Original Article

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.

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1. Introduction

Many social animals have marked preferences for particular individuals in their group, and these close social associations are referred to as friendships (Garber, 2008; Massen, Sterck, & de Vos, 2010; Schusterman, Reichmuth, & Kastak, 2000; Seyfarth & Cheney, 2012; Smuts, 1985). Comparable to human friendships, animal friendships are stable over time in several species (Massen & Sterck, 2013; Silk, Alberts, & Altmann, 2006; Silk et al., 2010a), including male–male and female–female friendships of wild and captive chimpanzees, *Pan troglodytes* (Koski, de Vries, van de Kraats, & Sterck, 2012; Langergraber, Mitani, & Vigilant, 2009; Mitani, 2009). 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 (Cameron, Setsaas, & Linklater, 2009; Frére et al., 2010; Silk, Alberts, & Altmann, 2003; Silk et al., 2009). Male–female friendships also increase infant survival (Huchard et al., 2013; Palombit, Seyfarth, & Cheney, 1997), and both male–female and male–male friendships can enhance male mating access or success (Connor, Heithaus, & Barre, 2001; Kulik, Muniz, Mundry, &

Widdig, 2011; Langergraber, Mitani, Watts, & Vigilant, 2013; Massen et al., 2012; Nishida & Hosaka, 1996; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Smuts, 1985).

However, what determines who is friends with whom is unclear. Some studies report that friendships are characterized by kinship (Chapais, 2001; Silk, 2002; Silk et al., 2006, 2010a; Silk, Alberts, Altmann, Cheney, & Seyfarth, 2012), rank- or age similarity (Silk et al., 2006, 2010a, 2012). Kinship-based friendship is likely formed through familiarity, Kinship-base friendship is likely formed through familiarity, and as relatedness favours cooperation through kin selection, the most commonly found form of friendship is that among kin. 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 (Langergraber et al., 2009; Mitani, 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

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(McPherson, Smith-Lovin, & Cook, 2001). Homophily among friends is described regarding age, ethnicity, class, education, interests (Marsden, 1988; McPherson et al., 2001; Shrum, Cheek, & MacD, 1988), and certain personality traits (Izard, 1960). Extraversion, Agreeableness and Openness (Digman, 1990) predicts friendships in adolescents and young adults (Nelson, Thorne, & Shapiro, 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 (Chiang & Takahashi, 2011; de Waal & Luttrell, 1988; Riolo, Cohen, & Axelrod, 2001; Rivas, 2009). 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, Both, Drent, & Tinbergen, 2004; Both, Dingemanse, Drent, & Tinbergen, 2005; Schuett, Tregenza, & Dall, 2010; Schuett, Godin, & Dall, 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, Silk, & Cheney, 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 affinitive 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 (Langergraber et al., 2009; Mitani, 2009), but male–female friendships also occur, both in the wild (Langergraber, Mitani, Watts, & Vigilant, 2010, Langergraber et al., 2013) and in captivity (Fraser, Schino, & Aureli, 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, Mitani, & Vigilant, 2007, Langergraber et al., 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.

2. Methods

2.1. 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 m^2, outside: 0.7 ha; Amersfoort: inside: 96 m^2, outside: 475 m^2) 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.

2.2. Measures and analyses

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

In addition, with targeted behavioural experiments on the same chimpanzees (10 experiments of novel object, novel food, predator models and foraging puzzles), Massen et al. (2013) identified several repeatable and contextually consistent variables. The experiments were performed in a group setting to enhance ecological validity; the results were not influenced by monopolisation of the devices, by rank or by sex (Massen et al., 2013). The variables formed two factors: Exploration Tendency-Persistence and Boldness (see Table 1 for the variables). The individual factor scores of these two factors were used in the current study as the *non-social* individual personality scores. The *social* personality trait scores were independent from the *non-social* personality trait scores (Spearman rank order correlations, range from r $= -0.31$ to r $= 0.12$, $P > 0.10$ in all correlations).

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

Table 1
Behaviours that characterize the personality dimensions used in this study.

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)	Frequency of play initiated and joined (incl. social and autoplay)	Self-scratching	Grooming density (no. of grooming partners out of all available partners)	No. of approaches to, and time spent in proximity of novel objects and puzzles	No. of approaches to predator models
Average no. of inds. in 2 m proximity but not in contact with the focal individual	Frequency of hugs, kisses, gentle touches, finger-to-mouth	Self-grooming	Grooming diversity (skew of grooming given)[**]	Time spent manipulating devices	Time in proximity of predator models
		Non-aggression	Inactivity	No. of tools used and modified in foraging tasks	

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).

