Manuscript submitted to *Animal Behaviour* on 20th December 2018

Title:

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

Author names:

Anja Ebenau[1,2,3], Christoph von Borell[3,4], Lars Penke[3,4], Julia Ostner[1,2,3] and Oliver Schülke[1,2,3]

Author affiliations:

[1]Department of Behavioral Ecology, Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology, University of Goettingen, Kellnerweg 6, 37077 Goettingen, Germany

[2]Research Group Social Evolution in Primates, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Goettingen, Germany

[3]Leibniz ScienceCampus Primate Cognition, Kellnerweg 4, 37077 Goettingen, Germany

[4]Biological Personality Psychology, Georg Elias Mueller Institute of Psychology, University of Goettingen, Goßlerstraße 14, 37073 Goettingen, Germany

Corresponding author:

Anja Ebenau, Department of Behavioral Ecology, Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology, University of Goettingen, Kellnerweg 6, 37077 Goettingen, Germany, Phone: +49 551 39 33926, Fax: +49 551 39 9637, E-Mail: aebenau@gwdg.de

ABSTRACT

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

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

INTRODUCTION

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

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

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

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

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

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

consistent across time and (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Personality homophily has been found in human spouses (e.g., Byrne, 1997; Klohnen & Luo, 2003; Youyou, Stillwell, Schwartz, & Kosinski, 2017) and improves reproductive success in monogamous rodents, birds, and fish (Ariyomo & Watt, 2013; Dingemanse, Both, Drent, & Tinbergen, 2004; Gabriel & Black, 2012; Rangassamy, Dalmas, Féron, Gouat, & Rödel, 2015; Schuett, Dall, & Royle, 2011). Similarity in certain personality traits is associated with the strength of social bonds in chimpanzees (Massen & Koski, 2014), higher-quality relationships in capuchin monkeys (Morton, Weiss, Buchanan-Smith, & Lee, 2015), relationship stability from one year to the next in juvenile rhesus macaques (Weinstein & Capitanio, 2012) and pairing-success of adult rhesus macaques in a laboratory setting (Capitanio, Blozis, Snarr, Steward, & McCowan, 2015). Beyond dyadic relationships, group-level similarity in personality traits facilitates cooperation among all group members in cooperative-breeding common marmosets (Koski & Burkart, 2015).

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

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

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

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

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

METHODS

Fieldwork was conducted in the Phu Khieo Wildlife Sanctuary (PKWS: 16°5'–35'N, 101°20'–55'E) which is part of the ca. 6500 km^2 interconnected and well-protected Western Isaan forest complex in north-eastern Thailand (Borries, Larney, Kreetiyutanont, & Koenig, 2002). The study area is covered by hill evergreen forest and harbours a diverse community of large mammals and predators (Borries et al., 2002) indicative of very low levels of human disturbance. The field site was established in 2005, study subjects lived in four fully habituated groups, and were followed from April 2014 (ASM and AOM group) or October 2014 (ASS and AOS group) through March 2016. Group sizes at the beginning of behavioural data collection are shown in Table A1.

Personality assessment

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

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

Table 1

Summary of integrative personality constructs of Assamese macaques, derived from behavioural codings$_{BC}$ and trait ratings$_{TR}$.

Personality traits	Description
Connectedness$_{BC}$	Frequent and diverse neighbours in 5m proximity and pronounced social tolerance, expressed as high rates of friendly approaches to and by others
Aggressiveness$_{BC}$	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

Behavioural data collection

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

Dyadic relationship measure

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

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

$$\mathrm{DSI} = \left(\frac{\frac{\mathrm{FP}_{ij}}{\mathrm{FP}_{ave}} + \frac{\mathrm{DP}_{ij}}{\mathrm{DP}_{ave}} + \frac{\mathrm{FB}_{ij}}{\mathrm{FB}_{ave}} + \frac{\mathrm{DB}_{ij}}{\mathrm{DB}_{ave}} + \frac{\mathrm{FG}_{ij}}{\mathrm{FG}_{ave}} + \frac{\mathrm{DG}_{ij}}{\mathrm{DG}_{ave}}}{6} \right)$$

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

Dominance rank

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

Statistical analyses

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

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

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

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

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

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

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: $\chi2 = 14.69$, df = 6, $P < 0.05$). The Connectedness
317 score (likelihood ratio test: $\chi2 = 5.14$, df = 1, $P = 0.023$) and the dominance rank difference
318 (likelihood ratio test: $\chi2 = 4.11$, 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

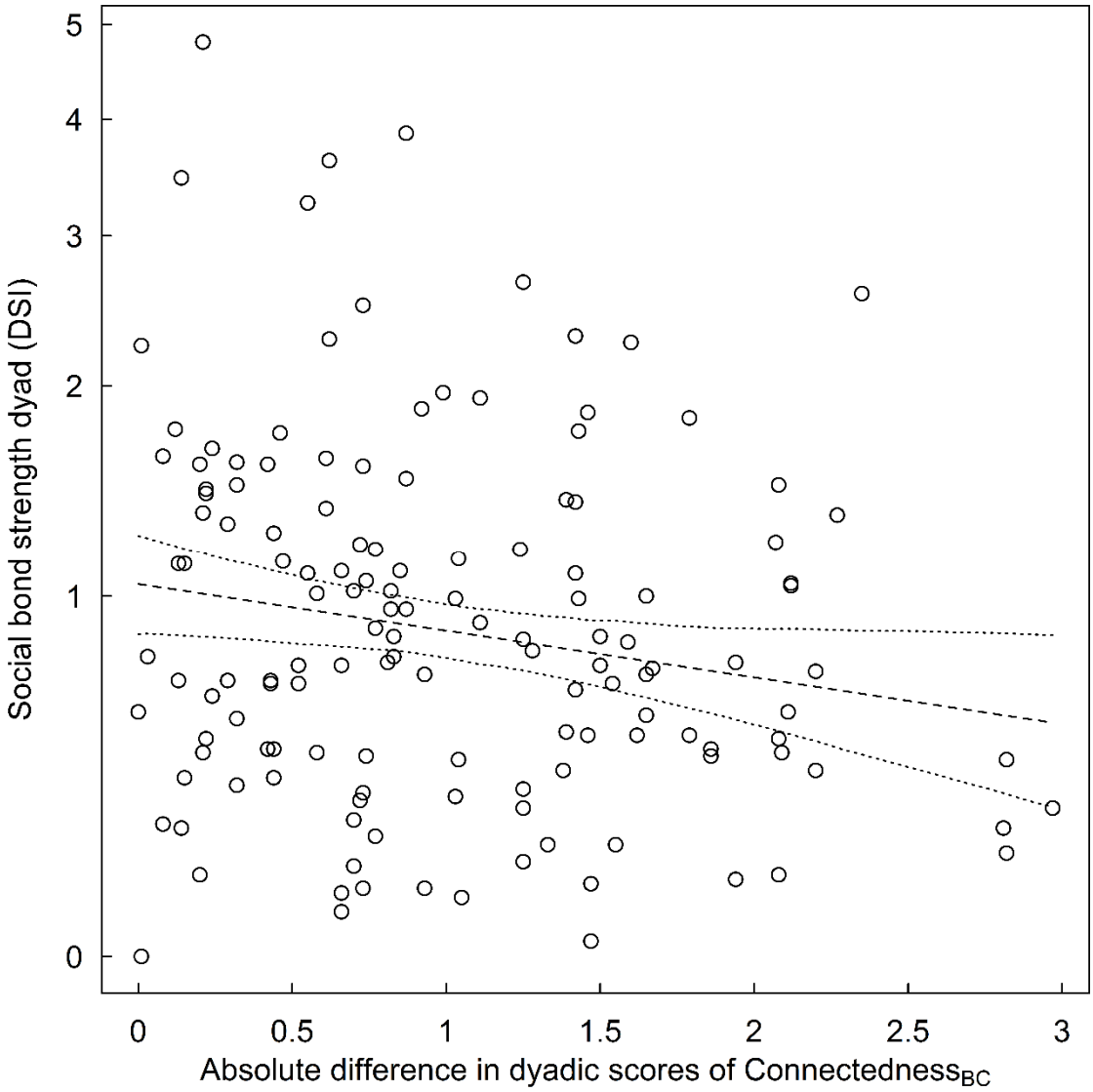
bonds). The raw data are quite scattered probably due to the relatively small sample size and relatively short period to measure the social bond strength. We pooled data from four different study groups and two time periods. These were rather stable periods within an unstable observation period with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

