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

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Abstract

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

Keywords: Chimpanzees, Friendship, Personality, Homophily Principle, Cooperation.

Introduction

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

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

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

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

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

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

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

Methods

Subjects and housing

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

Both groups were housed in zoo facilities containing an inside and an outside enclosure (Arnhem: inside: 368 m², outside: 0.7 ha; Amersfoort: inside: 96 m², outside: 475 m²) enriched with climbing facilities, nets, hay and other enrichment items such as footballs and cloths. In both zoos the animals were fed several times a day, with a diet consisting of fruit, vegetables, bread and seeds.

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

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

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

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

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

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

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

Results

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

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

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

Discussion

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

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

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

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

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

However, cooperative mobbing is not the only mutually beneficial form of cooperation in chimpanzees. Friends frequently exchange grooming, coalitionary support **in conflicts** and, in some populations, meat (captivity: Fraser et al., 2008; Koski et al., 2011; wild: Mitani, 2006; Gomes & Boesch, 2011). Post-hoc analysis on coalitionary support revealed that also in the Arnhem chimpanzees assessed in this 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

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

Considering further the found similarities with human friendship preference, in addition to the preferred similarity in gregariousness among friends, also similarity in boldness among unrelated friends agrees with the human data. In humans, boldness/shyness in the social realm is a characteristic of the Extraversion construct, similarly to gregariousness. In addition, also some of the absent effects in our study show some intriguing similarity to those found in humans. Namely, we found no effect of dyadic similarity or difference in Exploration-Persistence among friends. Our measure of Exploration-Persistence is close to the human constructs Openness (which includes intellectual curiosity) and Conscientiousness (which includes deliberation and self-control). Similarity in Openness is found among human friends, but it is hypothesised to influence friendship mainly via similar vocational choices and interests (McCrae, 1996). Similarity in Conscientiousness is not found to influence friendship choice in young adults (Selfhout et al., 2010), although individual's Conscientiousness and similarity in Conscientiousness is associated positively with friendship quality (Kurtz & Sherker, 2003; Jensen-Campbell & Malcolm, 2007). Moreover, we found no effect of similarity in Anxiety on friendship, 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

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

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

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

To conclude, we found that chimpanzee friendships are determined by

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

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

Social behavioral syndromes*				Non-social behavioral syndromes [§]	
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

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

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

[§] Data published in Massen et al. (2013).

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

Fixed Variable	Num. df	Denom. df	² ±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	0.006
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	0.009
Relatedness*Diff. Grooming Eq.	1	313.6	0.260±0.09	8.05	0.005
Relatedness*Diff. Anxiety	1	298.4	0.354±0.11	10.93	0.001
Relatedness*Diff. Positive affect	1	304.1	0.098±0.06	2.79	0.096

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

Fixed Variable	Num. df	Denom. df	² ±SE	F	P
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	0.010

Figure legends

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

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