioural and intrapersonal
83 characteristics, as well as sharing values, leads to trust and predicts friendships more than
84 dissimilar characteristics (Bahns, Crandall, Gillath, & Preacher, 2016; Curry & Dunbar, 2013;
85 Kandel, 1978; McPherson et al., 2001; Selfhout, Branje, & Meeus, 2007; Ziegler & Golbeck,
86 2007). Trust also plays a crucial role in forming and maintaining relationships in nonhuman
87 animals, particularly in non-kin (Dunbar, 2018; Engelmann & Herrmann, 2016; Massen &
88 Koski, 2014; Massen et al., 2015). Chimpanzees selectively trust bonded partners (Engelmann
89 & Herrmann, 2016), suggesting that trust in reciprocity is not unique to humans, but has
90 deeper evolutionary roots (Engelmann, Herrmann, & Tomasello, 2015). In male Barbary
91 macaques the probability that a bystander of an aggressive conflict rejects a recruitment for
92 help decreased with the strength of the affiliative relationship between the bystander and the
93 recruiter (Young et al., 2014), i.e. the individual in need can trust that bonded partners will
94 provide support.

95 Trust and reciprocity may be facilitated specifically via homophily in personality (Hampson,
96 2011; Massen, 2017; Massen & Koski, 2014; Scarr & McCartney, 1983). Personality is
97 defined as inter-individual differences in behaviour, affect and cognition that are relatively

98 consistent across time and (Réale, Reader, Sol, McDougall, & Dingemanse, 2007).

99 Personality homophily has been found in human spouses (e.g., Byrne, 1997; Klohnen & Luo,
100 2003; Youyou, Stillwell, Schwartz, & Kosinski, 2017) and improves reproductive success in
101 monogamous rodents, birds, and fish (Ariyomo & Watt, 2013; Dingemanse, Both, Drent, &
102 Tinbergen, 2004; Gabriel & Black, 2012; Rangassamy, Dalmas, Féron, Gouat, & Rödel,
103 2015; Schuett, Dall, & Royle, 2011). Similarity in certain personality traits is associated with
104 the strength of social bonds in chimpanzees (Massen & Koski, 2014), higher-quality
105 relationships in capuchin monkeys (Morton, Weiss, Buchanan-Smith, & Lee, 2015),
106 relationship stability from one year to the next in juvenile rhesus macaques (Weinstein &
107 Capitanio, 2012) and pairing-success of adult rhesus macaques in a laboratory setting
108 (Capitanio, Blozis, Snarr, Steward, & McCowan, 2015). Beyond dyadic relationships, group-
109 level similarity in personality traits facilitates cooperation among all group members in
110 cooperative-breeding common marmosets (Koski & Burkart, 2015).

111 Friends with similar personalities may perceive, interpret, and react to the world around them
112 in a similar way (neuronal homophily; Parkinson, Kleinbaum, & Wheatley, 2018). Friends
113 share dispositions and agree on values, opinions and activities, which may trigger a positive
114 affective response that increases enjoyment of each other's company, and strengthens the self-
115 concept (Baumeister & Leary, 1995; Campbell, Sedikides, Reeder, & Elliot, 2000; Clore &
116 Byrne, 1974; Hampson, 2011; Nelson, Thorne, & Shapiro, 2011; Nelson et al., 2011; Selfhout
117 et al., 2010). Personality similarity among friends may further reduce uncertainty during
118 acquaintanceship and enhances predictability by increasing the ease and clarity of
119 communication (Berger & Calabrese, 1975; Neyer, Banse, & Asendorpf, 1999; Selfhout et al.,
120 2010; van Zalk & Denissen, 2015). With respect to the "Big Five" personality model
121 (Digman, 1990; John, Srivastava, & Pervin, 1999), friends are mostly found to be similar in
122 two dimensions (e.g., Blaz, 1983; Caspi, Roberts, & Shiner, 2005; Feiler & Kleinbaum, 2015;

123 Jensen-Campbell et al., 2002: extraversion, a dimension capturing variation in activity,
124 sociability, positive emotionality, risk seeking and assertiveness, and agreeableness which
125 describes variation in being kind and considerate, empathic, prosocial and cooperative (van
126 Aken & Asendorpf, 2018). Given the potentially shared evolutionary history of social bonds
127 and human friendships (Baumeister & Leary, 1995; Seyfarth & Cheney, 2012; Silk, 2002),
128 and the fact that shared neural and physiological mechanisms underlie social behaviours in
129 humans and other animals (Brent, Chang, Gariépy, & Platt, 2014; Chang et al., 2013; Dunbar,
130 2010; Meunier, 2018), it has been proposed that homophily in human social partner choice
131 has a biological basis (Apicella, Marlowe, Fowler, & Christakis, 2012; Bahns et al., 2016; Fu
132 et al., 2012; Massen & Koski, 2014; Parkinson et al., 2018).

133 Here we investigated whether patterns of affiliation correspond to homophily in personality
134 traits in wild male Assamese macaques. Apart from an unpublished PhD thesis (Tkaczynski,
135 2017) these studies all used captive animals and assessed personality either with behavioural
136 or with trait rating (i.e. questionnaire) data. We add ecological validity by studying wild
137 animals. Male Assamese macaques are particularly well-suited for this study, because males
138 change groups several times during their life (Ostner, Vigilant, Bhagavatula, Franz, &
139 Schülke, 2013), and because males in the study population form differentiated social bonds
140 that convey fitness benefits via increased paternity success (Kalbitz, Ostner, & Schülke, 2016;
141 Schülke, Bhagavatula, Vigilant, & Ostner, 2010).

142 Instead of predicting homophily for a particular personality dimension, we followed an
143 explorative approach and expected to find homophily in any of the five personality traits we
144 defined for these males, namely Connectedness, Aggressiveness, Sociability, Vigilance, and
145 Confidence (Ebenau, Penke, Ostner, & Schülke, under review). In humans the social
146 personality traits extraversion and agreeableness are similar among friends, but other traits
147 may affect social partner choice as well: bonded partners are more similar in boldness in

148 chimpanzees (Massen & Koski, 2014) and traits like aggressiveness may be more relevant in
149 some species as it is shaping the social style in macaques (Adams et al., 2015). As closely
150 bonded individuals pull each other to similar ranks via support in agonistic interactions with
151 the benefits of increased access to food and mates (Chapais, 1995; Schülke et al., 2010), we
152 expected and therefore controlled for an effect of dominance rank difference on dyadic social
153 bond measures. We expect that similarity in personality predicts bond formation. To rule out
154 that this correlation results from bonded partners adapting their personalities over time, we
155 assess personality stability in males changing social groups during the study period, which is
156 accompanied by changing affiliation partners.

157

158 **METHODS**

159 Fieldwork was conducted in the Phu Khieo Wildlife Sanctuary (PKWS: 16°5'–35'N,
160 101°20'–55'E) which is part of the ca. 6500 km² interconnected and well-protected Western
161 Isaan forest complex in north-eastern Thailand (Borries, Larney, Kreetiyutanont, & Koenig,
162 2002). The study area is covered by hill evergreen forest and harbours a diverse community of
163 large mammals and predators (Borries et al., 2002) indicative of very low levels of human
164 disturbance. The field site was established in 2005, study subjects lived in four fully
165 habituated groups, and were followed from April 2014 (ASM and AOM group) or October
166 2014 (ASS and AOS group) through March 2016. Group sizes at the beginning of behavioural
167 data collection are shown in Table A1.