[*] 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).

occasions divided by dyadic summed observation time (focal data) or by the total number of scans where both individuals were present in group (scan data).

To assess who was contact-sitting with whom, we used both focal and scan observations. In the first sampling period in Arnhem (June 2002–August 2004) and Amersfoort (October 2009–April 2010), we conducted focal observations on all adolescent and adult members of the group in 10 min continuous observation sessions per individual, each observed once a day, four times a week. This added up to 873 h of focal data (mean = 39.7 h/individual) in Arnhem, and 219 h (mean 14.6 h/individual) in Amersfoort. From the focal data we calculated the dyadic summed contact-sitting occasions divided by the summed dyadic focal minutes. Contact-sitting was defined as sitting or lying in physical contact with another so that at least one body part was clearly touching another individual. Usually this involved at least a whole limb leaning on another individual's body or individuals sitting with sides or backs against each other. Each occasion of contact sitting was scored only once, irrespective of its duration (min. 1 min, max. 10 min). Two contact sitting episodes had to be separated by at least one full minute to be scored as independent occasions. To keep contact sitting independent of grooming, we considered all grooming as grooming only and thus did not score this as contact-sitting, also when contact-sitting led to grooming later, unless the dyad was physically separated in between (min. 1 minute) (Massen, Luyten, Spruijt, & Sterck, 2011). At the second sampling period, we conducted time-sample scan observations (Martin & Bateson, 1993) of all independent group members (i.e., excluding infants) in Arnhem (November 2010 - August 2011) and in Amersfoort (January 2011–September 2011). We conducted 2–4 group scans a day throughout the day, always with at least one hour in between each scan to assure that the scans were independent from each other. As before, grooming was only scored as grooming, and not as contact-sitting. Contact sitting was scored as a separate occasion in each scan, as the samples were separated by a considerable time gap. We collected 442 scans (110.5 separate days) of the group in Arnhem, and 204 scans (51 separate days) of the group in Amersfoort. Note, that whilst the measures of personality took into account the directionality of the behaviour (e.g. grooming given was separate from grooming received), contact-sitting was scored non-directionally. That is due to the inherent difficulty to assure with certainty who initiates an approach. A contact may be preceded by a subtle gaze or other cues, and individuals may also both move towards each other. Although the question of symmetry in friendships is important and valuable to address (Majolo, Ventura, & Schino, 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), and 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 and 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 (Chapais, 2001; Hamilton, 1964; 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.

3. 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
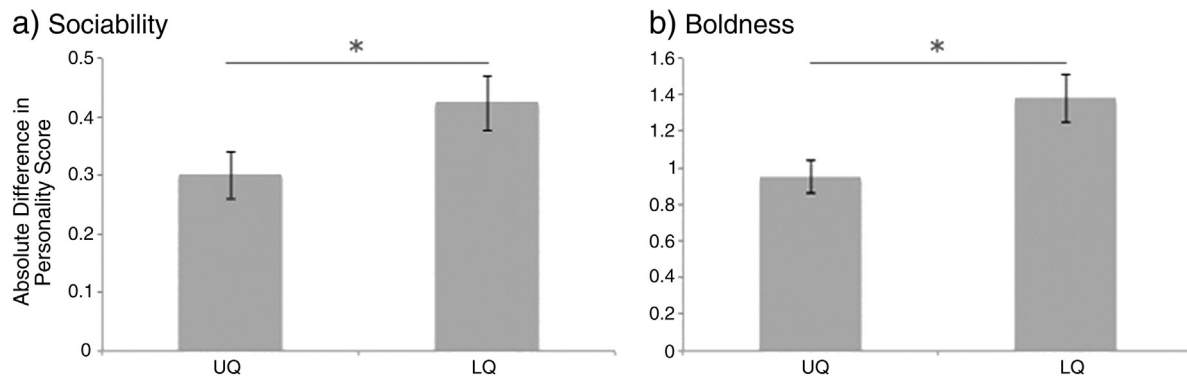
Fig. 1. Mean absolute difference in individual personality scores of individuals' a) Sociability (individual score range: −1.87 to −0.09), and b) Boldness (score range: −1.64−2.64), with those non-kin individuals that are in each individual's Upper Quartile of contact sitting; i.e. friends (UQ), and with those non-kin individuals that are in each individual's Lower Quartile of contact sitting; i.e. non-friends (LQ). *$P < 0.05$.

