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**Chimps of a feather sit together: chimpanzee friendships are based on homophily  
in personality**

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1 **Abstract**

2 Several recent studies show that animal friendships, like human friendships, are  
3 durable and have fitness benefits by increasing survival, infant survival, or  
4 reproductive success. However, the determinants of especially non-kin friendships are  
5 unclear. Human non-kin friendships are partly determined by similarity in personality.  
6 We investigated personality similarity of friends in 38 captive chimpanzees. Within-  
7 subject comparisons revealed that friends are more similar than non-friends in their  
8 Sociability and Boldness. Subsequent analyses, including both kin- and non-kin  
9 dyads, revealed higher similarity in Sociability among all individuals who sat in  
10 contact more often, while in Boldness and Grooming Equity the positive effect of  
11 similarity was only found in non-kin individuals' contact-sitting. Our results show  
12 that similar to humans, chimpanzees' friendships are related to homophily in certain  
13 personality characteristics, particularly those relevant for socio-positive and  
14 cooperative behaviour. We suggest that having friends similar to self in personality  
15 decreases uncertainty in interactions by promoting reliability especially in cooperative  
16 contexts, and is consequently adaptive. Further, we suggest that homophily in human  
17 friendships dates back at least to our last common ancestor with chimpanzees.

18

19 **Keywords:** Chimpanzees, Friendship, Personality, Homophily Principle,

20 Cooperation.

## 21 **Introduction**

22 Many social animals have marked preferences for particular individuals in their  
23 group, and these close social associations are referred to as friendships (Smuts, 1985;  
24 Schusterman et al., 2000; Garber, 2008; Massen et al., 2010; Seyfarth & Cheney,  
25 2012). Comparable to human friendships, animal friendships are stable over time in  
26 several species (Silk et al., 2006; Silk et al., 2010a; Massen & Sterck, 2013),  
27 including male-male and female-female friendships of wild and captive chimpanzees,  
28 *Pan troglodytes* (Mitani, 2009; Langergraber et al., 2009; Koski et al. 2012). Animal  
29 friendships can have positive fitness consequences. Overall, having many friends may  
30 enhance the chances of survival (McFarland & Majolo, 2013). Similarly, female-  
31 female friendships positively influence survival (Silk et al. 2010b), and also  
32 reproduction through increased infant survival (Silk et al., 2003; Silk et al., 2009;  
33 Cameron et al., 2009; Frère et al., 2010). Male-female friendships also increase infant  
34 survival (Palombit et al., 1997; Huchard et al., 2013), and both male-female and male-  
35 male friendships can enhance male mating access or success (Smuts, 1985; Nishida &  
36 Hosaka, 1996; Conner et al., 2001; Schülke et al. 2010; Kulik et al., 2011; Massen et  
37 al., 2012; Langergraber et al. 2013).

38 However, what determines who is friends with whom, is unclear. Some studies  
39 report that friendships are characterized by kinship (Chapais, 2001; Silk, 2002a; Silk  
40 et al., 2006; Silk et al., 2010a; Silk et al., 2012), rank- or age similarity (Silk et al.,  
41 2006; Silk et al., 2010a; Silk et al., 2012). Kinship-based friendship is likely formed  
42 through familiarity, and as relatedness favours cooperation through kin-selection, the  
43 most commonly found form of friendship. Friendships among unrelated age- and  
44 rank-peers may also be explained through familiarity or by competition over high-  
45 ranking partners, or potentially by paternal kinship (reviewed in Seyfarth & Cheney

46 2012). However, not all friendships, in all species are explained by these attributes.  
47 For example, in chimpanzees also unrelated, not age- or rank peer males form long-  
48 term bonds, and similar friendships are found among females (Mitani 2009;  
49 Langergraber et al., 2009). Similarly, in rhesus macaques the majority of strong bonds  
50 are formed among the matrilinear kin, yet some bonds among unrelated non-peers are  
51 highly affiliative and durable over many years (Massen & Sterck, 2013). Such  
52 friendships among unrelated individuals may be determined by additional factors,  
53 such as personality.

54 In humans, one of the most pervasive factors determining friendship is the  
55 principle of homophily, i.e. affinitive contacts occur at a higher rate among similar  
56 people than among dissimilar people (McPherson et al., 2001). Homophily among  
57 friends is described regarding age, ethnicity, class, education, interests (Shrum et al.,  
58 1988; Marsden, 1988; McPherson et al., 2001), and certain personality traits (Izard,  
59 1960). Similarity in Extraversion (Digman, 1990), Agreeableness and Openness  
60 predicts friendships in adolescents and young adults (Nelson et al., 2011; Selfhout et  
61 al., 2010), whereas similarity in Neuroticism or Conscientiousness does not (Selfhout  
62 et al., 2010, but see Kurtz & Sherker, 2003).