168

169 *Personality assessment*

170 We applied a multi-method approach based on analyses of trait ratings (TR) and behavioural
171 codings (BC), which allowed for testing construct validity of the quantified personality

172 structures (for details see Ebenau et al., under review). In brief, individuals were rated twice
173 in 2015 and 2016 on the 54 item Hominoid Personality Questionnaire (HPQ; King &
174 Figueredo, 1997; Weiss et al., 2009). Each adjective item was defined within the context of
175 general behaviours common to primates. For example, 'fearful' was defined as “Subject reacts
176 excessively to real or imagined threats by displaying behaviours such as screaming,
177 grimacing, running away or other signs of anxiety or distress.” Data were processed by
178 analysing rater performance, applying interrater-reliability (ICC; Shrout & Fleiss, 1979) with
179 a cut-off criterion of > 0.4 , and examining temporal stability from one year to the next. After
180 data reduction, 43 adjective items were submitted to factor analysis, revealing four
181 dimensions: Aggressiveness_{TR}, Confidence_{TR}, Activity_{TR} and Friendliness_{TR}. To validate the
182 rating data, behavioural codings were analysed for 24 adult males. Behavioural data were
183 collected from April 2014 to March 2016 concurrently for behavioural personality assessment
184 as well as for relationship measures, and is described in detail below. Eighteen temporally
185 stable variables were reduced to four factors: Connectedness_{BC}, Aggressiveness_{BC},
186 Sociability_{BC} and Vigilance_{BC}. Construct validity assessments suggested congruence between
187 most dimensions from trait ratings and behavioural codings, with the exception of the
188 Confidence_{TR} trait rating domain, which therefore was added as a fifth dimension to the
189 behavioural coding personality constructs (for details see Ebenau et al., under review).

190

191 **Table 1**

192 Summary of integrative personality constructs of Assamese macaques, derived from
193 behavioural codings_{SBC} and trait ratings_{STR}.

Personality traits	Description
Connectedness _{SBC}	Frequent and diverse neighbours in 5m proximity and pronounced social tolerance, expressed as high rates of friendly approaches to and by others
Aggressiveness _{SBC}	Quits body contact and grooming more than others, high rates of physical and mild aggression towards others
Sociability _{BC}	High rates of friendly behaviour and more time in body contact and grooming, as well as more frequent initiation of affiliations; more often outside the group centre
Vigilance _{BC}	High proportion of vigilant behaviour in activity budget
Confidence _{TR}	High scores of dominant, vigorous, bold and decisive attributes and leader qualities

194

195 *Behavioural data collection*

196 We collected 4628 hours of focal animal observations (Altmann, 1974) from 24 adult males
197 (mean per subject = 193 h; range = 86 h – 284 h) of the four study groups. These focal
198 animals were included in the study, since they were present more than three months within
199 one year of the two-year study period. Individuals were followed for 40 minutes with
200 continuous recording of all approaches and departures within 1.5 m of the focal animal, and
201 all affiliative and agonistic social interactions, with onset and termination for duration
202 behaviours (e.g., approaches, body contact and grooming), as well as with directionality and
203 the identities of interaction partners. Activity of the focal animal was recorded instantaneously
204 at 2-minutes intervals. Every 10 min we recorded the identities of all individuals within a 5 m
205 sphere around the focal animal. An effort was made to equally distribute observation time
206 across individuals and time of the day. Quantitative behavioural data collected with a
207 standardized ethogram were used to assess relationship strength.

208

209 *Dyadic relationship measure*

210 For relationship assessment, we used data of two half-year periods with rather stable male
211 group composition (October 2014–March 2015, October 2015–March 2016). Still, some adult
212 males were absent for some time within these periods. We set two criteria and only included
213 individuals, if they were either present in the group for at least half the time we spent with the
214 group within the half-year period, or their observation hours did not fall below half the group
215 mean within the half-year period. The remaining periods were too unstable to infer reliable
216 relationship measures due to migration events as well as alpha male rank changes. Two of
217 three adult males migrated from ASS into ASM group within the second year of observation,
218 leaving only one adult male, thus, just one half-year period (October 2014–March 2015) was
219 included for ASS group.

220 We used the dyadic sociality index (DSI; Silk, Cheney, & Seyfarth, 2013) to measure the
221 strength of dyadic relationships, with frequencies and durations of correlated affiliative
222 behaviours (mean $\tau_{(rw,ave)} = 0.491 \pm 0.103$), grooming, body contact and close proximity < 1.5
223 m. Since grooming frequencies between adult males tend to be quite low and to prevent
224 inflation effects, we excluded grooming from the calculation when the average frequency
225 across all dyads in a group was below 1.5. This was done for the second half-year period
226 (October 2015–March 2016) for ASM and AOS group. For body contact and close proximity,
227 we only included interactions longer than 10 seconds. Dyadic interaction rates and durations
228 of overlaid behavioural states were subtracted from one another, and calculations were
229 controlled for observation times of each partner. We calculated the index as follows:

230

231
$$DSI = \left(\frac{FP_{ij} + DP_{ij} + FB_{ij} + DB_{ij} + FG_{ij} + DG_{ij}}{FP_{ave} + DP_{ave} + FB_{ave} + DB_{ave} + FG_{ave} + DG_{ave}} \right)$$

232

233 Here ij is the male-male dyad, ave is the group mean across all male-male dyads, \mathbf{F} is the
234 frequency and \mathbf{D} the total duration of the behaviours: \mathbf{P} as close proximity < 1.5 m, \mathbf{B} as body
235 contact and \mathbf{G} as grooming. For a detailed description of dyadic CSI (i.e. DSI) calculation and
236 its application in male Assamese macaques see Kalbitz et al. (2016). The index is a linear
237 measure with a minimum of zero and a group mean of one, and increases with the strength of
238 the affiliative relationship between two partners. Weak relationships are defined by values
239 between zero and one, and values greater than 1 reflect stronger affiliative relationships (Silk,
240 Alberts, & Altmann, 2006).

241

242 *Dominance rank*

243 Male Assamese macaques can be ordered along a linear dominance hierarchy (Ostner,
244 Heistermann, & Schülke, 2008), where higher-ranked individuals dominate all individuals of
245 lower rank, thus all dyads have a dominant-subordinate relation. We calculated a dominance
246 hierarchy from decided dyadic agonistic interactions as well as unprovoked submissive
247 signals, e.g., silent-bared teeth (Ostner et al., 2008). Data on conflicts were recorded during
248 continuous and ad libitum sampling for the same half-year period as the dyadic relationship
249 measures. On average, we included in our analysis of dominance rank 13.7 and 16.3
250 interactions per individual in the two study periods respectively, which exceeds the value of
251 10 proposed for steep hierarchies (Sánchez-Tójar, Schroeder, & Farine, 2018). A winner/loser
252 matrix of these interactions was used to calculate the standardized normalized David's score
253 (nDS) using DomiCalc (“compete” R-package; Schmid & de Vries, 2013). Due to group
254 composition and alpha male rank changes we calculated an average rank for each period as a
255 sum of hierarchical rank multiplied by the number of months the rank position was occupied
256 divided by 6.

