Master Project submitted to obtain the degree of Master in Biology,
Specialisation: Evolution and Behaviour Biology

The influence of personality on relationship quality in bonobos

Jonas Verspeek

Promoter

Dr. Jeroen Stevens

CRC (KMDA)

In corporation with

Nicky Staes

Faculty of Science

Department of Biology

2014-2015

Universiteit Antwerpen

Acknowledgements

This thesis could never be written without the help of some people which therefore deserve a small but sincere mentioning on this page.

First of all, I would like to thank my promoter Dr. Jeroen Stevens for his help and guidance over the past year. Your advice during the observational period, your help during the analyses and the support I got in the writing process allowed me to experience the first exciting steps of behavioural research. I admire the commitment and fascination you have for all bonobo- and non-bonobo-related matters. Finally, in my opinion, this thesis indicates that even for dyads with low absolute differences in *forgetfulness scores*, informative cooperations can be found.

Next, I thank Nicky Staes, PhD student of Dr. Jeroen Stevens. Thank you for your help during the observational training period, for your statistical suggestions and your feedback on my work.

I am also grateful to the curator and keepers of the bonobos of the Wilhelma (Stuttgart) for allowing me to do observations and for opening the gate at the beginning and the end of each observation day. Also, thank you little happy man for your daily welcome at the Wilhelma zoo.

Then, I would like to thank Simon Braem, a biology student at the Ghent University, for his accompaniment during the observational period and his hilarious comments during the vocal recordings in Stuttgart.

Further, I would like to thank my family for their emotional and financial support and for their patience during the whole writing process. Next to them, I would also thank my friends for their advice and encouragement.

Finally, I am extremely grateful to Elien Romaen who has always been so involved and interested in this thesis and for her support the whole way through .

Table of contents

Abstracts

Human and animal friendships can have important effects on an individuals' fitness. Research usually focusses on how factors like age, sex, kinship, rank and tenure influence the strength of these relationships. Recent studies however suggest that similarity in personality may be a thriving factor as well . In this study we focus on whether homophily in personality, which is the preference to associate with individuals with more similar personalities, has an effect on the strength of relationships between dyads. Traditional studies measure the strength of dyadic friendships using only one or two behaviours, such as the amount of contact-sitting between the two individuals. As friendships are more complex, the use of a composite measure that includes several behaviours at once may be more accurate to describe relationships. To test this, we will measure dyadic friendships using both the conventional measure of contact-sitting, and a composite measure referred to as the relationship quality (RQ) model, which is calculated using principal component analysis (PCA). PCA revealed two components of RQ which were labelled Value, comprising the benefits resulting from relationships, and Compatibility, a measure for tolerance and affiliation between friends. Personality was determined using behavioural observations on 41 adult and adolescent bonobos (15 males, 26 females; aged between 6 and 63 years) housed in 5 European zoos (Frankfurt; Planckendael; Stuttgart; Twycross; Wuppertal). Mean focal time per individual was 17 h. We used factor analaysis to determine personality and found three traits that were labelled: Sociability, Positive Affect and Anxiety. Subsequently, the influence of similarity in these personality traits between friends on contact sitting, relationship Value and relationship Compatibility is determined. Analysis revealed that higher contact sitting and higher relationship Value were present between friends with similar Sociability. Homophily in personality may be adaptive when the relationship investment of both individuals is equal. Consequently, homophily in friendships is an evolutionary conserved trait as it is present in both humans and their closely related living relatives: chimpanzees and bonobos.