Table 2

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

Variable	Estimate	SE	CI_{lower}	CI_{upper}	$\chi 2$	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

(1)not shown, because having a limited interpretation.
(2)z-transformed, original values with mean ± SD: 1.18±0.79
(3)z-transformed, original values with mean ± SD: 1.24±0.85
(4)z-transformed, original values with mean ± SD: 1.01±0.70
(5)z-transformed, original values with mean ± SD: 1.10±1.10
(6)z-transformed, original values with mean ± SD: 1.12±0.92
(7)z-transformed, original values with mean ± SD: 2.98±1.88
(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

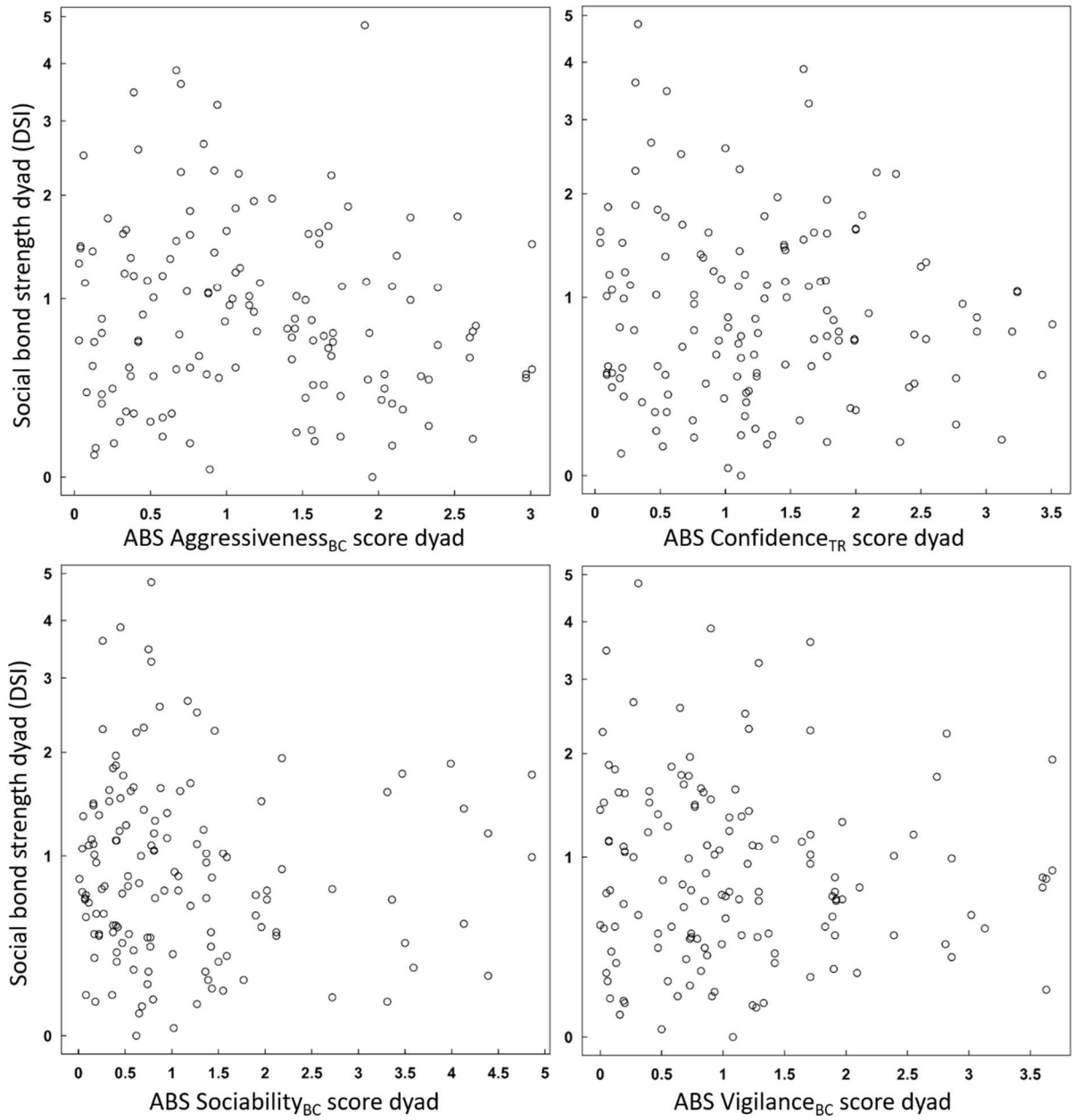


Figure 2: Other personality traits (absolute difference (ABS) in dyadic scores) with no effect on social bond strength (log standardized DSI). Total N with 101 dyads and 40 dominance rank differences. All variables z-transformed.

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

Friendship formation

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

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,

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

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

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

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

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

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

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

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

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

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

ACKNOWLEDGMENTS

We thank the National Research Council of Thailand (NRCT) and the Department of National Parks, Wildlife and Plant Conservation (DNP) for permission to conduct this study and for all the support granted (permit 0002/2424). We are grateful to I. Chatchawarn, J. Prabnasuk, K. Nitaya T. Wongsnak, M. Pongjantarasatien and K. Kreetiyutanont, M. Kumsuk, W. Saenphala (PKWS) for their cooperation over the years and permission to carry out this study. We thank A. Koenig and C. Borries, who developed the field site. Our special thanks goes to S. Jumrudwong, W. Nueorngshiyos, N. Juntuch, J. Wanart, R. Intalo, T. Kilawit, N. Pongangan, B. Klaewklar, N. Bualeng, D. Gutleb, P. Saisawatdikul, K. Srithorn, M. Swagemakers and T. Wisate for their excellent help in the field, and to P. Saisawatdikul and C. Haunhorst for their support. We thank Roger Mundry for the permission to use statistical packages developed by himself. This research was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – Project number 254142454 / GRK 2070.

REFERENCES

Adali, S., & Golbeck, J. (2012). Predicting Personality with Social Behavior. In *2012 IEEE/ACM International Conference on Advances in Social Networks Analysis and Mining* (pp. 302–309). https://doi.org/10.1109/ASONAM.2012.58

Adams, M., Bonaventura, M., Ostner, J., Schulke, O., De Marco, A., Thierry, B., … Weiss, A. (2015). Personality Structure and Social Style in Macaques. *Journal of Personality and Social Psychology*, *109*(2), 338–353. https://doi.org/10.1037/pspp0000041

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*, 227–267. https://doi.org/http://dx.doi.org/10.1163/156853974X00534.

Ambady, N., Bernieri, F. J., & Richeson, J. A. (2000). Toward a histology of social behavior: Judgmental accuracy from thin slices of the behavioral stream. In M. P. Zanna (Ed.), *Advances in experimental social psychology* (Vol. 32, pp. 201–271). San Diego, CA: Academic Press.