257

258 *Statistical analyses*

259 We ran a linear mixed model (Baayen, 2008) to evaluate the effect of absolute differences in
260 factor scores in each of the five personality dimensions (the more similar each social bond
261 pair, the smaller the difference values), on the response variable social bonds, i.e. DSI scores.
262 Due to the expected effect of absolute dominance rank differences on DSI, we included it as
263 fixed effect. Since group composition changed between years, the same groups in the two
264 consecutive years were handled separately, so we included a combined variable ‘group.year’
265 as fixed effect with 7 levels. As random effects we included ‘identity of dyad’ and
266 ‘dominance rank difference’, calculated per half year period, controlling for the fact that they
267 are dependent measures. Finally, random slopes were modelled for a dyads and dominance
268 rank difference variation in DSI along ‘group.year’. We did not predict interaction effects in
269 the model. The DSI scores were log transformed and all variables, except for ‘group.year’,
270 were z-transformed (to a mean of zero and a standard deviation of one). The model was fitted
271 in R (R Core Team 2017) using the function ‘lmer’ of the R-package ‘lme4’ (version 1.1-15;
272 Bates et al., 2014).

273 Our visual inspection of a qq-plot, and the residuals plotted against fitted values, did not
274 reveal obvious deviations from the model assumptions of normally distributed and
275 homogeneous residuals.

276 The function ‘vif’ of the R-package ‘car’ (Fox & Weisberg, 2011; applied to a standard linear
277 model excluding the random effects) indicated collinearity to be no issue (largest VIF=1.13;
278 (Fidell & Tabachnick, 2003; Field, 2000; Quinn & Keough, 2002; Zuur, Ieno, & Elphick,
279 2010). We tested the full against the null model, comprising only ‘group.year’ as fixed effect
280 and the random effects as described above. We fitted both models using Maximum
281 Likelihood (rather than Restricted Maximum Likelihood; Bolker et al., 2009) and conducted a
282 likelihood ratio test (R-function ‘anova’ with argument test set to "Chisq"; Dobson, 2010;

283 Forstmeier & Schielzeth, 2011). To extract p-values for the individual effects, we used the R-
284 function ‘drop1’ (with argument test set to "Chisq"; Barr, Levy, Scheepers, & Tily, 2013),
285 based on likelihood ratio tests comparing the full to respective reduced models. Confidence
286 intervals (lower: 2.5%, upper: 97.5%) for the estimates were computed with the function
287 ‘confint.merMod’ of the R-package ‘lme4’ (version 1.1-15; Bates et al., 2014). The sample
288 size for this model was a total of 140 observations made on 101 dyads and 40 absolute
289 dominance rank differences.

290 We tested for potential circularity problems arising from using the same behavioural variables
291 (body contact, grooming and friendly approach) to assess personality structure, as well as
292 affiliative relationship strength (DSI). In case of a circularity issue, on the one hand we would
293 expect a strong positive Pearson correlation between the two measures across individuals. We
294 correlated the individual personality scores with the sum DSI of the top two social bond
295 partners for each individual. On the other hand, across dyads we would expect a strong
296 positive correlation of DSI and the mean of both partners’ personality scores on a social
297 dimension. Pearson correlations with individual and dyadic Connectedness and Sociability
298 scores were performed for each half year period.

299 To assess whether males adjusted their personality after migrating into a new group with new
300 partners, we correlated each of the variables loading high on Connectedness (as quantified
301 from the two-year data collection period; Table 2) across the six migrating males from one
302 year to the next. We used Pearson correlation and variables were aggregated for April 2014–
303 March 2015 and April 2015–March 2016.

304

305

306

307 *Ethical statement*

308 Our animal research was completely non-invasive and approved by the Department of
309 National Parks, Wildlife and Plant Conservation (DNP), Thailand (permit 0002/2424). This
310 work followed the ASAB guidelines for the treatment of animals in behavioural research and
311 teaching, and adhered to standards as defined by the European Union Council Directive
312 2010/63/EU on the protection of animals used for scientific purposes.

313

314 **RESULTS**

315 The full model describing variation in dyadic relationship strength was significantly different
316 from the null model (likelihood ratio test: $\chi^2 = 14.69$, $df = 6$, $P < 0.05$). The Connectedness
317 score (likelihood ratio test: $\chi^2 = 5.14$, $df = 1$, $P = 0.023$) and the dominance rank difference
318 (likelihood ratio test: $\chi^2 = 4.11$, $df = 1$, $P = 0.043$) had significant effects on social bonds
319 (Table 2; Fig. 1 and 2). In accordance with previous findings, that closely bonded individuals
320 pull each other to similar ranks (Schülke et al., 2010), we found that bond strength was
321 associated with similarity in dominance rank. The smaller the Connectedness score of a dyad,
322 i.e. the more similar two partners are in that personality dimension, the higher the DSI score,
323 i.e. the stronger the social bond. Since all variables entered into the model were z-
324 standardized, the results can be interpreted as follows: if the absolute difference in the
325 Connectedness score of a dyad increases one standard deviation then social bond strength will
326 decrease by about 0.18 standard deviations, with all other control variables held on average.
327 In other words, if the Connectedness score of a dyad increases one unit then social bond
328 strength will decrease about 0.09 units.

329 The graph shows that with high difference scores in Connectedness, the DSI of a dyad is far
330 below the meaningful threshold of one, which marks strong social relationships (i.e. social

331 bonds). The raw data are quite scattered probably due to the relatively small sample size and
 332 relatively short period to measure the social bond strength. We pooled data from four different
 333 study groups and two time periods. These were rather stable periods within an unstable
 334 observation period with alpha rank changes and migration events, which are influencing the
 335 social bonds of all group members. However, the narrow confidence intervals of the model
 336 prediction are indicative of reliable results. The personality effects are rather small like in the
 337 other primate studies (effect range: |0.043–2.02|; Capitanio et al., 2015; Massen & Koski,
 338 2014; Morton et al., 2015; Weinstein & Capitanio, 2012) as well as in humans (Feiler &
 339 Kleinbaum, 2015; Jensen-Campbell et al., 2002; Roberts, Kuncel, Shiner, Caspi, & Goldberg,
 340 2007).

341 **Table 2**

342 Effects of personality similarity on the strength of dyadic social bonds. Bond strength is the
 343 log standardized dyadic composite sociality score (DSI), and similarity in each of five
 344 personality dimensions was modelled as the absolute difference in personality scores between
 345 partners and dominance similarity as absolute dominance rank difference. All variables z-
 346 transformed. Significant results marked in bold.