Vriendschappen tussen mensen en dieren onderling hebben belangrijke consequenties voor de fitness van de betrokken individuen. De meeste onderzoekers bekijken echter enkel de invloed van dispositionele factoren op deze relaties terwijl persoonlijkheden evenwel een groot effect kunnen hebben. Bovendien maken de meeste studies gebruik van conventionele maten, bestaande uit slechts één gedrag, voor vriendschap. Aangezien individuen in meer dan één aspect verschillen, zou het gebruik van een samengestelde maat voor vriendschap een meer correct resultaat geven. Daarom wordt er in deze studie nagegaan of homofilie in persoonlijkheden, de voorkeur om met vergelijkbare persoonlijkheden om te gaan, in zes verschillende groepen bonobos aanwezig is, door gebruik te maken van zowel een conventionele als een samengestelde maat voor vriendschap. *Principle Component Analysis* (PCA) wordt gebruikt om de componenten van relatiekwaliteit te achterhalen. De componenten Waarde en Compatibiliteit werden gevonden welke respectievelijk de voordelen die uit relaties gehaald kunnen worden en een maat voor de tolerantie en verbondenheid tussen individuen zijn. Zowel de Waarde als de Compatibiliteit van relaties worden gebruikt als samengestelde maat voor vriendschap. Door gebruik te maken van gedragsobservaties werden de persoonlijkheden van 41 adulte en adolescente bonobos (15 mannen, 26 vrouw, leeftdij variëerd van 6 tot 63 jaar) bepaald. Via factor analyse vinden we drie persoonlijkheidsfactoren: *Sociability*, *Positive affect* en *Anxiety*. Verder wordt de invloed van vergelijkbare persoonlijkheden tussen individuen op zowel contact-zitten als de Waarde en Compatibiliteit voor relaties bepaald. Analyses wezen uit dat vrienden met vergelijkbare *Sociability* meer in contact zitten en een hogere relatie Waarde hebben. Homofilie in persoonlijkheden is mogelijks adaptief aangezien reciprociteit in investeringen aan relaties meer betrouwbaar zouden kunnen zijn. Tenslotte blijkt dat homofilie in vriendschappen een gemeenschappelijk kenmerk is voor zowel de mens als zijn nauwe verwanten chimpansees en bonobos.

Human and animal friendships have important effects on different aspects of an individuals' live. However, most researchers only focus on the influence of factors like age, sex, kinship, rank and tenure on these valuable relationships, while similarity in personality may have an important effect as well. Moreover, most studies use measures of friendships which include only few behaviours to determine friendship quality. Since individuals may differ in more than one behaviour, using a composite of several behaviours may therefore be more accurate. In this study homophily in personality, the preference to associate with similar personalities, between dyads, a group of two persons, is studied using both a simple measure consisting of one behaviour, contact sitting, and another consisting of several behaviours. We use a statistical procedure which converts the set of behaviours into a few components of relationship quality. We find two components labelled Value, comprising the benefits resulting from relationships, and Compatibility, a measure for tolerance and affiliation between friends. These components are used as a composite measure of friendship. Further, from the personality analysis, three traits are found: Sociability, Positive Affect and Anxiety. Subsequently, the influence of similarity in these personality traits between friends on contact sitting, relationship Value and relationship Compatibility is determined. Analysis revealed that higher contact sitting and higher relationship Value were present between friends with similar Sociability. Homophily in personality may be adaptive as relationship investment of both individuals may be equal. Consequently, homophily in friendships is a common trait for both humans and closely related chimpanzees and bonobos.

1. Introduction

Darwin's *On the Origin of Species by Means of Natural Selection, Or the Preservation of Favoured Races in the Struggle for Life* (1859) raised the idea of evolution by natural selection. This revolutionary work changed human self-image (Wilson, 2006) and has been seen as one of the most important publications in biology. Phenotypics were seen as the results of the genetic information, the element on which natural selection acts (Bock, 2003; Réale, 2007), while behaviour was considered to be coincidental variation. However, individuals often display consistent differences in behaviour. These differences are present in a wide range of contexts and species (Dall *et al.*, 2004). This variation has long been interpreted as the results of inaccurate measurements or non-adaptive variation around an adaptive mean (Groothuis & Carere, 2005) but now has become a major interest for evolutionary and behavioural biologists (Dall *et al.*, 2004; van Oers *et al.*, 2005; Cote & Clobert, 2007; Wolf *et al.*, 2007; Groothuis & Trillmitch, 2011; Koski, 2011; Dirienzo & Hedrick, 2014). In the last decades, more research has shown that seemingly independent behaviours were linked to one another (Groothuis & Carere, 2005; Groothuis & Trillmitch, 2011). Moreover, these correlated behaviours have important implications for relations between individuals. Recently several studies in humans and non-human primates have found that individuals with higher similarities in these correlated behaviours share more affiliation or have higher quality relationships (McPherson *et al*., 2001; Massen & Koski, 2014; Carter *et al*., 2015; Morton *et al.*, 2015)