Antal, T., Ohtsuki, H., Wakeley, J., Taylor, P. D., & Nowak, M. A. (2009). Evolution of cooperation by phenotypic similarity. *Proceedings of the National Academy of Sciences*, *106*(21), 8597–8600. https://doi.org/10.1073/pnas.0902528106

Apicella, C. L., Marlowe, F. W., Fowler, J. H., & Christakis, N. A. (2012). Social networks and cooperation in hunter-gatherers. *Nature*, *481*(7382), 497–501. https://doi.org/10.1038/nature10736

Ariyomo, T. O., & Watt, P. J. (2013). Disassortative mating for boldness decreases reproductive success in the guppy. *Behavioral Ecology*, *24*(6), 1320–1326. https://doi.org/10.1093/beheco/art070

Aron, A., & Aron, E. N. (1996). Self and self-expansion in relationships. In G. J. O. Fletcher & J. Fitness (Eds.), *Knowledge structures in close relationships: A social psychological approach* (pp. 325–344). New Jersey: Lawrence Erlbaum Associates.

601 Asakawa-Haas, K., Schiestl, M., Bugnyar, T., & Massen, J. J. M. (2016). Partner Choice in
602 Raven (Corvus corax) Cooperation. *PLOS ONE*, *11*(6), e0156962.
603 https://doi.org/10.1371/journal.pone.0156962
604 Ashton, M. C., Paunonen, S. V., Helmes, E., & Jackson, D. N. (1998). Kin Altruism,
605 Reciprocal Altruism, and the Big Five Personality Factors. *Evolution and Human*
606 *Behavior*, *19*(4), 243–255. https://doi.org/10.1016/S1090-5138(98)00009-9
607 Baayen, R. H. (2008). *Analyzing linguistic data: a practical introduction to statistics*.
608 Cambridge: Cambridge University Press.
609 Bahns, A. J., Crandall, C. S., Gillath, O., & Preacher, K. J. (2016). Similarity in relationships
610 as niche construction: Choice, stability, and influence within dyads in a free choice
611 environment. *Journal of Personality and Social Psychology*, *112*(2), 329–355.
612 https://doi.org/10.1037/pspp0000088
613 Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for
614 confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*,
615 *68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001
616 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting Linear Mixed-Effects Models
617 using lme4. *Journal of Statistical Software*, *67*, 1–48.
618 https://doi.org/arxiv.org/abs/1406.5823
619 Baumeister, R. F., & Leary, M. R. (1995). The need to belong: desire for interpersonal
620 attachments as a fundamental human motivation. *Psychological Bulletin*, *117*(3), 497–
621 529.
622 Berger, C. R., & Calabrese, R. J. (1975). Some Explorations in Initial Interaction and Beyond:
623 Toward a Developmental Theory of Interpersonal Communication. *Human*
624 *Communication Research*, *1*(2), 99–112. https://doi.org/10.1111/j.1468-
625 2958.1975.tb00258.x

626 Berghänel, A., Ostner, J., Schröder, U., & Schülke, O. (2011). Social bonds predict future
627 cooperation in male Barbary macaques, Macaca sylvanus. *Animal Behaviour*, *81*(6),
628 1109–1116. https://doi.org/10.1016/j.anbehav.2011.02.009
629 Bergmüller, R., Schürch, R., & Hamilton, I. M. (2010). Evolutionary causes and
630 consequences of consistent individual variation in cooperative behaviour.
631 *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1553),
632 2751–2764. https://doi.org/10.1098/rstb.2010.0124
633 Bergmüller, R., & Taborsky, M. (2007). Adaptive behavioural syndromes due to strategic
634 niche specialization. *BMC Ecology*, *7*(1), 12. https://doi.org/10.1186/1472-6785-7-12
635 Blaz, M. (1983). Perceived Extraversion in a Best Friend. *Perceptual and Motor Skills*, *56*(3),
636 891–894. https://doi.org/10.2466/pms.1983.56.3.891
637 Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H.,
638 & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for
639 ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135.
640 https://doi.org/10.1016/j.tree.2008.10.008
641 Borries, C., Larney, E., Kreetiyutanont, K., & Koenig, A. (2002). The diurnal primate
642 community in a dry evergreen forest in Phu Khieo Wildlife Sanctuary, Northeast
643 Thailand, *50*(1), 75–88.
644 Braun, A., & Bugnyar, T. (2012). Social bonds and rank acquisition in raven nonbreeder
645 aggregations. *Animal Behaviour*, *84*(6), 1507–1515.
646 https://doi.org/10.1016/j.anbehav.2012.09.024
647 Brent, L. J. N., Chang, S. W. C., Gariépy, J.-F., & Platt, M. L. (2014). The neuroethology of
648 friendship. *Annals of the New York Academy of Sciences*, *1316*(1), 1–17.
649 https://doi.org/10.1111/nyas.12315
650 Brosnan, S. F., & de Waal, F. B. M. (2002). A proximate perspective on reciprocal altruism.
651 *Human Nature*, *13*(1), 129–152. https://doi.org/10.1007/s12110-002-1017-2

652 Brosnan, S. F., Hopper, L. M., Richey, S., Freeman, H. D., Talbot, C. F., Gosling, S. D., …
653 Schapiro, S. J. (2015). Personality influences responses to inequity and contrast in
654 chimpanzees. *Animal Behaviour*, *101*, 75–87.
655 https://doi.org/10.1016/j.anbehav.2014.12.019
656 Brown, S. L., & Brown, R. M. (2006). Selective Investment Theory: Recasting the Functional
657 Significance of Close Relationships. *Psychological Inquiry*, *17*(1), 1–29.
658 https://doi.org/10.1207/s15327965pli1701_01
659 Byrne, D. (1997). An Overview (and Underview) of Research and Theory within the
660 Attraction Paradigm. *Journal of Social and Personal Relationships*, *14*(3), 417–431.
661 https://doi.org/10.1177/0265407597143008
662 Campbell, W. K., Sedikides, C., Reeder, G. D., & Elliot, A. J. (2000). Among friends? An
663 examination of friendship and the self-serving bias. *British Journal of Social*
664 *Psychology*, *39*(2), 229–239. https://doi.org/10.1348/014466600164444
665 Campennì, M., & Schino, G. (2014). Partner choice promotes cooperation: The two faces of
666 testing with agent-based models. *Journal of Theoretical Biology*, *344*, 49–55.
667 https://doi.org/10.1016/j.jtbi.2013.11.019
668 Capitanio, J. P., Blozis, S. A., Snarr, J., Steward, A., & McCowan, B. J. (2015). Do 'birds of a
669 feather flock together' or do 'opposites attract'? Behavioral responses and
670 temperament predict success in pairings of rhesus monkeys in a laboratory setting.
671 *American Journal of Primatology*, e22464. https://doi.org/10.1002/ajp.22464
672 Carson, R. C. (1969). *Interaction concepts of personality*. Oxford, England: Aldin Publishing
673 Co.
674 Caspi, A., & Herbener, E. S. (1990). Continuity and change: Assortative marriage and the
675 consistency of personality in adulthood. *Journal of Personality and Social*
676 *Psychology*, *58*(2), 250–258.

677 Caspi, A., Roberts, B. W., & Shiner, R. L. (2005). Personality development: Stability and
678 change. *Annual Review of Psychology*, 453–484.
679 https://doi.org/10.1146/annurev.psych.55.090902.141913
680 Chang, S. W. C., Brent, L. J. N., Adams, G. K., Klein, J. T., Pearson, J. M., Watson, K. K., &
681 Platt, M. L. (2013). Neuroethology of primate social behavior. *Proceedings of the*
682 *National Academy of Sciences*, *110*(S2), 10387–10394.
683 https://doi.org/10.1073/pnas.1301213110
684 Chapais, B. (1995). Alliances as a means of competition in primates: Evolutionary,
685 developmental, and cognitive aspects. *American Journal of Physical Anthropology*,
686 *38*(S21), 115–136. https://doi.org/10.1002/ajpa.1330380607
687 Chen, X., Fu, F., & Wang, L. (2009). Social tolerance allows cooperation to prevail in an
688 adaptive environment. *Physical Review E*, *80*(5), 51104.
689 https://doi.org/10.1103/PhysRevE.80.051104
690 Cheney, D. L. (2011). Extent and limits of cooperation in animals. *Proceedings of the*
691 *National Academy of Sciences*, *108*(S2), 10902–10909.
692 https://doi.org/10.1073/pnas.1100291108
693 Chiang, Y.-S., & Takahashi, N. (2011). Network Homophily and the Evolution of the Pay-It-
694 Forward Reciprocity. *Plos One*, *6*(12). https://doi.org/10.1371/journal.pone.0029188
695 Clore, G. L., & Byrne, D. (1974). A reinforcement-affect model of attraction. *Foundations of*
696 *Interpersonal Attraction*, 143–170.
697 Clutton-Brock, T. H., Russell, A. F., & Sharpe, L. L. (2003). Meerkat helpers do not
698 specialize in particular activities. *Animal Behaviour*, *66*(3), 531–540.
699 https://doi.org/10.1006/anbe.2003.2209
700 Connor, R. C., Heithaus, M. R., & Barre, L. M. (2001). Complex social structure, alliance
701 stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the*