Variable	Estimate	SE	CI _{lower}	CI _{upper}	χ^2	Df	P
(Intercept)	-0.01	0.16	-0.33	0.31	(1)	(1)	(1)
Aggressiveness _{BC} score ⁽²⁾	-0.09	0.08	-0.24	0.07	1.32	1	0.251
Confidence _{TR} score ⁽³⁾	-0.02	0.08	-0.19	0.16	0.03	1	0.853
Connectedness _{BC} score ⁽⁴⁾	-0.18	0.08	-0.33	-0.02	5.14	1	0.023
Sociability _{BC} score ⁽⁵⁾	-0.03	0.08	-0.19	0.13	0.14	1	0.706
Vigilance _{BC} score ⁽⁶⁾	-0.10	0.08	-0.26	0.05	1.77	1	0.183
Dominance rank difference ⁽⁷⁾	-0.19	0.09	-0.37	-0.01	4.11	1	0.043
Group.year	(8)	(8)	(8)	(8)	3.81	6	0.702

347 ⁽¹⁾not shown, because having a limited interpretation.

348 ⁽²⁾z-transformed, original values with mean \pm SD: 1.18 \pm 0.79

349 ⁽³⁾z-transformed, original values with mean \pm SD: 1.24 \pm 0.85

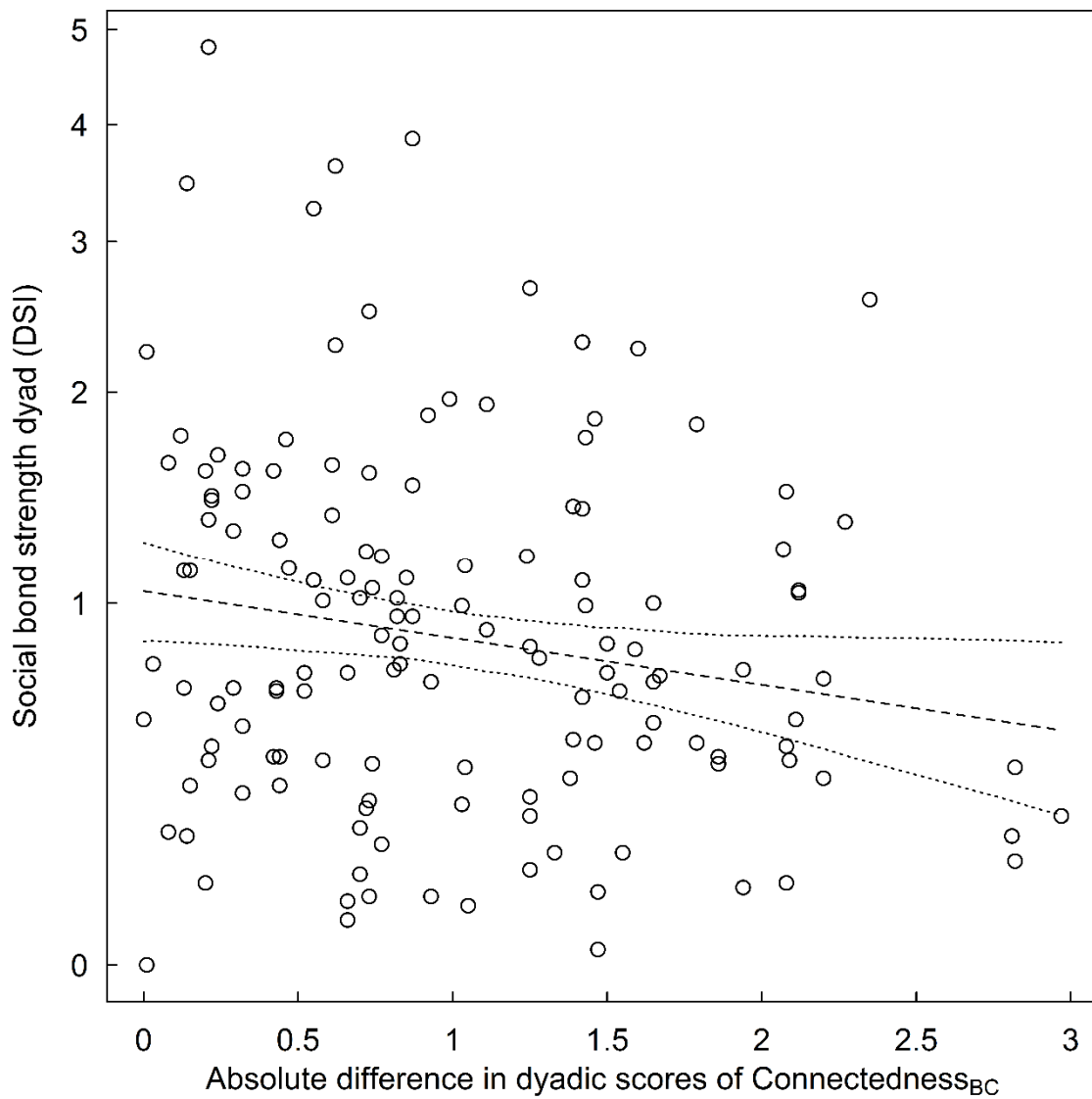
350 ⁽⁴⁾z-transformed, original values with mean \pm SD: 1.01 \pm 0.70