1.1. Personality in animals

Consistent physiological or behavioural differences between individuals, consisting of more than one feature, have been classified as temperament, behavioural syndromes, coping styles, coping strategies and personalities (Koolhaas *et al.*, 1999; Dall *et al.*, 2004; Groothuis & Carere, 2005; van Oers *et al*, 2005; Groothuis & Trillmitch, 2011; Koski, 2011). Empirical results from more than 60 species, going from primates to insects, indicate that animal behaviour is indeed less flexible and arbitrary than previously thought (Wolf, *et al*, 2007). Individuals differ in suites of often heritable and correlated traits (Dingemanse *et al.*, 2002). Most investigated personality traits in literature involve risk-taking behaviour because fear has an important survival value in wild animals (Boissy, 1995; Freeman & Gosling, 2010). Boldness towards predators and aggressiveness towards conspecifics for example are two traits that seem to be strongly correlated (Wolf *et al.*, 2007). Risk taking individuals in intraspecific fights will also

risk more against predators. This shy/bold feature has been studied in several species like primates, cats, fishes, birds, reptiles and even in humans (Clarke & Boinski, 1995; Lopez *et al.*, 2003; Ward *et al.*, 2004; Groothuis & Carere, 2005; Sinn *et al.*, 2007; Beaton *et al.*, 2008; Cole & Quinn, 2014; Pritchard *et al.*, 2014).

The adaptive value of animal personalities has long been a mystery. A more flexible structure of behaviour should provide a selective advantage (Coleman & Wilson, 1998; Wilson, 1998; Dall *et al.*, 2004; Bergmüller *et al.*, 2010; Koski, 2011). In contrast, Wolf *et al.* (2007) showed that animal personalities could be adaptive. Their theory was based on the fact that individuals put different effort in current and future reproduction. Following life-history theory, individuals should adjust their risk-taking behaviour to their expected future fitness (Clark, 1994). Therefore, individuals with low reproductive expectations should be relatively shy and risk-prone because they have little to lose (Wolf *et al.*, 2007).

Personality in a social context has an important consequence for group living animals. However, less research is done on personality differences in social behaviour (Koski, 2011). An individual's reaction to the presence or absence of conspecifics and the tendency to seek other's proximity is called Sociability (Koksi, 2011). Group composition in sticklebacks (Ward *et al.*, 2004), cooperation in several species (Bergmüller *et al.*, 2004), likelihood of having children and sexual activity in humans (Nettle, 2005; Jokela *et al.*, 2009) are different aspects that are influenced by Sociability. In baboons, more sociable females experience lower glucocorticoid levels, reproduce more successfully and have higher lifetime fitness than non-sociable females (Silk, 2002; Silk *et al.*, 2007; Silk *et al.*, 2009). Consequently, personalities greatly influence social relationships between individuals.