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 (Table 2, 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 (Tables 2 and 3, Fig. 2). 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.

4. 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 in the group, whilst in captivity strong bonds among related females exist (Crockford et al., 2013; Fraser et al., 2008; Koski et al., 2012; Mitani, 2009; Nishida & Hosaka, 1996; Langergraber et al., 2007, 2009, 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 2 m), 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, Settle, &

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).

Fixed variable	Num. df	Denom. df	β ± SE	F	P
Maternal relatedness	1	309.0	0.111 ± 0.07	2.42	0.120
Sex combination	2	142.8	−0.010 ± 0.02	1.18	0.309
			0.007 ± 0.02		
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

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.
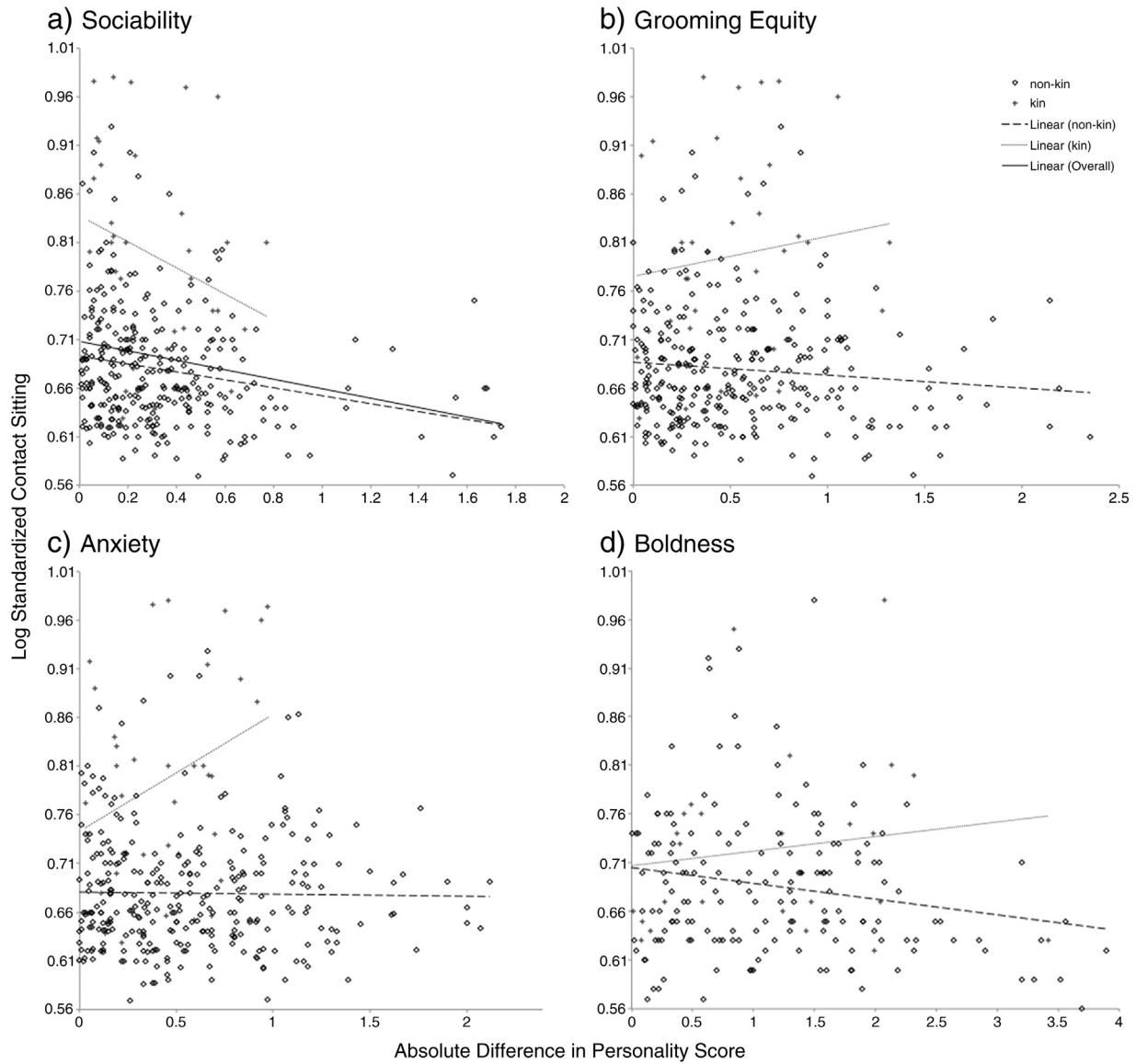Bold typeface indicates significance at the level alpha < 0.05.