351 ⁽⁵⁾z-transformed, original values with mean \pm SD: 1.10 \pm 1.10

352 ⁽⁶⁾z-transformed, original values with mean \pm SD: 1.12 \pm 0.92

353 ⁽⁷⁾z-transformed, original values with mean \pm SD: 2.98 \pm 1.88

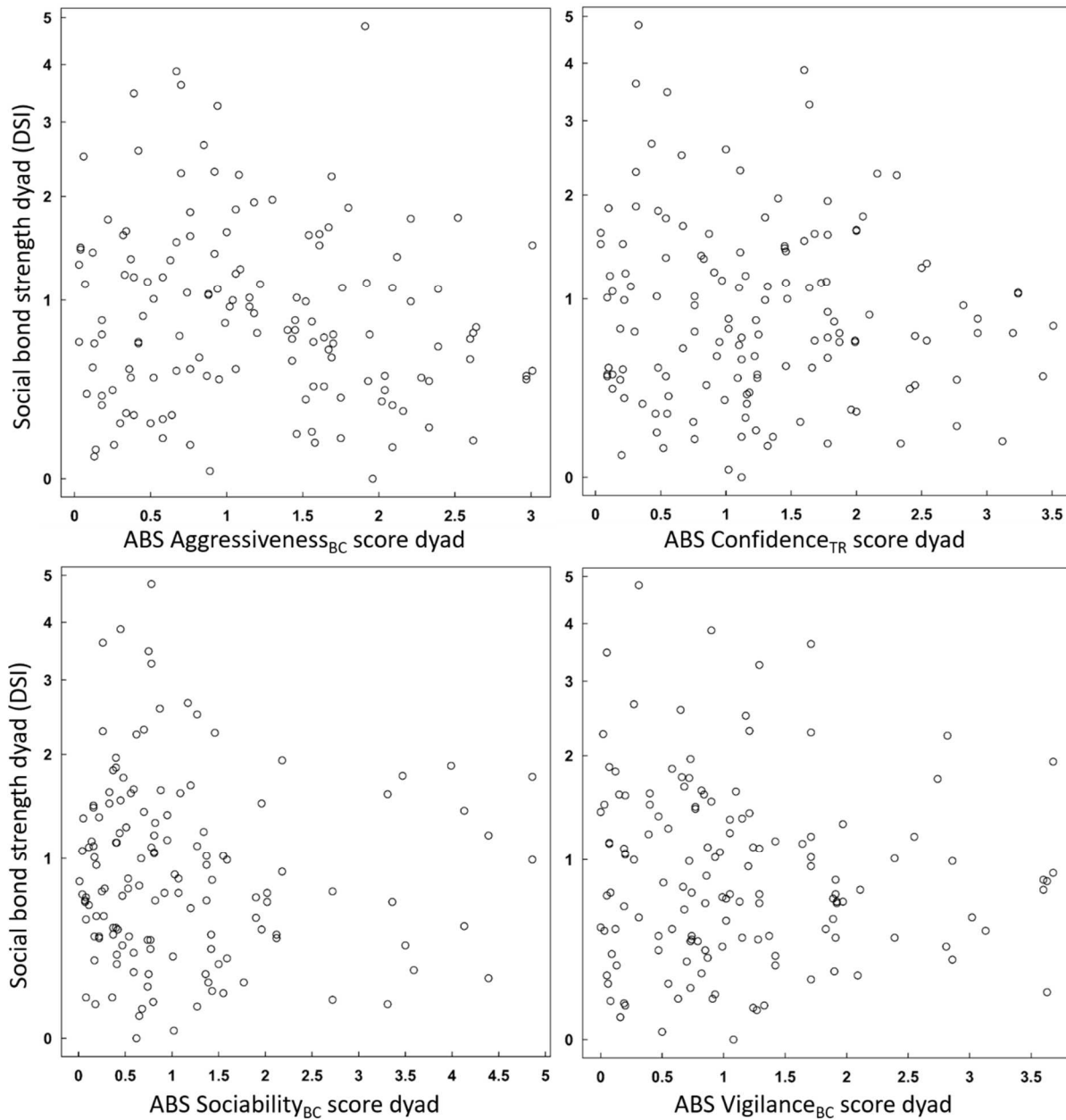
354 ⁽⁸⁾7 levels of group.year reveal no effect and are not shown.



355

356 **Figure 1:** Effect of personality similarity on bond strength. Linear mixed model plot with the
357 significant effect of absolute difference in dyadic scores of Connectedness on log
358 standardized social bond strength (DSI). The dashed line is the model prediction and dotted
359 lines represent its bootstrapped 95% confidence intervals. Total N with 101 dyads and 40
360 dominance rank differences. All variables z-transformed.

361



362

363 **Figure 2:** Other personality traits (absolute difference (ABS) in dyadic scores) with no effect
364 on social bond strength (log standardized DSI). Total N with 101 dyads and 40 dominance
365 rank differences. All variables z-transformed.

366

367 The strength of affiliative relationships was explicitly related to the similarity in personality
368 between partners and did not result from dyads or individuals scoring high or low on social
369 personality dimensions. DSI did not correlate with mean Connectedness of a dyad (Oct2014–
370 Mar2015: $r_{\text{dyadic}} = 0.139$, $p = 0.227$, $n = 77$; Oct2015–Mar2016: $r_{\text{dyadic}} = 0.054$, $p = 0.675$, $n = 63$)
371 and mean Sociability scores per dyad (Oct2014–Mar2015: $r_{\text{dyadic}} = -0.135$, $p = 0.242$, $n = 77$;
372 Oct2015–Mar2016: $r_{\text{dyadic}} = 0.246$, $p = 0.052$, $n = 63$; Fig. A1). Similarly, the strength of the
373 strongest bonds this individual formed (i.e. sum of top two DSI values) did not correlate with
374 individual Connectedness (Oct2014–Mar2015: $r_{\text{individual}} = 0.076$, $p = 0.722$, $n = 24$; Oct2015–
375 Mar2016: $r_{\text{individual}} = -0.004$, $p = 0.985$, $n = 21$) and Sociability scores (Oct2014–Mar2015:
376 $r_{\text{individual}} = -0.155$, $p = 0.471$, $n = 24$; Oct2015–Mar2016: $r_{\text{individual}} = 0.168$, $p = 0.468$, $n = 21$;
377 Fig. A2).

378

379 *Friendship formation*

380 For our small subset of six migrating individuals, the variables loading on the Connectedness
381 dimension were positively correlated from before to after the migration for variables active,
382 alone, neighbour diversity and tolerance (mean $r = 0.817$; $p = 0.02$ – 0.1 ; Table 3), with the
383 exception of friendly approach ($r = 0.041$; $p = 0.94$; Table 3).

384

385 **Table 3**

386 Stability in variables loading on the Connectedness personality domain in six males that
387 changed groups.

Behavioural variable	Pearson's r	p -value
active	0.879	0.02
alone	0.724	0.10
friendly approach	0.041	0.94
neighbour diversity	0.860	0.03
tolerance	0.805	0.05

388

389

390 **DISCUSSION**

391 Consistent with the idea that partner choice in social bond formation is guided by personality
392 homophily, male Assamese macaques chose bond partners with similar levels of
393 Connectedness. Similarity in Connectedness most likely predicted social bond formation and
394 not the other way around, because males did not change their personality after migrating to a
395 new group. In the following we will compare these results with personality homophily in
396 humans, discuss its adaptive value, evidence from animal mating pairs and other types of
397 animal social bonds, and why partners are similar in social personality traits and not in other
398 dimensions. We discuss the role of tolerance in bonding and cooperation and their neural
399 basis and consider alternative theories for the social effects of partners' personality.

400 Our result that individuals more similar in Connectedness form stronger social bonds supports
401 the hypothesis of a shared evolutionary origin of personality homophily as partner choice
402 strategy in human and non-human primates (Bahns et al., 2016; Massen & Koski, 2014). In
403 humans the personality dimensions most closely matched in friends are extraversion and
404 agreeableness (e.g., Blaz, 1983; Caspi et al., 2005; Dishion, Patterson, Stoolmiller, & Skinner,

405 1991; Ilmarinen, Vainikainen, Verkasalo, & Lönnqvist, 2017; Maaß, Lämmle, Bensch, &
406 Ziegler, 2016; Markey & Kurtz, 2006; van Zalk & Denissen, 2015; Youyou et al., 2017),
407 which partly resembles our findings. Aspects of the Connectedness trait, like proximity, social
408 tolerance, and friendly approach, roughly correspond to the sociable or affiliative facets of
409 extraversion associated with enjoyment of social interactions (Denissen & Penke, 2008). Our
410 sociability domain (i.e. high rates of friendly behaviour and more time in body contact and
411 grooming, as well as more frequent initiation of affiliations) has more overlap with the
412 agreeableness dimension in humans, where individuals scoring higher in agreeableness are
413 more interested in maintaining positive social relationships (Denissen & Penke, 2008). Unlike
414 in humans, homophily regarding this second social personality dimension did not predict
415 social bonds.