1.1.1. Measuring personality in animals

Different methods of data collection have been used over time to measure personality. Traditional personality studies commonly use subjective rating methods (Freeman & Gosling, 2010; Freeman *et al.*, 2011; Watters & Powell, 2012). People, familiar with the study object, rate the animals on a set of traits or adjectives. These terms are typically accompanied by clarifying definitions. This method takes variability due to noise as well as cross-situational consistency into account. However, the subjective judgement by the observer and the difficulty to interpret comparisons between individuals belonging to different groups along with the fact that raters may give more weight to salient events make this method less suitable than behavioural coding. The latter involves observing animals and recording their behaviour in

terms of bout frequencies or duration. This observational method requires less subjective judgement by the observer and makes it a lot easier to make direct comparisons between animals. On the other hand, it's a very time consuming process (Freeman *et al.*, 2011). Behavioural coding is used in 74% of the published personality studies (Watters & Powell, 2012). Both methods can be used in naturalistic and experimental conditions. In experimental studies, animals are observed in response to a particular stimulus or experiment (Freeman & Gosling, 2010).

In psychology, personality studies often yield multidimensional models like for example the Five-Factor model in humans (Digman, 1990; Goldberg *et al*, 1996; Massen *et al.*, 2013). Each of the following five dimensions or factors comprises more smaller traits: 1) Extraversion, 2) Agreeableness, 3) Conscientiousness, 4) Emotional Stability (or sometimes Neuroticism) and 5) Intellect (or imagination or openness) (Goldberg *et al.*, 1996).

However in behavioural ecology, previous studies on animal personalities commonly focus on single behavioural dimensions such as shy and bold (Gosling, 2001) or behaviours like contact-sitting (Massen *et al.*, 2013). Recently, more studies implement different behavioural variables to obtain multi-dimensional personalities (e.g. Koski, 2011).

1.1.2. Personality in primates

Non-human primate personality has received an increasing interest (Pritchard *et al.*, 2014). Research on this matter is strategically important because of the recent evolutionary split between non-human primate species and humans. Therefore several personality traits may be homologous between these taxonomic groups. Research on nonhuman primate personality started in the 1930s with Crawford (1938) developing a reliable rating scale to assess personality of chimpanzees. In 1940 Yerkes determined chimpanzee personality by recording the frequency and duration of different behaviours in a natural setting. After this influencing work, other studies of primate personality were still uncommon until the 1960s and 70s. In the 1990s, Jane Goodall described the personalities of wild chimpanzees. Her findings were criticized as being anthropomorphic (Weiss *et al.*, 201). Decades later, other critics like Uher (2008) and Wynne (2009) state that assigning human-like traits like personality to animals is contaminated by anthropomorphism. However, no empirical studies support these claims (Weiss *et al.*, 2012).

In the last two decades, more studies focused on differences in personality in great apes (Uher & Asendorf, 2007; Uher *et al.*, 2007; Freeman & Gosling, 2010; Massen *et al.*, 2013).

Freeman and Gosling's review (2010) revealed that of all 496 (or more) primate species (Species Survival Commision, 2015), only 28 (7%) have been studied in relation to personality. Moreover, of the 28 studied species, the representation is strongly biased towards just a few. Namely, the rhesus macaque was studied in 40% of the reviewed articles. This is due to the fact that this primate species is commonly found in laboratory settings because of its physiological and anatomical similarity to humans and the ease with which it can be maintained and bred (Mitruka, 1976). Chimpanzees (21%) are the second most commonly studied species in primate research. Baboons (6%) and vervet monkeys (5%) are two other primate species were a lot of research has been done on personality differences.

In 1938 Meredith P. Crawford introduced a rating scale for determining personality in chimpanzees. This was one of the first articles studying individual differences in nonhuman primates. However, further research on this matter only flourished in the 1980s (Freeman & Gosling, 2010). As in all personality studies, the first assessment methods used subjective rating to determine personality in chimpanzees (Bard & Gardner, 1996; King & Figueredo, 1997; Freeman & Gosling, 2010; Massen *et al.*, 2013). These results showed that chimpanzee personalities consist of one chimpanzee-specific trait named Dominance and a five factor construct comparable to the human five-factor model (King & Figueredo, 1990): Agreeableness, Conscientiousness, Extraversion, Neuroticism and Openness (Digman, 1990; King & Figueredo, 1990; Weiss, 2012). Chimpanzee personalities therefore contain several social as well as non-social factors.