Royal Society of London B: Biological Sciences, *268*(1464), 263–267. https://doi.org/10.1098/rspb.2000.1357

Costa Jr, P. T., & McCrae, R. R. (1992). Four ways five factors are basic. *Personality and Individual Differences*, *13*(6), 653–665. https://doi.org/10.1016/0191-8869(92)90236-I

Cronin, K. A. (2012). Prosocial behaviour in animals: the influence of social relationships, communication and rewards. *Animal Behaviour*, *84*(5), 1085–1093. https://doi.org/10.1016/j.anbehav.2012.08.009

Cullum, J., & Harton, H. C. (2007). Cultural Evolution: Interpersonal Influence, Issue Importance, and the Development of Shared Attitudes in College Residence Halls. *Personality and Social Psychology Bulletin*, *33*(10), 1327–1339. https://doi.org/10.1177/0146167207303949

Currarini, S., Jackson, M. O., & Pin, P. (2009). An Economic Model of Friendship: Homophily, Minorities, and Segregation. *Econometrica*, *77*(4), 1003–1045. https://doi.org/10.3982/ECTA7528

Curry, O., & Dunbar, R. M. (2013). Do Birds of a Feather Flock Together? *Human Nature*, *24*(3), 336–347. https://doi.org/10.1007/s12110-013-9174-z

Davis, J. L., & Rusbult, C. E. (2001). Attitude alignment in close relationships. *Journal of Personality and Social Psychology*, *81*(1), 65.

Denissen, J. J. A., & Penke, L. (2008). Motivational individual reaction norms underlying the Five-Factor model of personality: First steps towards a theory-based conceptual framework. *Journal of Research in Personality*, *42*(5), 1285–1302. https://doi.org/10.1016/j.jrp.2008.04.002

DeScioli, P., & Kurzban, R. (2009). The Alliance Hypothesis for Human Friendship. *Plos One*, *4*(6). https://doi.org/10.1371/journal.pone.0005802

726 Digman, J. M. (1990). Personality Structure: Emergence of the Five-Factor Model. *Annual*
727 *Review of Psychology*, *41*(1), 417–440.
728 https://doi.org/10.1146/annurev.ps.41.020190.002221
729 Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of
730 avian personalities in a fluctuating environment. *Proceedings of the Royal Society B-*
731 *Biological Sciences*, *271*(1541), 847–852. https://doi.org/10.1098/rspb.2004.2680
732 Dishion, T. J., Patterson, G. R., Stoolmiller, M., & Skinner, M. L. (1991). Family, school, and
733 behavioral antecedents to early adolescent involvement with antisocial peers.
734 *Developmental Psychology*, *27*(1), 172.
735 Dobson, A. J. (2010). *An introduction to generalized linear models* (2nd ed.). Chapman and
736 Hall/CRC. Boca Raton.
737 Drea, C. M., & Carter, A. N. (2009). Cooperative problem solving in a social carnivore.
738 *Animal Behaviour*, *78*(4), 967–977. https://doi.org/10.1016/j.anbehav.2009.06.030
739 Dunbar, R. I. M. (2010). The social role of touch in humans and primates: Behavioural
740 function and neurobiological mechanisms. *Neuroscience & Biobehavioral Reviews*,
741 *34*(2), 260–268. https://doi.org/10.1016/j.neubiorev.2008.07.001
742 Dunbar, R. I. M. (2018). The Anatomy of Friendship. *Trends in Cognitive Sciences*, *22*(1),
743 32–51. https://doi.org/10.1016/j.tics.2017.10.004
744 Ebenau, A., Penke, L., Ostner, J., & Schülke, O. (under review). Integrative personality
745 assessment in wild Assamese macaques (Macaca assamensis). *Journal of*
746 *Comparative Psychology*
747 Engelmann, J. M., & Herrmann, E. (2016). Chimpanzees Trust Their Friends. *Current*
748 *Biology*, *26*(2), 252–256. https://doi.org/10.1016/j.cub.2015.11.037
749 Engelmann, J. M., Herrmann, E., & Tomasello, M. (2015). Chimpanzees trust conspecifics to
750 engage in low-cost reciprocity. *Proceedings of the Royal Society of London B:*
751 *Biological Sciences*, *282*(1801). https://doi.org/10.1098/rspb.2014.2803

752 English, S., Nakagawa, S., & Clutton-Brock, T. H. (2010). Consistent individual differences
753 in cooperative behaviour in meerkats (Suricata suricatta). *Journal of Evolutionary*
754 *Biology*, *23*(8), 1597–1604. https://doi.org/10.1111/j.1420-9101.2010.02025.x
755 Feiler, D. C., & Kleinbaum, A. M. (2015). Popularity, Similarity, and the Network
756 Extraversion Bias. *Psychological Science*, *26*(5), 593–603.
757 https://doi.org/10.1177/0956797615569580
758 Fessler, D. M. T., & Holbrook, C. (2014). Marching into battle: synchronized walking
759 diminishes the conceptualized formidability of an antagonist in men. *Biology Letters*,
760 *10*(8), 20140592. https://doi.org/10.1098/rsbl.2014.0592
761 Fidell, L. S., & Tabachnick, B. G. (2003). Preparatory data analysis. In J. A. Schinka & W. F.
762 Velicer (Eds.), *Handbook of psychology: Research methods in psychology* (Vol. 2, pp.
763 115–141). New Jersey: John Wiley & Sons.
764 Field, A. (2000). *Discovering statistics using SPSS for Windows: Advanced techniques for*
765 *beginners (Introducing Statistical Methods series)*. Sage publications.
766 Fiske, A. P., & Haslam, N. (1996). Social cognition is thinking about relationships. *Current*
767 *Directions in Psychological Science*, *5*(5), 143–148.
768 Flynn, E. G., Laland, K. N., Kendal, R. L., & Kendal, J. R. (2013). Target article with
769 commentaries: Developmental niche construction. *Developmental Science*, *16*(2),
770 296–313. https://doi.org/10.1111/desc.12030
771 Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models:
772 overestimated effect sizes and the winner's curse. *Behavioral Ecology and*
773 *Sociobiology*, *65*(1), 47–55. https://doi.org/10.1007/s00265-010-1038-5
774 Fowler, J. H., Settle, J. E., & Christakis, N. A. (2011). Correlated genotypes in friendship
775 networks. *Proceedings of the National Academy of Sciences of the United States of*
776 *America*, *108*(5), 1993–1997. https://doi.org/10.1073/pnas.1011687108