416 The main selective advantage of personality similarity in friendships as well as animal social
417 bonds may result from a more reliable and thus more successful cooperation among
418 individuals with similar (cooperative) behavioural tendencies via facilitated coordination,
419 communication and reciprocity, as well as reduced uncertainty and conflict (Asakawa-Haas,
420 Schiestl, Bugnyar, & Massen, 2016; Bahns et al., 2016; Chiang & Takahashi, 2011; Curry &
421 Dunbar, 2013; Fu et al., 2012; Gabriel & Black, 2012; Koski & Burkart, 2015; Massen &
422 Koski, 2014; Riolo et al., 2001; Schuett et al., 2011). Humans cultivate cooperative
423 relationships sustained by emotional closeness and reciprocity of support (Dunbar, 2018;
424 Hruschka & Henrich, 2006; Rand & Nowak, 2013; Wrzus & Neyer, 2016)(Dunbar, 2018;
425 Hruschka & Henrich 2006; Rand & Nowack, 2013; Wrzus & Neyer, 2016), whereby people
426 preferentially form ties with others who share similar cooperative behavioural tendencies
427 (Apicella et al., 2012). Extraversion and agreeableness are linked to motivation for
428 cooperative activities as well as cooperative skills. For instance, people scoring high in these
429 dimensions have greater enthusiasm toward cooperation and are more trusting of others

430 (Adali & Golbeck, 2012; Ashton, Paunonen, Helmes, & Jackson, 1998; Hirsh & Peterson,
431 2009; Lu & Argyle, 1991; Ross, Rausch, & Canada, 2003; but see also: Koole, Jager, van den
432 Berg, Vlek, & Hofstee, 2001).

433 Animal mating pairs of partners with similar level in exploration tendency (rodents:
434 Rangassamy et al., 2015; Steller's jays: Gabriel & Black, 2012; great tits: Dingemanse et al.,
435 2004; zebra finches: Schuett et al., 2011) and boldness (guppies: Ariyomo & Watt, 2013)
436 express higher reproductive success, and successful cooperative-breeding common marmosets
437 show group-level similarity in both traits (Koski & Burkart, 2015). The role of similarity in
438 social personality traits remains underexplored. Exploration may be more directly linked to
439 helping behaviour, as demonstrated in a cooperative-breeding cichlid (Bergmüller &
440 Taborsky, 2007) and choices for breeding partners may differ in choices for other partnerships
441 where social personality traits may be more relevant (Koski, 2014).

442 Across group members, chimpanzees and Capuchin monkeys show proximity driven, i.e.
443 social tolerance related, personality homophily in social relationships (Massen & Koski, 2014;
444 Morton et al., 2015). Further, in a trait rating study with juvenile rhesus macaques, an
445 equitability dimension (e.g., calmer, more easygoing, less active), which also includes aspects
446 of social tolerance, correlated with relationship stability (Weinstein & Capitanio, 2012).
447 However, in a social network study with wild Barbary macaques, it was not similarity in
448 social tolerance but excitability (contains elements related to low impulse control: excitable,
449 impulsive, erratic and disorganized) that was correlated with spatial association (Tkaczynski,
450 2017), albeit this effect was not seen in grooming networks.

451 More generally, social tolerance (i.e. tolerating the proximity of others), as well as social
452 grooming behaviour, are considered as prerequisites for animal social bonds, and, like
453 friendships, they are further assumed to require mutuality and positive interactions (Asakawa-
454 Haas et al., 2016; Brosnan et al., 2015; Massen, Sterck, & De Vos, 2010; van Zalk &

455 Denissen, 2015; Watts, 2002). Considering homophily in Connectedness as partner choice
456 mechanisms in Assamese macaques, similar needs of proximity and similar level of social
457 tolerance (scoring either high or low in Connectedness), may be associated with increased
458 trust in reciprocal relations with bond partners, to maintain bonds and facilitate cooperation
459 (Campenni & Schino, 2014; Laakasuo, Rotkirch, Berg, & Jokela, 2016; Massen & Koski,
460 2014). Cooperative success and bond maintenance are intertwined regarding social bonds as
461 alliances that generate adaptive benefits via support in critical situations (DeScioli &
462 Kurzban, 2009; Massen & Koski, 2014; Schülke et al., 2010; Seyfarth & Cheney, 2012).
463 Mutual coalitionary support helps bond partners to attain and maintain high social status,
464 which is linked to reproductive success in male Assamese macaques (Schülke et al., 2010;
465 Sukmak, Wajjwalku, Ostner, & Schülke, 2014). In Barbary macaques, it was demonstrated
466 experimentally that strong social bonds positively influenced the maintenance of cooperation
467 over a long period (Molesti & Majolo, 2016).

468 Social tolerance (or other traits in other species) may be correlated with cooperativeness,
469 given that correlations between different behaviours are assumed to occur among different
470 functional contexts (behavioural syndromes: Bergmüller, Schürch, & Hamilton, 2010; Sih,
471 Bell, & Johnson, 2004; see also cooperative syndromes in cooperative breeding meerkats:
472 Clutton-Brock, Russell, & Sharpe, 2003; English, Nakagawa, & Clutton-Brock, 2010 and
473 cichlids: Schürch & Heg, 2010). Social tolerance could as well be functionally related to
474 variation in other cognitive abilities or styles to negotiate the social landscape, which in turn
475 affect cooperation (Fiske & Haslam, 1996; Moreira et al., 2013; Seyfarth & Cheney, 2015;
476 Sih & Del Giudice, 2012). Differences in social awareness or sensitivity, comprising the
477 ability to monitor the cooperative tendencies of others, may favour the evolution of consistent
478 individual differences in cooperation (Korman, Voiklis, & Malle, 2015; McNamara, Stephens,
479 Dall, & Houston, 2009; Seyfarth & Cheney, 2015; cognitive syndromes: Sih & Del Giudice,

480 2012). It was recently demonstrated that chimpanzees high in Extraversion (corresponding to
481 Assamese' Connectedness) and assumingly more sensitive to inter-individual interactions,
482 have been more sensitive to inequity in outcomes between themselves and a social partner in
483 an experimental condition (Brosnan et al., 2015). In sum, homophily in social tolerance in
484 Assamese macaques may either be related to similar cooperative tendencies or similar social
485 sensitivity in bonded partners leading to enhanced cooperative success, probably because of
486 increased trust in compatible partner.