63 From an evolutionary point of view, as friendships take investment of energy,  
64 time and trust, it is beneficial to maintain bonds with individuals that are more  
65 trustworthy. Similarity in characteristics may increase trust through a similar affective  
66 state during interaction (Clore & Byrne, 1974) or by facilitating reciprocity among  
67 individuals with similar behavioural tendencies (de Waal & Luttrell, 1988; Riolo et  
68 al., 2001; Rivas, 2009; Chiang & Takahashi, 2011). It is therefore plausible that  
69 similarity in characteristics may promote friendship also in nonhuman animals.  
70 However, despite evidence for personality similarity in mating partners in many pair-

71 bonded species (Dingemanse et al., 2004; Both et al., 2005; Schuett et al., 2010;  
72 2011; Gabriel & Black 2012), thus far empirical evidence of similarity promoting  
73 animal friendship is lacking. For example, chacma baboons' (*Papio hamadryas*  
74 *ursinus*) highest quality bonds were recently found among individuals with  
75 consistently high rates of touching, embracing and grunting to lower-ranking females  
76 (Seyfarth et al, 2012). However, whether the partners had a similar personality, i.e.  
77 whether friendship formation was assortative according to personality, was not  
78 directly assessed.

79 In this study, we assessed whether similarity in personality influences  
80 chimpanzee friendships. We considered friendships as highly affiliative bonds among  
81 and between adult and adolescent males and females that are characterized by high  
82 rates of sitting in contact (see Methods). Chimpanzees tend to form long-term bonds  
83 mainly with same-sex partners (Mitani, 2009; Langergraber et al., 2009), but male-  
84 female friendships also occur, both in the wild (Langergraber et al., 2010; 2013) and  
85 in captivity (Fraser et al. 2008; Koski et al., 2012). Although many long-term bonds in  
86 males occur between kin, relatedness does not necessarily determine friendship  
87 among either sex class (Langergraber et al., 2007; 2009). However, in captive  
88 conditions females often remain in their natal group, resulting in matrilinear  
89 relationships. Relationships among maternally related individuals are indeed often  
90 strongly bonded (Koski et al. 2012). Therefore, in this study we assessed the effect of  
91 personality on strong bonds with particular others both among unrelated and related  
92 individuals of both sex.

93

## 94 **Methods**

### 95 *Subjects and housing*

96 We studied two captive chimpanzee (*Pan troglodytes*) colonies housed in Dierenpark  
97 Amersfoort ( $n = 14-15$ , three adult or adolescent males, and 11-12 adult or adolescent  
98 females) and Burgers' Zoo, Arnhem ( $n = 15-22$ , three to five adolescent or adult  
99 males, and 12-17 adult females), The Netherlands. In addition, both groups contained  
100 infants and juveniles. However, we did not include them in our analyses since their  
101 behaviour and proximity patterns are heavily dependent on those of their mothers. For  
102 family trees and dates of birth, please see Electronic Supplementary Materials (ESM).  
103 Ages ranged from 1.5 to 47 years in Amersfoort and 5 to 53 years in Arnhem. In  
104 chimpanzees, sexual maturity is reached at the age of 9 and old age starts at the age of  
105 30. Consequently, both groups contained both males and females of all life-stages,  
106 which represents the natural group composition of chimpanzees in the wild (Goodall,  
107 1986).

108 Both groups were housed in zoo facilities containing an inside and an outside  
109 enclosure (Arnhem: inside: 368 m<sup>2</sup>, outside: 0.7 ha; Amersfoort: inside: 96 m<sup>2</sup>,  
110 outside: 475 m<sup>2</sup>) enriched with climbing facilities, nets, hay and other enrichment  
111 items such as footballs and cloths. In both zoos the animals were fed several times a  
112 day, with a diet consisting of fruit, vegetables, bread and seeds.

113 Both zoos are members of the European Association of Zoo and Aquaria and  
114 thus fulfil the legal and ethical regulations on captive animal welfare. Due to the non-  
115 invasive character of the study, our study did not meet the definition of an animal  
116 experiment as mentioned in Article 1 of the Dutch 'Experiments on Animals Act'.  
117 Consequently, the ethics committee of Utrecht University waived the need for  
118 approval, and thus the experiments comply with the Dutch law.

119

120 *Measures and Analyses*

**Kommentar [SK1]:**

IF added, then let's be open. Arn had at time 1 many juveniles, not just one male, whilst Afoort had zero. At time 2 I guess there was just one in each then? I added the info concerning Arnhem in S1 table. Will you add the young present in Afoort? I don't know who it is...