777 Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression* (2nd ed.). Sage:
778 Thousand Oaks CA.
779 Fu, F., Nowak, M. A., Christakis, N. A., & Fowler, J. H. (2012). The Evolution of
780 Homophily. *Scientific Reports*, *2*, 845. https://doi.org/10.1038/srep00845
781 Gabriel, P. O., & Black, J. M. (2012). Behavioural Syndromes, Partner Compatibility and
782 Reproductive Performance in Steller's Jays. *Ethology*, *118*(1), 76–86.
783 https://doi.org/10.1111/j.1439-0310.2011.01990.x
784 Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., &
785 Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees.
786 *Behavioral Ecology and Sociobiology*, *67*(3), 373–381.
787 https://doi.org/10.1007/s00265-012-1457-6
788 Hampson, S. E. (2011). Personality Processes: Mechanisms by Which Personality Traits 'Get
789 Outside the Skin'. *Annual Review of Psychology*, *63*(1), 315–339.
790 https://doi.org/10.1146/annurev-psych-120710-100419
791 Hirsh, J. B., & Peterson, J. B. (2009). Extraversion, neuroticism, and the prisoner's dilemma.
792 *Personality and Individual Differences*, *46*(2), 254–256.
793 https://doi.org/10.1016/j.paid.2008.10.006
794 Hruschka, D. J., & Henrich, J. (2006). Friendship, cliquishness, and the emergence of
795 cooperation. *Journal of Theoretical Biology*, *239*(1), 1–15.
796 https://doi.org/10.1016/j.jtbi.2005.07.006
797 Ilmarinen, V.-J., Vainikainen, M.-P., Verkasalo, M. J., & Lönnqvist, J.-E. (2017).
798 Homophilous Friendship Assortment Based on Personality Traits and Cognitive
799 Ability in Middle Childhood: The Moderating Effect of Peer Network Size. *European*
800 *Journal of Personality*, *31*(3), 208–219. https://doi.org/10.1002/per.2095
801 Jensen-Campbell, L. A., Adams, R., Perry, D. G., Workman, K. A., Furdella, J. Q., & Egan,
802 S. K. (2002). Agreeableness, extraversion, and peer relations in early adolescence:

803 Winning friends and deflecting aggression. *Journal of Research in Personality*, *36*(3),
804 224–251. https://doi.org/10.1006/jrpe.2002.2348
805 John, O., Srivastava, S., & Pervin, L. (1999). The Big Five trait taxonomy: History,
806 measurement, and theoretical perspectives. In L. A. Pervin & O. P. John (Eds.),
807 *Handbook of Personality: Theory and Research* (Vol. 2, pp. 102–138). New York:
808 Guilford Press.
809 Kalbitz, J., Ostner, J., & Schülke, O. (2016). Strong, equitable and long-term social bonds in
810 the dispersing sex in Assamese macaques. *Animal Behaviour*, *113*, 13–22.
811 https://doi.org/10.1016/j.anbehav.2015.11.005
812 Kandel, D. B. (1978). Homophily, Selection, and Socialization in Adolescent Friendships.
813 *American Journal of Sociology*, *84*(2), 427–436. https://doi.org/10.1086/226792
814 King, J. E., & Figueredo, A. J. (1997). The Five-Factor Model plus Dominance in
815 Chimpanzee Personality. *Journal of Research in Personality*, *31*(2), 257–271.
816 https://doi.org/10.1006/jrpe.1997.2179
817 Klohnen, E. C., & Luo, S. (2003). Interpersonal attraction and personality: What is attractive–
818 self similarity, ideal similarity, complementarity or attachment security? *Journal of*
819 *Personality and Social Psychology*, *85*(4), 709.
820 Koole, S. L., Jager, W., van den Berg, A. E., Vlek, C. A., & Hofstee, W. K. (2001). On the
821 social nature of personality: Effects of extraversion, agreeableness, and feedback
822 about collective resource use on cooperation in a resource dilemma. *Personality and*
823 *Social Psychology Bulletin*, *27*(3), 289–301.
824 https://doi.org/doi.org/10.1177/0146167201273003
825 Korman, J., Voiklis, J., & Malle, B. F. (2015). The social life of cognition. *The Changing*
826 *Face of Cognition*, *135*, 30–35. https://doi.org/10.1016/j.cognition.2014.11.005
827 Koski, S. E. (2014). Broader horizons for animal personality research. *Ecology and Evolution*,
828 *2*(70), 1–6. https://doi.org/10.3389/fevo.2014.00070

829 Koski, S. E., & Burkart, J. M. (2015). Common marmosets show social plasticity and group-
830 level similarity in personality. *Scientific Reports*, *5*, 8878.
831 https://doi.org/10.1038/srep08878
832 Laakasuo, M., Rotkirch, A., Berg, V., & Jokela, M. (2017). The Company You Keep:
833 Personality and Friendship Characteristics. *Social Psychological and Personality*
834 *Science*, *8*(1), 66–73. https://doi.org/10.1177/1948550616662126
835 Laland, K., Odling-Smee, J., & Endler, J. (2017). Niche construction, sources of selection and
836 trait coevolution. *Interface Focus*, *7*(5), 20160147.
837 https://doi.org/10.1098/rsfs.2016.0147
838 Laubu, C., Dechaume-Moncharmont, F.-X., Motreuil, S., & Schweitzer, C. (2016).
839 Mismatched partners that achieve postpairing behavioral similarity improve their
840 reproductive success. *Science Advances*, *2*(3), e1501013.
841 https://doi.org/10.1126/sciadv.1501013
842 Lu, L., & Argyle, M. (1991). Happiness and cooperation. *Personality and Individual*
843 *Differences*, *12*(10), 1019–1030.
844 Maaß, U., Lämmle, L., Bensch, D., & Ziegler, M. (2016). Narcissists of a Feather Flock
845 Together: Narcissism and the Similarity of Friends. *Personality and Social Psychology*
846 *Bulletin*, *42*(3), 366–384. https://doi.org/10.1177/0146167216629114
847 Majolo, B., Ames, K., Brumpton, R., Garratt, R., Hall, K., & Wilson, N. (2006). Human
848 friendship favours cooperation in the Iterated Prisoner's Dilemma. *Behaviour*,
849 *143*(11), 1383–1395. https://doi.org/10.1163/156853906778987506
850 Markey, P. M., & Kurtz, J. E. (2006). Increasing Acquaintanceship and Complementarity of
851 Behavioral Styles and Personality Traits Among College Roommates. *Personality and*
852 *Social Psychology Bulletin*, *32*(7), 907–916.
853 https://doi.org/10.1177/0146167206287129

854 Marshall-Pescini, S., Schwarz, J. F. L., Kostelnik, I., Virányi, Z., & Range, F. (2017).
855 Importance of a species' socioecology: Wolves outperform dogs in a conspecific
856 cooperation task. *Proceedings of the National Academy of Sciences*, *114*(44), 11793–
857 11798. https://doi.org/10.1073/pnas.1709027114
858 Massen, J. J. M. (2017). Friendships in Animals. In J. Vonk & T. Shackelford (Eds.),
859 *Encyclopedia of Animal Cognition and Behavior* (pp. 1–6). Cham: Springer
860 International Publishing.
861 Massen, J. J. M., & Koski, S. E. (2014). Chimps of a feather sit together: chimpanzee
862 friendships are based on homophily in personality. *Evolution and Human Behavior*,
863 *35*(1), 1–8. https://doi.org/10.1016/j.evolhumbehav.2013.08.008
864 Massen, J. J. M., Ritter, C., & Bugnyar, T. (2015). Tolerance and reward equity predict
865 cooperation in ravens (*Corvus corax*). *Scientific Reports*, *5*, 15021.
866 https://doi.org/10.1038/srep15021
867 Massen, J., Sterck, E., & Vos, H. de. (2010). Close social associations in animals and humans:
868 functions and mechanisms of friendship. *Behaviour*, *147*(11), 1379–1412.
869 https://doi.org/10.1163/000579510X528224
870 McNamara, J. M., Stephens, P. A., Dall, S. R., & Houston, A. I. (2009). Evolution of trust and
871 trustworthiness: social awareness favours personality differences. *Proceedings of the*
872 *Royal Society B: Biological Sciences*, *276*(1657), 605–613.
873 https://doi.org/10.1098/rspb.2008.1182
874 McPherson, M., Smith-Lovin, L., & Cook, J. M. (2001). Birds of a feather: Homophily in
875 social networks. *Annual Review of Sociology*, *27*, 415–444.
876 https://doi.org/10.1146/annurev.soc.27.1.415
877 Meunier, H. (2018). The Pertinence of Studying Neuroethology in Nonhuman Primates for
878 Human Behavior in Groups and Organizations. *Organizational Research Methods*.
879 https://doi.org/10.1177/1094428118756741