487 Friends show similar neural responses to the same stimuli and thus react to the world around
488 them in a similar way, presumably due to similar dispositions, pre-existing knowledge,
489 opinions, interests, and values (Parkinson et al., 2018). Such similar neural responses are
490 proposed to enhance social interactions and friendship formation via positive affective
491 processes, increased predictability and facilitated communication (Berger & Calabrese, 1975;
492 Neyer et al., 1999; Selfhout et al., 2010; van Zalk & Denissen, 2015). The same line of
493 argument may apply to animal social bonds. Similarity in personality, or possibly social
494 tolerance traits in particular, may trigger basic neural and physiological mechanisms
495 (underlying social interactions in humans and other animals: e.g., Brent 2014; Chang et al.,
496 2013; Dunbar, 2010), in the bond partner in a similar way, which in turn may facilitate
497 attitudinal or emotionally based partner choice (Fruteau, Voelkl, Van Damme, & Noë, 2009;
498 Fu et al., 2012; Parkinson et al., 2018; Schino & Aureli, 2009). Koski & Burkhardt (2015)
499 propose that similar affective states may facilitate behavioural synchrony, contingency and
500 reciprocity in a cognitively inexpensive way (Brosnan & de Waal, 2002; Fessler & Holbrook,
501 2014). Not alone that long-term relationships may be reliably maintained via emotionally
502 based reciprocity (Schino & Aureli, 2016), positive affect and common psychological
503 mechanisms may allow for quick assessment in bond formation as well, since it is known in

504 humans that similar people relate with each other quite rapidly and without concise choice
505 (Ambady, Bernieri, & Richeson, 2000; Bahns et al., 2016; Sunnafrank & Ramirez, 2004).

506 Alternative theories in human personality research claim that ‘opposites attract’. Interpersonal
507 theory (Carson, 1969), proposes that dominance invites submission and vice versa, while
508 partners mutually reinforce each other’s dispositional tendencies. Self-expansion theory (Aron
509 & Aron, 1996) suggests that people accommodate to each other’s distinctiveness to expand
510 their selves. Empirical studies often found mixed evidence. For instance, friends were either
511 very similar or very different regarding extraversion-introversion (Nelson et al., 2011).

512 Pairings of rhesus macaques in a laboratory setting were successful for females similar in
513 Emotionality, but only for those males with both dyad members scoring low (but not
514 moderate or high) on Gentle and Nervous temperament (Capitanio et al., 2015). Yet,
515 researchers mostly agree that homophily plays an important role in long-term relationships.

516 When people form relationships with dissimilar individuals these are rather short-lived task-
517 oriented ties, like professional collaborations (Currarini, Jackson, & Pin, 2009; Fu et al., 2012;
518 McPherson et al., 2001; Moody, 2004; Parkinson et al., 2018; Rivera et al., 2010).

519 Another alternative theoretical account for the observed correlations between personality and
520 social relationships invokes social influence and predicts that friends may become more
521 similar over time, and individuals may potentially converge their attitudes to one another to be
522 more liked (normative) or to be more right (informational) (Cullum & Harton, 2007; Davis &
523 Rusbult, 2001). Likewise, there is evidence for post pairing adjustment (associated with
524 improved reproductive success) with reactive partners becoming more proactive in
525 monogamous fish (Laubu, Dechaume-Moncharmont, Motreuil, & Schweitzer, 2016).

526 Consistent with our finding that personality similarity most likely predicts social bond
527 formation in Assamese macaques, human studies demonstrated that similarity matters early in
528 acquaintanceship, and established attitudes, values and personality seem generally less

529 amenable to influence (Bahns et al., 2016; Costa & McCrae, 1992; Papadopoulou, 2016).

530 Still, not many studies considered social influence, and further research is needed especially

531 in the realm of animal social bonds.

532 In fact, human psychology research even goes beyond the statement of selectivity in

533 friendships, and proposes that people engage in niche construction when they seek out social

534 environments, such as friendships (e.g., Kandel, 1978; Bahns et al., 2016; Papadopoulou,

535 2016). In short, Niche Construction Theory (NCT; Odling-Smee, Laland, & Feldman, 2003),

536 refers to evolutionary processes as constant and cyclical transactions between the organisms,

537 their socio-physical environment and their genetic heritage, whereby organisms modify their

538 own (and/or each other's) environments through the metabolic, physiological and behavioural

539 activities, as well as through their choices (Flynn, Laland, Kendal, & Kendal, 2013; Laland,

540 Odling-Smee, & Endler, 2017; Odling-Smee et al., 2013). Recent studies investigated

541 friendship dyads in adults and children in a real-life setting, and newly formed relationships

542 were tracked over some period (Bahns et al., 2016; Papadopoulou, 2016). These studies

543 support previous findings and state that humans actively choose similar minded (e.g., on

544 personality or attitudes) friends to construct stable, satisfying social niches, that are

545 compatible with their dispositions, and further promote cooperation and well-being (Bahns et

546 al., 2016; Caspi & Herbener, 1990; Hampson, 2011; Papadopoulou, 2016; Scarr &

547 McCartney, 1983).

548 In sum, our results support the idea of a fundamental biological basis of homophily as partner

549 choice strategy in human and non-human animals (Apicella et al., 2012; Bahns et al. 2016; Fu

550 et al., 2012; Massen & Koski, 2014). Specifically, homophily in social tolerance traits may

551 play an important role considering the potential relatedness of human personality traits

552 extraversion and agreeableness with the Connectedness domain in Assamese macaques plus

553 the evidence from other primate studies relating personality and social bonds (Massen &

554 Koski, 2014; Morton et al., 2015; Weinstein & Capitanio, 2012). Further, social tolerance is
555 key in social bonds and cooperative success (e.g., raven: Asakawa-Haas et al., 2016; Massen
556 et al., 2015; hyena: Drea & Carter, 2009; primates: Hare, Melis, Woods, Hastings, &
557 Wrangham, 2007; Werdenich & Huber, 2002; theoretical model: Chen, Fu, & Wang, 2009).
558 To gauge the generality of these findings, additional primate and particularly other animal
559 studies are needed to elucidate the importance of similarity in social tolerance in the process
560 of social bond formation.

