



## Original Article

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

Jorg J.M. Massen<sup>a,\*</sup>, Sonja E. Koski<sup>b,1</sup>

<sup>a</sup> Department of Cognitive Biology, University of Vienna, 1090 Vienna, Austria

<sup>b</sup> Anthropological Institute und Museum, University of Zürich

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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; Frère 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 matrilineal 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

\* Corresponding author. Department of Cognitive Biology, University of Vienna Althanstrasse 14, 1090 Vienna, Austria.

E-mail address: [jorgmassen@gmail.com](mailto:jorgmassen@gmail.com) (J.J.M. Massen).

<sup>1</sup> Shared first authorship due to equal contribution.

(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 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 (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:  $368\text{ m}^2$ , outside:  $0.7\text{ ha}$ ; Amersfoort: inside:  $96\text{ m}^2$ , outside:  $475\text{ m}^2$ ) 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 ( $N_{\text{total}} = 90$ ), 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

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