880 Molesti, S., & Majolo, B. (2016). Cooperation in wild Barbary macaques: factors affecting
881 free partner choice. *Animal Cognition*, *19*(1), 133–146.
882 https://doi.org/10.1007/s10071-015-0919-4
883 Moody, J. (2004). The structure of a social science collaboration network: Disciplinary
884 cohesion from 1963 to 1999. *American Sociological Review*, *69*(2), 213–238.
885 https://doi.org/10.1177/000312240406900204
886 Moreira, J., Vukov, J., Sousa, C., Santos, F. C., d'Almeida, A. F., Santos, M. D., & Pacheco,
887 J. M. (2013). Individual memory and the emergence of cooperation. *Animal*
888 *Behaviour*, *85*(1), 233–239. https://doi.org/10.1016/j.anbehav.2012.10.030
889 Morton, F. B., Weiss, A., Buchanan-Smith, H. M., & Lee, P. C. (2015). Capuchin monkeys
890 with similar personalities have higher-quality relationships independent of age, sex,
891 kinship and rank. *Animal Behaviour*, *105*, 163–171.
892 https://doi.org/10.1016/j.anbehav.2015.04.013
893 Nelson, P. A., Thorne, A., & Shapiro, L. A. (2011). I'm Outgoing and She's Reserved: The
894 Reciprocal Dynamics of Personality in Close Friendships in Young Adulthood.
895 *Journal of Personality*, *79*(5), 1113–1147. https://doi.org/10.1111/j.1467-
896 6494.2011.00719.x
897 Neyer, F. J., Banse, R., & Asendorpf, J. B. (1999). The Role of Projection and Empathic
898 Accuracy in Dyadic Perception between Older Twins. *Journal of Social and Personal*
899 *Relationships*, *16*(4), 419–442. https://doi.org/10.1177/0265407599164001
900 Noë, R. (2006). Cooperation experiments: coordination through communication versus acting
901 apart together. *Animal Behaviour*, *71*(1), 1–18.
902 https://doi.org/10.1016/j.anbehav.2005.03.037
903 Nowak MA, Tarnita CE, Antal T (2010). Evolutionary dynamics in structured populations.
904 *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 19–30.
905 https://doi.org/10.1098/rstb.2009.0215

906 Odling-Smee, J., Erwin, D. H., Palkovacs, E. P., Feldman, M. W., Laland, K. N., & Handling
907 Editor James Thomson. (2013). Niche Construction Theory: A Practical Guide for
908 Ecologists. *The Quarterly Review of Biology*, *88*(1), 3–28.
909 https://doi.org/10.1086/669266
910 Olson, K. R., & Spelke, E. S. (2008). Foundations of cooperation in young children.
911 *Cognition*, *108*(1), 222–231. https://doi.org/10.1016/j.cognition.2007.12.003
912 Ostner, J., Heistermann, M., & Schülke, O. (2008). Dominance, aggression and physiological
913 stress in wild male Assamese macaques (Macaca assamensis). *Hormones and*
914 *Behavior*, *54*(5), 613–619. https://doi.org/10.1016/j.yhbeh.2008.05.020
915 Ostner, J., & Schülke, O. (2014). The evolution of social bonds in primate males. *Behaviour*,
916 *151*(7), 871 – 906. https://doi.org/10.1163/1568539X-00003191
917 Ostner, J., & Schülke, O. (2018). Chapter Four - Linking Sociality to Fitness in Primates: A
918 Call for Mechanisms. In M. Naguib, L. Barrett, S. D. Healy, J. Podos, L. W. Simmons,
919 & M. Zuk (Eds.), *Advances in the Study of Behavior* (Vol. 50, pp. 127–175).
920 Academic Press. https://doi.org/10.1016/bs.asb.2017.12.001
921 Ostner, J., Vigilant, L., Bhagavatula, J., Franz, M., & Schülke, O. (2013). Stable heterosexual
922 associations in a promiscuous primate. *Animal Behaviour*, *86*(3), 623–631.
923 https://doi.org/10.1016/j.anbehav.2013.07.004
924 Papadopoulou, M. (2016). The 'space'of friendship: young children's understandings and
925 expressions of friendship in a reception class. *Early Child Development and Care*,
926 *186*(10), 1544–1558.
927 Parkinson, C., Kleinbaum, A. M., & Wheatley, T. (2018). Similar neural responses predict
928 friendship. *Nature Communications*, *9*(1), 332. https://doi.org/10.1038/s41467-017-
929 02722-7

930 Perry, S., Barrett, H. C., & Manson, J. H. (2004). White-faced capuchin monkeys show triadic
931 awareness in their choice of allies. *Animal Behaviour*, *67*(1), 165–170.
932 https://doi.org/10.1016/j.anbehav.2003.04.005
933 Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*.
934 Cambridge University Press.
935 R Core Team (2017). R: A language and environment for statistical computing. R Foundation
936 for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.
937 Rand, D. G., & Nowak, M. A. (2013). Human cooperation. *Trends in Cognitive Sciences*,
938 *17*(8), 413–425. https://doi.org/10.1016/j.tics.2013.06.003
939 Rangassamy, M., Dalmas, M., Féron, C., Gouat, P., & Rödel, H. G. (2015). Similarity of
940 personalities speeds up reproduction in pairs of a monogamous rodent. *Animal*
941 *Behaviour*, *103*, 7–15. https://doi.org/10.1016/j.anbehav.2015.02.007
942 Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating
943 animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291–
944 318. https://doi.org/10.1111/j.1469-185X.2007.00010.x
945 Riolo, R. L., Cohen, M. D., & Axelrod, R. (2001). Evolution of cooperation without
946 reciprocity. *Nature*, *414*(6862), 441–443.
947 Rivera, M. T., Soderstrom, S. B., & Uzzi, B. (2010). Dynamics of Dyads in Social Networks:
948 Assortative, Relational, and Proximity Mechanisms. *Annual Review of Sociology*,
949 *36*(1), 91–115. https://doi.org/10.1146/annurev.soc.34.040507.134743
950 Roberts, B. W., Kuncel, N. R., Shiner, R., Caspi, A., & Goldberg, L. R. (2007). The Power of
951 Personality: The Comparative Validity of Personality Traits, Socioeconomic Status,
952 and Cognitive Ability for Predicting Important Life Outcomes. *Perspectives on*
953 *Psychological Science*, *2*(4), 313–345. https://doi.org/10.1111/j.1745-
954 6916.2007.00047.x