Also, I noticed that in period 1 Ituri was only 6-7 years old... so technically a juvie. I included her anyway, as she is independent enough... but I keep quiet about that detail ;)

121 Each individual's personality was characterised by the personality traits found in our  
122 previous studies (Koski, 2011; Massen et al., 2013). Here, we provide a brief  
123 summary of the findings in these studies. Koski (2011) identified high repeatability  
124 (i.e. temporal consistency within-individuals and variation between-individuals) in 15  
125 bottom-up derived behavioural variables recorded during the daily behaviour of 75  
126 chimpanzees. The variables formed five independent behavioural syndromes in a  
127 factor analysis: Sociability, Positive Affect, Grooming Equity, Anxiety, and Activity.  
128 The study included the Arnhem group but not the Amersfoort group. In a later  
129 analysis with identical measures the Amersfoort chimpanzees were assessed and the  
130 behaviours found to be similarly repeatable (Koski SE, unpublished). In a subsequent  
131 factor analysis including the Amersfoort chimpanzees ( $N_{\text{total}}=90$ ), the solution was  
132 nearly identical with the findings of Koski (2011), with the exception of the fifth  
133 factor, which was not sustained. Therefore, in the current study we included the four  
134 retained factors: Sociability, Positive Affect, Anxiety and Grooming Equity (see  
135 Table 1 for the variables and Table S2 for the variable loadings). The individual factor  
136 scores of the four factors were used in the current study as the *social* personality  
137 scores. Note, that Grooming Equity is not a dyadic measure of reciprocity; it indicates  
138 the skew and spread of individual's grooming efforts among the group.

139 In addition, with targeted behavioural experiments on the same chimpanzees  
140 (10 experiments of novel object, novel food, predator models and foraging puzzles),  
141 Massen et al. (2013) identified several repeatable and contextually consistent  
142 variables. The experiments were performed in a group setting to enhance ecological  
143 validity; the results were not influenced by monopolisation of the devices, by rank or  
144 by sex (Massen et al. 2013). The variables formed two factors: Exploration Tendency-  
145 Persistence and Boldness (see Table 1 for the variables). The individual factor scores

**Kommentar [SK2]:** This is consider to have been a typo from the referee... variation-between is not a word ;)

146 of these two factors were used in the current study as the *non-social* individual  
147 personality scores. The *social* personality trait scores were independent from the *non-*  
148 *social* personality trait scores (Spearman rank order correlations, range from  $r = -0.31$   
149 to  $r = 0.12$ ,  $P > 0.10$  in all correlations).

150 We used contact sitting as a measure of relationship quality (Massen et al.,  
151 2010) of the dyads in both groups, while keeping it independent from the social  
152 measures (e.g. grooming) used to assess personality (Koski, 2011). Contact sitting and  
153 other proximity measures are reliable proxies to differentiate affiliative relationships  
154 among animals, including kin vs. non-kin (Chapais, 2001; Silk, 2002), and, generally,  
155 'friends' vs. 'non-friends' (Massen et al., 2010; Fraser et al. 2008), and are also  
156 known to be reliable predictors of human friendships (Hinde, 1981) even in  
157 contemporary Western societies (Hill & Dunbar, 2003). We considered contact-sitting  
158 to be an active choice of affiliation of dyads, as it can be very easily refused or broken  
159 by an unwilling partner. We derived dyadic contact-sitting values from focal and scan  
160 data (Martin & Bateson, 1993), corrected by the sampling effort (i.e., dyadic no. of  
161 independent contact sitting occasions divided by dyadic summed observation time  
162 (focal data) or by the total number of scans where both individuals present in group  
163 (scan data).

164 To assess who was contact-sitting with whom, we used both focal and scan  
165 observations. In the first sampling period in Arnhem (June 2002 – August 2004) and  
166 Amersfoort (October 2009 – April 2010), we conducted focal observations on all  
167 adolescent and adult members of the group in 10 min continuous observation sessions  
168 per individual, each observed once a day, four times a week. This added up to 873 hrs  
169 of focal data (mean = 39.7 h/individual) in Arnhem, and 219 h (mean 14.6  
170 h/individual) in Amersfoort. From the focal data we calculated the dyadic summed

**Kommentar [SK3]:** Changed the wording slightly not to give the impression that we would consider bonds in kin to be 'non friendships'