Fig. 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.

Christakis, 2011; but see Boardman, Domingue, & Fletcher, 2012). Interestingly, DRD2 receptor density is associated with social detachment and aloofness (Farde, Gustavsson, & Jönsson, 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

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).

Fixed variable	Num. df	Denom. df	$\beta \pm$ 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	2.35	0.101
			-0.014 ± 0.03		
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**

The full model was similar to the one with social personality scores (Table 2).

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

We hypothesise that similarity in Boldness, Sociability and Grooming Equity is adaptive through facilitating mutual benefits in many cooperative situations, especially among unrelated individuals (see a similar argument for mate choice: Schuett et al., 2010). In ultimate terms, kin-friendship is favoured by kin selection, whilst non-kin friendship may gain selective advantage from more reliable cooperation. This suggestion is supported by theoretical models on the positive effect of homophily on the maintenance and evolution of cooperation (Riolo et al., 2001; Rivas, 2009; Chiang & Takahashi, 2011). Similarly bold and similarly sociable individuals may become bonded partners because of increasing trust in each other's behaviour, promoted either through similar behavioural tendencies that facilitate reciprocity, maintenance of a similar affective state during interactions, or both. Indeed, in experimental conditions chimpanzee friends cooperate better than non-friends (Melis, Hare, & Tomasello, 2006), although it is not clear whether this stems from similarity in personality. In addition, our hypothesis of the evolutionary benefits of homophily is consistent with the positive group-level assortment with regard to boldness in fish (Croft et al., 2009; Schürch, Rothenberger, & Heg, 2010), and the similarity in personality of mating partners in many species (Dingemanse et al., 2004; Both et al., 2005; Sinn, Apiolaza, & Moltschaniwskyj, 2006; Schuett, Godin, & Dall, 2011; Gabriel & Black, 2012). For example, zebra finches actively choose males that have a similar personality to their own (Schuett, Dall, & Tregenza, 2011), 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, Godin, & Dall, 2011). Our results suggest that homophily in personality regarding coordination and cooperation is 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 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 proneness to stress, and overall emotionality; Costa & McCrae, 1992). Thus, it appears that what draws and keeps friends together in both chimpanzees and humans is similarity in gregariousness, assertiveness and boldness, but not in persistence and goal-orientation or curiosity.

However, in humans there is also a known effect of dissimilarity in friendships, which may be beneficial due to friends adopting complementary roles and thus avoiding competition (niche specialization: humans: Hruschka, 2010; see psychological support in complementary roles: Nelson et al., 2011; in other social animals: Bergmüller & Taborsky, 2010). In collaborative work situations, heterophily appears to increase benefits for collaborative interaction partners by complementation of individual skills to the collective benefit (Rivera, Soderstrom, & Uzzi, 2010). However, such multiparty collaborations do not exist in chimpanzees, and in dyadic friendship niche specialization is rather unlikely, considering the types of behaviours that chimpanzee friends cooperate in. Accordingly, we found no heterophily effects, apart from a tentative one regarding Anxiety among related friends, apparently driven by mother-offspring relationships (Fig. S1). However, this is to be interpreted with great caution due to a small number of mother-offspring dyads in the data. Whilst intriguing and worth addressing in further studies, homophily appears to be a stronger determinant than heterophily of friendships in these groups of chimpanzees. We hypothesise that it is because of homophily's benefits in dyadic cooperative contexts. In humans, it is consistently found that dyadic friendships are characterised by tolerance to imbalance of exchanged favours and by less active tracking of those favours than with non-friends (e.g. Hruschka, 2010; Xue & Silk, 2012), which likely promotes coordination 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, Dall, et al., 2011). 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, Denissen, Branje, & Meeus, 2009; Linden-Andersen, Markiewicz, & Doyle, 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, Denissen, & Miller, 2007; Tschirren & Bensch, 2010) and remarkably stable within life-phases (chimpanzees: Koski, 2011; humans: Caspi, Roberts, & Shiner, 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.

Supplementary Materials

Acknowledgments

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