955 Ross, S. R., Rausch, M. K., & Canada, K. E. (2003). Competition and Cooperation in the
956 Five-Factor Model: Individual Differences in Achievement Orientation. *The Journal*
957 *of Psychology*, *137*(4), 323–337. https://doi.org/10.1080/00223980309600617
958 Sánchez-Tójar, A., Schroeder, J., & Farine, D. R. (2018). A practical guide for inferring
959 reliable dominance hierarchies and estimating their uncertainty. *Journal of Animal*
960 *Ecology*, *87*(3), 594–608. https://doi.org/10.1111/1365-2656.12776
961 Scarr, S., & McCartney, K. (1983). How People Make Their Own Environments: A Theory of
962 Genotype → Environment Effects. *Child Development*, *54*(2), 424–435.
963 https://doi.org/10.2307/1129703
964 Schino, G. (2007). Grooming and agonistic support: a meta-analysis of primate reciprocal
965 altruism. *Behavioral Ecology*, *18*(1), 115–120. https://doi.org/10.1093/beheco/arl045
966 Schino, G., & Aureli, F. (2009). Chapter 2 Reciprocal Altruism in Primates: Partner Choice,
967 Cognition, and Emotions. In *Advances in the Study of Behavior* (Vol. Volume 39, pp.
968 45–69). Academic Press. https://doi.org/10.1016/S0065-3454(09)39002-6
969 Schino, G., & Aureli, F. (2016). Reciprocity in group-living animals: partner control versus
970 partner choice. *Biological Reviews*, n/a-n/a. https://doi.org/10.1111/brv.12248
971 Schmid, V. S., & de Vries, H. (2013). Finding a dominance order most consistent with a
972 linear hierarchy: an improved algorithm for the I&SI method. *Animal Behaviour*,
973 *86*(5), 1097–1105. https://doi.org/10.1016/j.anbehav.2013.08.019
974 Schuett, W., Dall, S. R. X., & Royle, N. J. (2011). Pairs of zebra finches with similar
975 'personalities' make better parents. *Animal Behaviour*, *81*(3), 609–618.
976 https://doi.org/10.1016/j.anbehav.2010.12.006
977 Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social Bonds Enhance
978 Reproductive Success in Male Macaques. *Current Biology*, *20*(24), 2207–2210.
979 https://doi.org/10.1016/j.cub.2010.10.058

Schürch, R., & Heg, D. (2010). Variation in helper type affects group stability and reproductive decisions in a cooperative breeder. *Ethology*, *116*(3), 257–269. https://doi.org/10.1111/j.1439-0310.2009.01738.x

Selfhout, M., Burk, W., Branje, S., Denissen, J., van Aken, M., & Meeus, W. (2010). Emerging Late Adolescent Friendship Networks and Big Five Personality Traits: A Social Network Approach. *Journal of Personality*, *78*(2), 509–538. https://doi.org/10.1111/j.1467-6494.2010.00625.x

Selfhout, M. H., Branje, S. J., & Meeus, W. H. (2007). Similarity in adolescent best friendships: The role of gender. *Netherlands Journal of Psychology*, *63*(2), 42–48. https://doi.org/10.1007/BF03061061

Seyfarth, R. M., & Cheney, D. L. (2012). The Evolutionary Origins of Friendship. *Annual Review of Psychology*, *63*(1), 153–177. https://doi.org/10.1146/annurev-psych-120710-100337

Seyfarth, R. M., & Cheney, D. L. (2015). Social cognition. *Animal Behaviour*, *103*, 191–202. https://doi.org/10.1016/j.anbehav.2015.01.030

Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin*, *86*, 420–428. https://doi.org/http://dx.doi.org/10.1037/0033-2909.86.2.420

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, *19*(7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1603), 2762–2772. https://doi.org/10.1098/rstb.2012.0216

Silk, J. B. (2002). Using the'F'-word in primatology. *Behaviour*, *139*, 421–446. https://doi.org/10.1163/156853902760102735

1006 Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical*
1007 *Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 539–559.
1008 https://doi.org/10.1098/rstb.2006.1994
1009 Silk, J. B., Alberts, S. C., & Altmann, J. (2006). Social relationships among adult female
1010 baboons (Papio cynocephalus) II. Variation in the quality and stability of social bonds.
1011 *Behavioral Ecology and Sociobiology*, *61*(2), 197–204.
1012 https://doi.org/10.1007/s00265-006-0250-9
1013 Silk, J., Cheney, D., & Seyfarth, R. (2013). A practical guide to the study of social
1014 relationships. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(5), 213–225.
1015 https://doi.org/10.1002/evan.21367
1016 Sukmak, M., Wajjwalku, W., Ostner, J., & Schülke, O. (2014). Dominance rank, female
1017 reproductive synchrony, and male reproductive skew in wild Assamese macaques.
1018 *Behavioral Ecology and Sociobiology*, *68*(7), 1097–1108.
1019 https://doi.org/10.1007/s00265-014-1721-z
1020 Sunnafrank, M., & Ramirez, A. (2004). At First Sight: Persistent Relational Effects of Get-
1021 Acquainted Conversations. *Journal of Social and Personal Relationships*, *21*(3), 361–
1022 379. https://doi.org/10.1177/0265407504042837
1023 Tkaczynski, P. (2017). *The Behavioural Ecology of Personality in Wild Barbary Macaques*
1024 (Doctoral dissertation). University of Roehampton, Roehampton.
1025 van Aken, M. A. G., & Asendorpf, J. B. (2018). Personality and peer relationships. In K. H.
1026 Rubin, W. M. Bukowski, & B. Laursen (Eds.), *Handbook of peer interactions,*
1027 *relationships, and groups* (pp. 159–176). New York, US: Guilford Press.
1028 van Zalk, M., & Denissen, J. (2015). Idiosyncratic versus social consensus approaches to
1029 personality: Self-view, perceived, and peer-view similarity. *Journal of Personality and*
1030 *Social Psychology*, *109*(1), 121. https://doi.org/10.1037/pspp0000035

1031 Voelkl, B., & Kasper, C. (2009). Social structure of primate interaction networks facilitates
1032 the emergence of cooperation. *Biology Letters*, rsbl20090204.
1033 https://doi.org/10.1098/rsbl.2009.0204
1034 Watts, D. P. (2002). Reciprocity and interchange in the social relationships of wild male
1035 chimpanzees. *Behaviour*, *139*(2), 343–370.
1036 https://doi.org/10.1163/156853902760102708
1037 Weinstein, T. A. R., & Capitanio, J. P. (2012). Longitudinal Stability of Friendships in
1038 Rhesus Monkeys (Macaca mulatta): Individual- and Relationship-Level Effects.
1039 *Journal of Comparative Psychology*, *126*(1), 97–108.
1040 https://doi.org/10.1037/a0025607
1041 Weiss, A., Inoue-Murayama, M., Hong, K.-W., Inoue, E., Udono, T., Ochiai, T., … King, J.
1042 E. (2009). Assessing chimpanzee personality and subjective well-being in Japan.
1043 *American Journal of Primatology*, *71*(4), 283–292. https://doi.org/10.1002/ajp.20649
1044 Wood, R. I., Kim, J. Y., & Li, G. R. (2016). Cooperation in rats playing the iterated Prisoner's
1045 Dilemma game. *Animal Behaviour*, *114*, 27–35.
1046 https://doi.org/10.1016/j.anbehav.2016.01.010
1047 Wrzus, C., & Neyer, F. J. (2016). Co-Development of Personality and Friendships Across the
1048 Lifespan. *European Psychologist*, *21*(4), 254–273. https://doi.org/10.1027/1016-
1049 9040/a000277
1050 Young, C., Majolo, B., Schülke, O., & Ostner, J. (2014). Male social bonds and rank predict
1051 supporter selection in cooperative aggression in wild Barbary macaques. *Animal*
1052 *Behaviour*, *95*, 23–32. https://doi.org/10.1016/j.anbehav.2014.06.007
1053 Youyou, W., Stillwell, D., Schwartz, H. A., & Kosinski, M. (2017). Birds of a Feather Do
1054 Flock Together. *Psychological Science*, *28*(3), 276–284.
1055 https://doi.org/10.1177/0956797616678187

1056 Ziegler, C.-N., & Golbeck, J. (2007). Investigating interactions of trust and interest similarity.
1057 *Decision Support Systems*, *43*(2), 460–475. https://doi.org/10.1016/j.dss.2006.11.003
1058 Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid
1059 common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14.
1060 https://doi.org/10.1111/j.2041-210X.2009.00001.x