171 contact-sitting occasions divided by the summed dyadic focal minutes. Contact-sitting  
172 was defined as sitting or lying in physical contact with another so that at least one  
173 body part was clearly touching another individual. Usually this involved at least a  
174 whole limb leaning on another individual's body or individuals sitting with sides or  
175 backs against each other. Each occasion of contact sitting was scored only once,  
176 irrespective of its duration (min. 1 min, max. 10 min). Two contact sitting episodes  
177 had to be separated by at least one full minute to be scored as independent occasions.  
178 To keep contact sitting independent of grooming, we considered all grooming as  
179 grooming only and thus did not score this as contact-sitting, also when contact-sitting  
180 led to grooming later, unless the dyad was physically separated in between (min. 1  
181 minute) (Massen *et al.* 2011). At the second sampling period, we conducted time-  
182 sample scan observations (Martin & Bateson 1993) of all independent group members  
183 (i.e., excluding infants) in Arnhem (November 2010 - August 2011) and in  
184 Amersfoort (January 2011 - September 2011). We conducted 2-4 group-scans a day  
185 throughout the day, always with at least one hour in between each scan to assure that  
186 the scans were independent from each other. As before, grooming was only scored as  
187 grooming, and not as contact-sitting. Contact sitting was scored as a separate occasion  
188 in each scan, as the samples were separated by a considerable time gap. We collected  
189 442 scans (110.5 separate days) of the group in Arnhem, and 204 scans (51 separate  
190 days) of the group in Amersfoort. Note, that whilst the measures of personality took  
191 into account the directionality of the behaviour (e.g. grooming given was separate  
192 from grooming received), contact-sitting was scored non-directionally. That is due to  
193 the inherent difficulty to assure with certainty who initiates an approach. A contact  
194 may be preceded by a subtle gaze or other cues, and individuals may also both move  
195 towards each other. Although the question of symmetry in friendships is important

196 and valuable to address (Majolo et al. 2010), we could not account for potential  
197 asymmetry in the initiation of contact-sitting.

198 We standardized the raw contact-sitting data into z-scores (per zoo) before  
199 pooling the data of the two zoos. Furthermore, we added five to each z-score to obtain  
200 positive values only, and thereafter log transformed these dyadic data to create a  
201 normal distribution.

202 Owing to demographic changes, the sample sizes differed between analyses.  
203 In the analysis of the effects of the *social* personality traits on friendship  $N = 37$  (8  
204 males, 29 females); in the analysis of the effects of the *non-social* personality traits on  
205 friendship  $N = 29$  (6 males, 23 females). For each individual we calculated per period,  
206 which of its non-kin group members were in its Upper and Lower Quartile (UQ & LQ  
207 respectively) with regard to contact-sitting. Since individuals may differ in the degree  
208 of contact sitting preferences (i.e., they sit in contact frequently with many  
209 individuals, or sit in contact very frequently with few individuals), individuals had a  
210 different number of individuals in their UQ and LQ (UQ: Mean = 3.4, Range = 1-6;  
211 LQ: Mean = 3.5, Range = 1-6). To assess individuals' personality similarity with their  
212 friends and non-friends from each individual's personal perspective, we compared  
213 pair-wise the mean absolute difference in personality scores between an individual  
214 and its UQ non-kin animals ('friends'), with that between the individual and its non-  
215 kin LQ animals ('non-friends'), using Wilcoxon signed ranks tests. The analysis was  
216 repeated for every personality dimension, using the time-corresponding friendship  
217 classification.

218 Next, we used Linear Mixed Models (LMM) to assess the influence of dyadic  
219 sex-combination, absolute age difference, maternal relatedness, and the absolute  
220 differences in personality scores on friendship. Maternal relatedness was based on

221 known pedigrees (i.e., mother-offspring relationships) and was entered as Sewall  
222 Wright's (1922) coefficient of relatedness  $r$ , ranging between 0.125 and 0.5 (Hamilton  
223 1964; Chapais 2001; Silk 2002). The dyadic contact-sitting score was the response  
224 variable. Sex-combination was entered into the LMM as a fixed factor and age  
225 difference, maternal relatedness and the differences in personality scores as fixed  
226 covariates. In addition, the location (Zoo) and the two subjects of each dyad were  
227 entered as random factors. We ran two sets of models, the first with the social  
228 personality scores and the corresponding contact-sitting scores, and the second with  
229 the non-social personality scores and the corresponding contact-sitting scores. We ran  
230 the models including all two-way interaction effects and reduced the models by  
231 excluding non-significant interaction effects. The model choice was based on  
232 comparisons of the Akaike Information Criteria (AIC). For reasons of clarity, here we  
233 only present the best fitting models.

234

## 235 **Results**

236 First, we compared the mean absolute difference in personality scores between an  
237 individual and its non-kin friends, i.e., individuals in its upper quartile of contact-  
238 sitting, to those between the individual and its non-kin non-friends, i.e., individuals in  
239 its lower quartile of contact-sitting. We found that friends were significantly more  
240 similar (i.e. had a smaller absolute difference) than non-friends in their scores of  
241 Sociability (Wilcoxon signed ranks test:  $T^+ = 502$ ,  $N = 37$ ,  $P = 0.023$ ) and Boldness  
242 ( $T^+ = 354$ ,  $N = 29$ ,  $P = 0.003$ ) (Fig. 1). We found no difference between friends' and  
243 non-friends' absolute personality difference with regard to personality scores of  
244 Grooming Equity, Anxiety, Positive Affect or Exploration-Persistence ( $P > 0.10$ ).