561

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575

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1063 **APPENDIX**

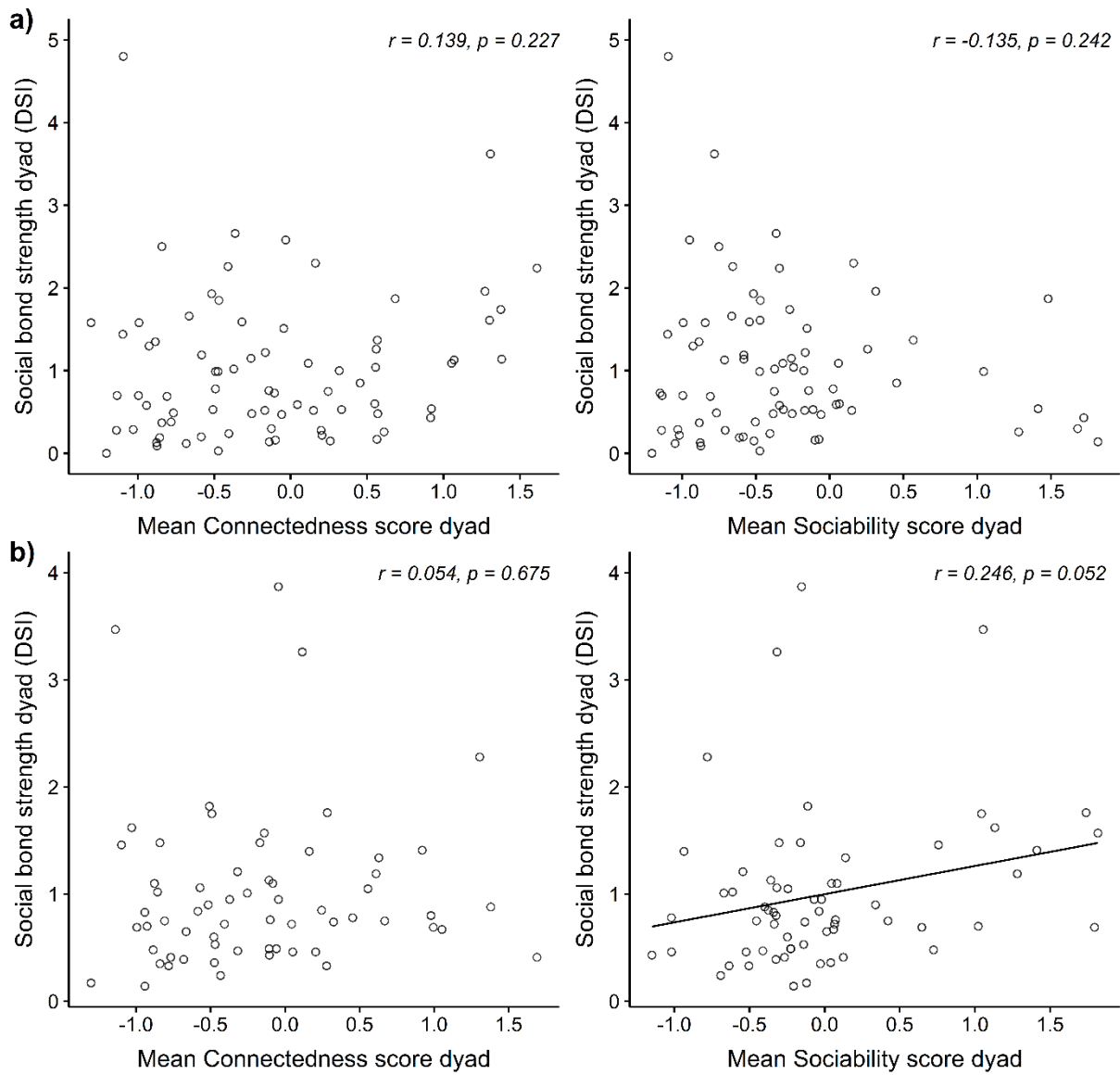
1064 **Table A1**

1065 Group composition with age-sex classes at onset of study.

Group	Adult males	Subadult males	Juvenile males	Infant males	Adult females	Juvenile females	Infant females	Total
ASM	8	6	10	3	10	12	3	52
AOM	10	3	8	1	14	10	5	51
ASS	4	2	2	4	9	7	1	28
AOS	5	0	2	2	6	5	1	21
All	27*	11	22	10	39	34	10	153

1066 *24 adult males were included in the analysis because 3 individuals emigrated.

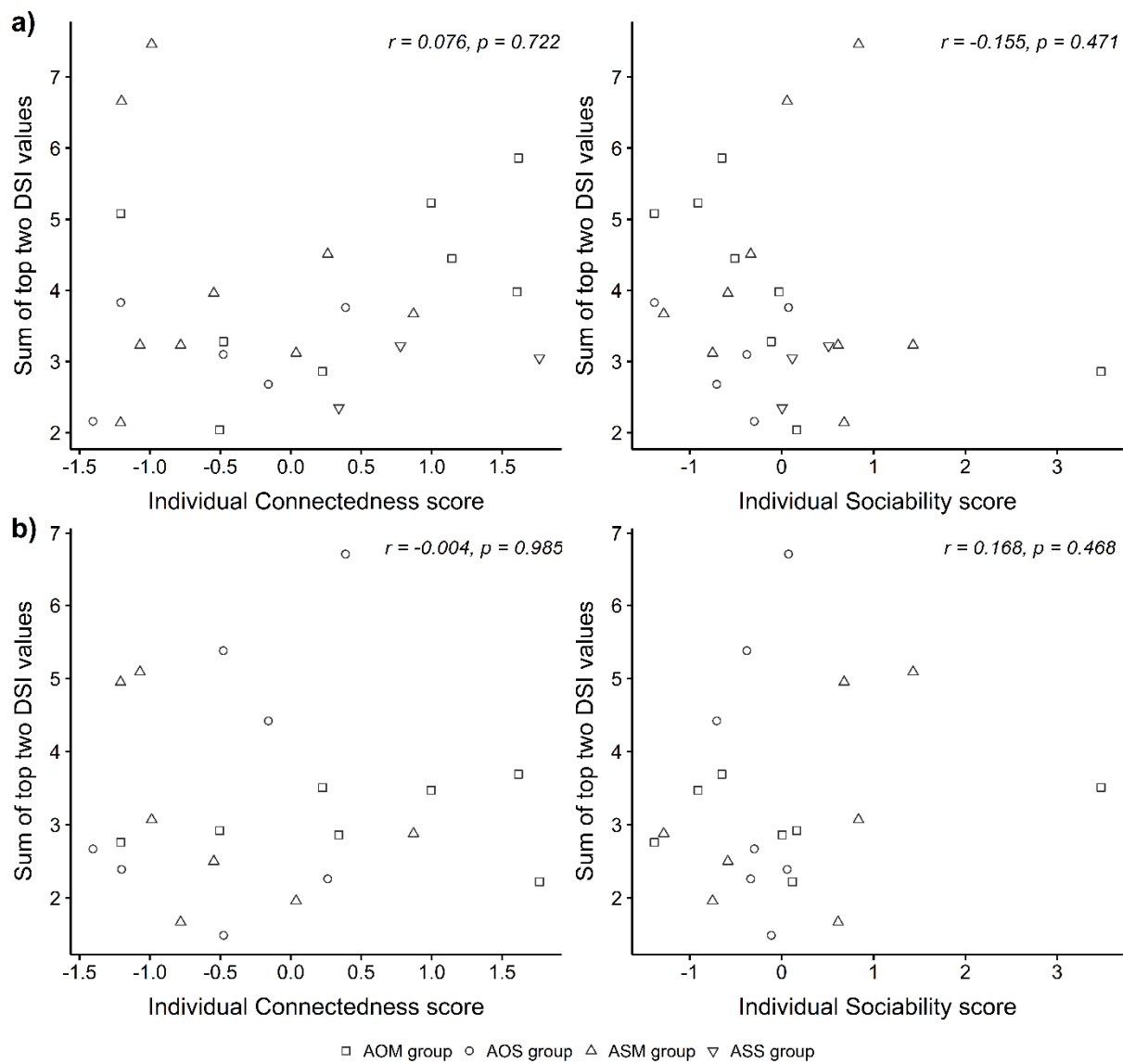
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1069 **Figure A1:** Pearson correlation of mean personality scores per dyad with DSI scores for every
1070 half year period. a) Oct2014–Mar2015 with n=77. b) Oct2015–Mar2016 with n=63.

1071



1072

1073 **Figure A2:** Pearson correlation of individual personality scores with sum of top two DSI
1074 values for every half year period. a) Oct2014–Mar2015 with n=24. b) Oct2015–Mar2016 with
1075 n=21.

1076