1061

1062

APPENDIX

Table A1

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

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

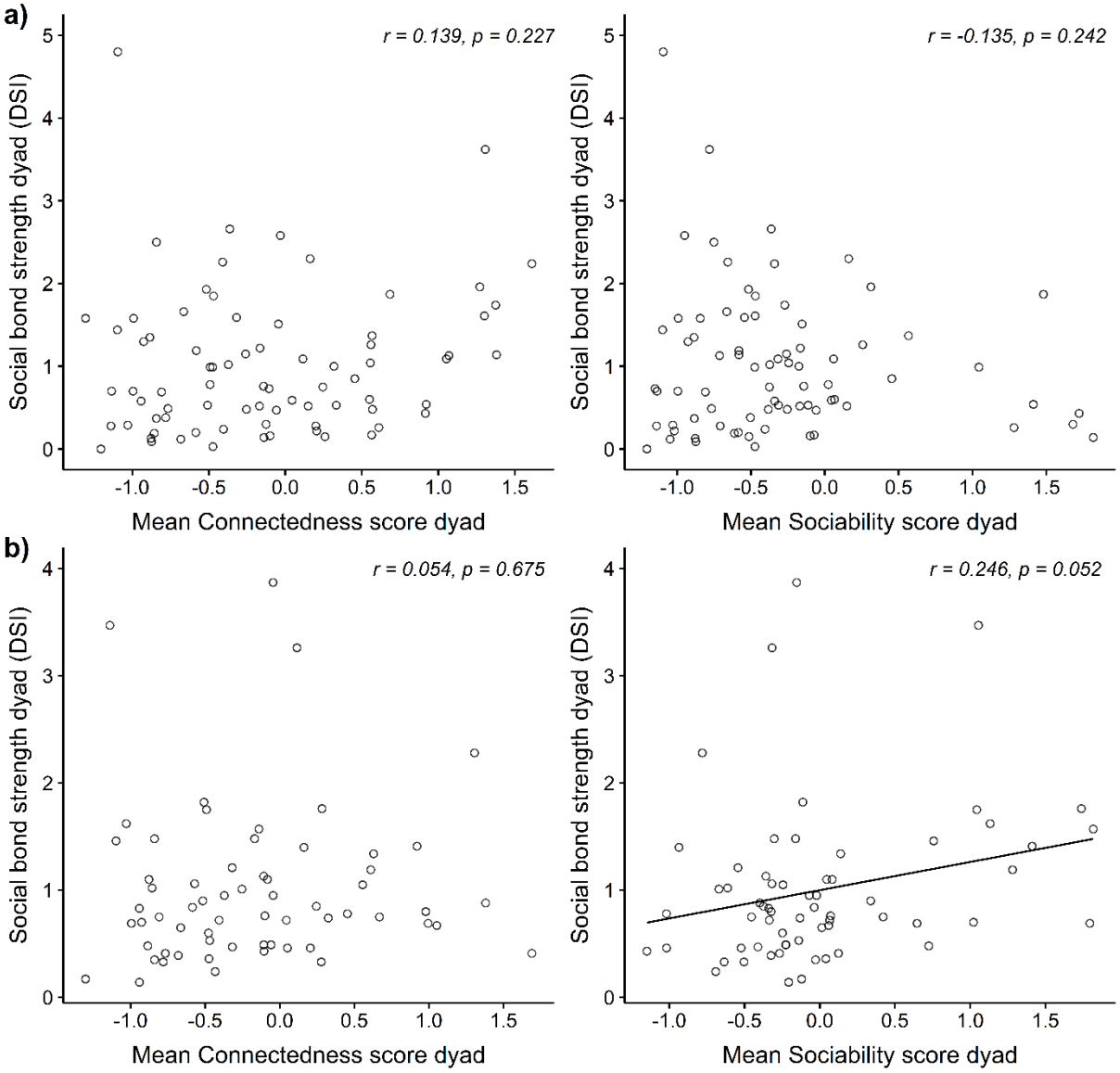


Figure A1: Pearson correlation of mean personality scores per dyad with DSI scores for every half year period. a) Oct2014–Mar2015 with n=77. b) Oct2015–Mar2016 with n=63.

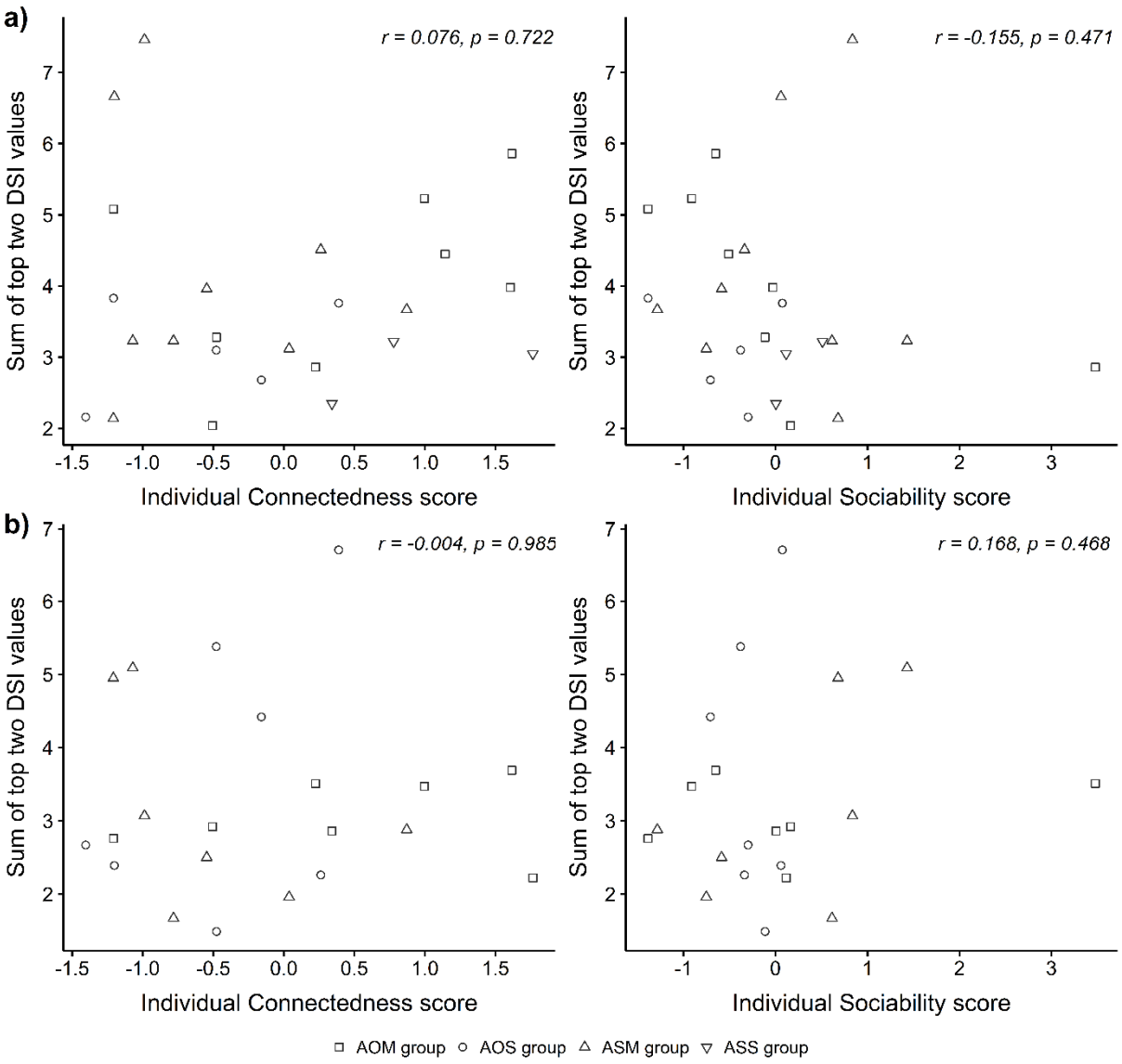


Figure A2: Pearson correlation of individual personality scores with sum of top two DSI values for every half year period. a) Oct2014–Mar2015 with n=24. b) Oct2015–Mar2016 with n=21.