245           Second, we assessed whether friendship among all dyads, including kin, is  
246 predicted by dyadic similarity in the six personality trait dimensions, age difference,  
247 sex-combination, or relatedness. In the best-fitting model we found one significant  
248 main effect (Table 2). The absolute difference in Sociability had a significant negative  
249 effect on contact sitting; i.e. the more similar two individuals were with regard to  
250 Sociability, the more often they sat together in contact (Fig. 2a). This effect was  
251 similar for both kin and non-kin relationships, although among kin it was stronger, as  
252 indicated by a significant interaction effect (Tables 2 & 3, Fig. 2). Also, there was a  
253 significant interaction effect of Grooming Equity and Boldness with relatedness on  
254 contact sitting: the effect was negative among unrelated individuals, and positive or  
255 neutral among kin. The interaction of Anxiety difference and relatedness showed a  
256 strong positive effect among kin, while among non-kin the relationship was neutral.  
257 However, a more detailed investigation of these interactions per kin-class (i.e.,  $r = 0.5$ ,  
258  $0.25$ , or  $0.125$ ) revealed that the patterns among kin are relatively unclear (see ESM),  
259 and should be taken with caution due to the relatively small samples per kin-class.  
260 Nonetheless, patterns of non-kin differed from those of related individuals.

261           Unfortunately, we could not test the potentially confounding factor of  
262 dominance hierarchy (Silk et al., 2006; 2010a; 2012), because an absence of formal  
263 submission signals among females in these groups prevented a reliable assessment of  
264 the dominance hierarchy. However, in our earlier study we found no relationship  
265 between individuals' estimated, categorical rank positions and personality scores  
266 (Massen et al, 2013). Therefore, the influence of personality similarity on friendship  
267 is unlikely to be mediated by rank.

268

269 **Discussion**

270 We found that similarity in certain aspects of chimpanzee personality influence  
271 dyadic friendship, as assessed by contact sitting. Similar scores in Sociability were  
272 found in both kin and non-kin friends, indicating that similarly sociable individuals  
273 were sitting together, even when controlling for dyadic sex-combination and age  
274 difference. Indeed, sex-combination, age-difference or maternal relatedness did not as  
275 such predict dyadic friendship scores. This corroborates the patterns found in the wild  
276 and in previous captive studies, where strong friendships are found in all sex  
277 combinations, across ages and among both related and unrelated individuals, although  
278 wild females rarely have related adult females on the group, whilst in captivity strong  
279 bonds among related females exist (Koski et al., 2012; Fraser et al., 2008; Mitani,  
280 2009; Nishida & Hosaka, 1996; Langergraber et al., 2007, 2009, 2013; Crockford et  
281 al., 2013). Similarity in Boldness and Grooming Equity also positively influenced  
282 non-kin friendships, but not friendships among kin. Finally, kin friends appeared to  
283 have high dissimilarity regarding Anxiety, although this result should be considered  
284 as tentative.

285 Our measure of Sociability consisted of individual grooming frequency and  
286 duration, and the average number of individuals in close proximity (but not contact-  
287 sitting) per moment in time (see Table 1). The latter represents an individual's  
288 average tendency to be in close proximity to others (within 2m), as it was sampled  
289 only once a day at the beginning of the individual's focal session. As such, sociability  
290 is similar to the human Extraversion, especially its gregariousness facet (Costa &  
291 McCrae, 1992). Human friends are also preferentially similar in Extraversion (Nelson  
292 et al., 2011), further supported by similarity of the dopamine receptor DRD2 genotype  
293 in friendship networks (TaqI A polymorphism: Fowler et al., 2011; but see Boardman  
294 et al., 2012). Interestingly, DRD2 receptor density is associated with social

295 detachment and aloofness (Farde et al., 1997). Thus, a similar gregariousness  
296 tendency appears to be preferred among friends in humans and chimpanzees.

297 An obvious alternative explanation for the chimpanzee pattern may be that  
298 particularly sociable individuals sit together simply because less sociable individuals  
299 avoid them. However, there were also friendships among individuals with similarly  
300 *low* scores of Sociability. Moreover, the same effect was found when comparing the  
301 mean difference in sociability scores of the best and the worst friends at the individual  
302 level. These aspects support our interpretation of preferential association of similar  
303 individuals.

304 Homophily in Boldness and Grooming Equity was found only among non-kin  
305 friends. Similarity in Boldness may be especially beneficial in cooperation,  
306 considering that our measures of Boldness concerned behaviour in a predatory context  
307 (modelled by an artificial leopard and snake). Effective mobbing of a predator  
308 requires coordination and cooperation, which may be facilitated by trust in another's  
309 similarly active participation. Arguably, in this context, the benefit concerns  
310 specifically equally bold individuals, because bolder individuals with a high mobbing  
311 propensity would not benefit from associating with shier individuals with a low  
312 mobbing propensity, whereas shy individuals would benefit from associating with  
313 bolder ones.

314 However, cooperative mobbing is not the only mutually beneficial form of  
315 cooperation in chimpanzees. Friends frequently exchange grooming, coalitionary  
316 support **in conflicts** and, in some populations, meat (captivity: Fraser et al., 2008;  
317 Koski et al., 2011; wild: Mitani, 2006; Gomes & Boesch, 2011). Post-hoc analysis on  
318 coalitionary support revealed that also in the Arnhem chimpanzees assessed in this  
319 study (unfortunately, we did not have appropriate data available for the Amersfoort

320 chimpanzees), friends support each other in conflicts significantly more often than  
321 non-friends (coalition frequency / opportunity to support: UQ vs. LQ of non-kin  
322 contact sitting, Wilcoxon signed ranks:  $T^+ = 90$ ,  $N = 22$ ,  $P = 0.016$ ; Fig. S2).  
323 Therefore, if personality similarity is sufficiently beneficial in some cooperative  
324 contexts, such as grooming and coalitions, the consequent friendship of similar  
325 individuals is beneficial also in other cooperative contexts.

326 We hypothesise that similarity in Boldness, Sociability and Grooming Equity  
327 is adaptive through facilitating mutual benefits in many cooperative situations,  
328 especially among unrelated individuals (see a similar argument for mate choice:  
329 Schuett et al., 2010). In ultimate terms, kin-friendship is favoured by kin selection,  
330 whilst non-kin friendship may gain selective advantage from more reliable  
331 cooperation. This suggestion is supported by theoretical models on the positive effect  
332 of homophily on the maintenance and evolution of cooperation (Riolo et al., 2001;  
333 Rivas, 2009; Chiang & Takahashi, 2011). Similarly bold and **similarly** sociable  
334 individuals may become bonded partners because of increasing trust in each other's  
335 behaviour, promoted either through similar behavioural tendencies that facilitate  
336 reciprocity, maintenance of a similar affective state during interactions, or both.  
337 Indeed, in experimental conditions chimpanzee friends cooperate better than non-  
338 friends (Melis et al., 2006), although it is not clear whether this stems from similarity  
339 in personality. In addition, our hypothesis of the evolutionary benefits of homophily is  
340 consistent with the positive group-level assortment with regard to boldness in fish  
341 (Croft et al., 2009; Schürch et al., 2010), and the similarity in personality of mating  
342 partners in many species (Dingemanse et al., 2004; Both et al., 2005; Sin et al., 2006;  
343 Schuett et al., 2011; Gabriel & Black, 2012). For example, zebra finches actively  
344 choose males that have a similar personality to their own (Schuett et al., 2011a), and

345 in an independent study pairs with a similar personality raised chicks in better  
346 condition than those with a different personality, and the effect was not dependent on  
347 genetic factors (Schuett et al., 2011b). Our results suggest that homophily in  
348 personality regarding coordination and cooperation are not limited to mating pairs, but  
349 may apply to beneficial social relations in general. It would be informative to assess  
350 whether similar homophily among cooperative friends is also found in the wild  
351 chimpanzees, where forms of cooperation include behaviours less common or absent  
352 in captivity (i.e., border patrols, inter-group encounters, hunting).

353 Considering further the found similarities with human friendship preference,  
354 in addition to the preferred similarity in gregariousness among friends, also similarity  
355 in boldness among unrelated friends agrees with the human data. In humans,  
356 boldness/shyness in the social realm is a characteristic of the Extraversion construct,  
357 similarly to gregariousness. In addition, also some of the absent effects in our study  
358 show some intriguing similarity to those found in humans. Namely, we found no  
359 effect of dyadic similarity or difference in Exploration-Persistence among friends.  
360 Our measure of Exploration-Persistence is close to the human constructs Openness  
361 (which includes intellectual curiosity) and Conscientiousness (which includes  
362 deliberation and self-control). Similarity in Openness is found among human friends,  
363 but it is hypothesised to influence friendship mainly via similar vocational choices  
364 and interests (McCrae, 1996). Similarity in Conscientiousness is not found to  
365 influence friendship choice in young adults (Selfhout et al., 2010), although  
366 individual's Conscientiousness and similarity in Conscientiousness is associated  
367 positively with friendship quality (Kurtz & Sherker, 2003; Jensen-Campbell &  
368 Malcolm, 2007). Moreover, we found no effect of similarity in Anxiety on friendship,  
369 nor is it found in human Neuroticism (which concerns both baseline and reactive



370 proneness to stress, and overall emotionality; Costa & McCrae 1992). Thus, it appears  
371 that what draws and keeps friends together in both chimpanzees and humans is  
372 similarity in gregariousness, assertiveness and boldness, but not in persistence and  
373 goal-orientation or curiosity.

374 However, in humans there is also a known effect of dissimilarity in  
375 friendships, which may be beneficial due to friends adopting complementary roles and  
376 thus avoiding competition (niche specialization: humans: Hruschka, 2010; see  
377 psychological support in complementary roles: Nelson et al. 2011; in other social  
378 animals: Bergmüller & Taborsky, 2010). In collaborative work situations, heterophily  
379 appears to increase benefit for collaborative interaction partners by complementation  
380 of individual skills to the collective benefit (Rivera et al. 2010). However, such  
381 multiparty collaborations do not exist in chimpanzees, and in dyadic friendships niche  
382 specialization is rather unlikely, considering the types of behaviours that chimpanzee  
383 friends cooperate in. Accordingly, we found no heterophily effects, apart from a  
384 tentative one regarding Anxiety among related friends, apparently driven by mother-  
385 offspring relationships (Fig. S1). However, this is to be interpreted with great caution  
386 due to a small number of mother-offspring dyads in the data. Whilst intriguing and  
387 worth addressing in further studies, homophily appears to be a stronger determinant  
388 than heterophily of friendships in these groups of chimpanzees. We hypothesise that it  
389 is because of homophily's benefits in dyadic cooperative contexts. In humans, it is  
390 consistently found that dyadic friendships are characterised by tolerance to imbalance  
391 of exchanged favours and by less active tracking of those favours than with non-  
392 friends (e.g. Xue & Silk, 2012; Hruschka, 2010), which likely promotes coordination  
393 and commitment to enhance reliable cooperation whilst it relaxes the need to keep

394 track of the exchanges. It is plausible that homophily brings forward similar  
395 psychological and evolutionary benefits also in chimpanzees.

396         Regarding proximate mechanisms of friendship formation, homophily may be  
397 more relevant for non-kin, because relatives are likely to bond through long-term  
398 familiarity, whilst unrelated individuals may engage in active friendship formation  
399 based on the other's characteristics (cf. Schuett et al., 2011a). Alternatively,  
400 assortment based on personality may be passive, because bold and sociable  
401 individuals are more likely to establish relationships with anyone, and thus more  
402 likely to find each other. Conversely, shier and less sociable individuals interact with  
403 others less frequently, but when they bond, they are more likely to seek similarly shy  
404 and 'aloof' individuals. If similarity thereafter promotes mutually beneficial  
405 interactions, it maintains durable bonds.

406         A cautionary note concerns the difficulty to disentangle causality in our data:  
407 do chimpanzees choose friends of similar personality, or do chimpanzees that are  
408 close with each other develop similar personalities? For example, in humans  
409 perceived similarity in personality enhances friendship intensity, yet in turn, the  
410 intensity of friendship also enhances the perceived similarity in personality (Selfhout  
411 et al., 2009; Linden-Andersen et al., 2009). However, in our data homophilic  
412 preferences were less apparent among related individuals who nonetheless are often in  
413 each other's proximity, which suggests that friends were chosen according to their  
414 similarity in personality and not the other way around. In addition, personality is  
415 known to be heritable (Penke et al., 2007; Tschirren & Bensch, 2010) and remarkably  
416 stable within life-phases (chimpanzees: Koski, 2011; humans: Caspi et al., 2005),  
417 which also supports the causal effect of similarity.

418         To conclude, we found that chimpanzee friendships are determined by

419 similarity in personality, specifically in Sociability, Boldness, and Grooming Equity.  
420 We suggest that similarity in these personality traits is adaptive, because it may  
421 enhance partner reliability in cooperative interactions, including grooming,  
422 cooperative defence, and coalitionary support in aggression. Similarity in these  
423 characteristics may be especially relevant in bonds among unrelated individuals. Our  
424 results resemble homophily found in human friendships. This suggests that the  
425 mechanisms of friendship formation and/or maintenance are similar in ourselves and  
426 our closest living relatives.

427

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440

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661

662 **Table 1.** Behaviours that characterize the personality dimensions used in this study.  
 663 Each dimension is an independent factor in a factor analysis (social behavioural  
 664 syndromes) or a principal component analysis (non-social behavioural syndromes).  
 665 The factors are derived based on a parallel analysis. The traits that loaded negatively  
 666 in the analysis are indicated here as their polar opposites (i.e. negative loading of  
 667 ‘aggression’ is here ‘non-aggression’ and negative loading of ‘activity’ is here  
 668 ‘inactivity’). All variables in the analyses are repeatable and based on behavioural  
 669 observations (social traits) and experiments (non-social traits).  
 670

Social behavioral syndromes*				Non-social behavioral syndromes <sup>5</sup>	
Sociability	Positive affect	Anxiety	Grooming Equity	Exploration-Persistence	Boldness
Frequency of grooming given and received (to all partners, analysed as separate variables)  Average no. of inds. in 2m proximity but not in contact with the focal individual	Frequency of play initiated and joined (incl. social and autoplay)  Frequency of hugs, kisses, gentle touches, finger-to-mouth	Self-scratching  Self-grooming  Non-aggression	Grooming density (no. of grooming partners out of all available partners)  Grooming diversity (skew of grooming given)**  Inactivity	No. of approaches to, and time spent in proximity of novel objects and puzzles  Time spent manipulating devices  No. of tools used and modified in foraging tasks	No. of approaches to predator models  Time in proximity of predator models

671 \* Data published in Koski (2011); the variable loadings in the FA including also the Amersfoort  
 672 chimpanzees is shown in SEM (see Table S2).

673 \*\* not measured in Amersfoort, thus excluded in the current analyses.

674 <sup>5</sup> Data published in Massen et al. (2013).  
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677

678 **Table 2.** The best-fitting model showing the factors influencing the log of the standardized  
679 dyadic contact-sitting frequency during the study period in which the *social* personality scores  
680 were obtained, assessed with a Linear Mixed Model (LMM). Dyadic sex-combination was  
681 entered as a fixed factor, and absolute age difference, maternal relatedness of the dyad (as the  
682 real  $r$ , ranging between 0.0125 and 0.5 (Chapais, 2001; Silk, 2002)), and the dyadic absolute  
683 differences in personality scores were fixed covariates. Additionally, all two-way interactions  
684 between dispositional (personality) effects and non-dispositional (age, sex and relatedness)  
685 effects were tested in the full model, and Zoo, individual A of the dyad and Individual B of  
686 the dyad were entered as random factors.

Fixed Variable	Num. df	Denom. df	$\eta^2 \pm SE$	<i>F</i>	<i>P</i>
Maternal Relatedness	1	309.0	0.111±0.07	2.42	0.120
Sex Combination	2	142.8	-0.010±0.02 0.007±0.02	1.18	0.309
Age Difference	1	307.7	-0.000±0.00	1.24	0.266
Difference in Sociability	1	219.9	-0.043±0.02	7.64	<b>0.006</b>
Difference in Grooming Equity	1	220.5	-0.002±0.01	0.03	0.871
Difference in Anxiety	1	232.8	0.006±0.01	0.52	0.472
Difference in Positive affect	1	142.5	-0.006±0.01	0.42	0.520
Relatedness*Diff. Sociability	1	317.0	-0.491±0.19	6.86	<b>0.009</b>
Relatedness*Diff. Grooming Eq.	1	313.6	0.260±0.09	8.05	<b>0.005</b>
Relatedness*Diff. Anxiety	1	298.4	0.354±0.11	10.93	<b>0.001</b>
Relatedness*Diff. Positive affect	1	304.1	0.098±0.06	2.79	0.096

687

688

689

690 **Table 3.** The best-fitting model showing the factors influencing the log of the standardized  
 691 dyadic contact sitting frequency during the study period in which the *non-social* personality  
 692 scores were obtained, assessed with a Linear Mixed Model (LMM). The full model was  
 693 similar to the one with social personality scores (Table 1).

<b>Fixed Variable</b>	<b>Num. df</b>	<b>Denom. df</b>	<b><math>\beta \pm SE</math></b>	<b>F</b>	<b>P</b>
Maternal Relatedness	1	173.4	0.070±0.06	0.01	0.908
Sex Combination	2	90.3	0.018±0.03 -0.014±0.03	2.35	0.101
Age Difference	1	186.3	-0.000±0.00	0.33	0.564
Difference in Exploration	1	187.4	0.002±0.01	0.10	0.754
Difference in Boldness	1	175.5	-0.008±0.01	1.42	0.235
Relatedness*Diff. Boldness	1	173.2	0.119±0.05	6.76	<b>0.010</b>

694  
 695

696 **Figure legends**

697 **Figure 1.** Mean absolute difference in individual personality scores of individuals'  
698 a) Sociability (individual score range: -1.87 - -0.09), and b) Boldness  
699 (score range : -1.64 – 2.64), with those non-kin individuals that are in each  
700 individual's Upper Quartile of contact sitting; i.e. friends (UQ), and with  
701 those non-kin individuals that are in each individual's Lower Quartile of  
702 contact sitting; i.e. non-friends (LQ). \*  $P < 0.05$

703

704 **Figure 2.** Relation between Contact-sitting (log of standardized values) and the  
705 absolute difference in dyadic personality scores of a) Sociability, b)  
706 Grooming Equity, c) Anxiety, and d) Boldness, and the effect of maternal  
707 relatedness on this relation.