Behavioural measures were needed to complement these subjective ratings and to compare with non-primate species (Weiss *et al.*, 2013). Early studies on personality in chimpanzees only included young individuals or small sample sizes (e.g. Anestis et al., 2005). Others didn't even assess the basic criteria for personality such as temporal repeatability or contextual consistency (Massen *et al.*, 2013). The first broad-scale behavioural study on chimpanzee personality was performed by Koski (2011). She included 75 chimpanzees of both sexes from multiple captive populations and found 15 repeatable behavioural variables. Further, within-individual consistency and between-individual variation in a range of ecologically and evolutionary relevant social behavioural patterns were measured. All behavioural variables were structured into five independent dimensions: Sociability, Positive Affect, Equitability, Anxiety and Activity.

1.2. Friendships in animals

Using this 'F'-word implies that the close and affiliative bonds between animals are roughly analogous to human friendships and serve similar emotional, psychological and adaptive functions (Silk, 2002). However, in this study, the word friendship will be used as a synonym for the close and affiliative bonds between animals without referring to the anthropological features of human friendships.

For group living animals, reproductive success is strongly influenced by social interactions. The presence of familiar conspecifics for example buffers the effect of induced stress (Seeman & McEwen, 1996) and lowers the basal cortisol levels in male baboons (Sapolsky *et al.*, 1997). Most primate species therefore live in social groups. It is important to notice that sociality will only evolve if the benefits of close associations will exceed the costs of group living, such as competition between group members over food or safety. Relationships also implicate series of interactions over time between two (or more) individuals known to each other and can therefore be influenced by the history of past interactions (Hinde, 1976). Relationship quality therefore plays an important role in group living species. Variation in the quality of relationships between individuals, groups and even species has already been used to determine the function of social interactions like mother-infant relations (Weaver & de Waal, 2002) and post-conflict behaviour (Koski *et al.*, 2007) on reproductive success and infant survival (Silk *et al.*, 2003, 2009; Silk, 2007). However, the sources of variation in relationship quality have received less attention.

1.2.1. Measuring friendships

Measuring relationship quality is still under debate. In the past, most researchers used conventional measures of friendships which include only one or just a few behaviours like for example agonistic support (Cooper *et al.*, 2005), grooming (Majolo *et al.*, 2005), proximity (Massen & Koski, 2014) or time spent in proximity and grooming (Carter *et al.*, 2015) to assess relationship quality. Other studies used broad categories like kinship and age-sex combinations. Affiliation, tolerance and agonistic support between kin lead to a higher inclusive fitness (Silk, 2002, 2007; Surbeck *et al.*, 2011) and therefore kinship has often been used as an indirect measure for relationship quality (Aureli, 1992; Chapais *et al.*, 2001).

Friendships can also be studied using the three-factor model of relationship quality, proposed by Cords and Aureli (2000) which contains following components: Value, Compatibility and Security. The Value of a relationship comprises the benefits that result from that relationship like food sharing or forming coalitions. Therefore it should be better to form close associations

with more valuable partners. The Compatibility between two partners measures the tolerance and affiliation between the subjects based on previous interactions. Compatibility is important as it influences accessibility of the social partner. The predictability and consistency of the behaviour of both partners over time prescribes the Security of a relationship (Cords & Aureli, 2000; Fraser *et al.*, 2008; Massen *et al.*, 2010). Different studies used the relative frequency of social interactions, linked to one or two of these components, as a measure for relationship quality (Silk, 2002; Fraser *et al.*, 2008). Agonistic support (Cooper *et al.*, 2005) and grooming (Majolo *et al.*, 2005) are examples which have been used as measures of relationship Value while grooming rates and proximity have also been used as measures of Compatibility (Koski *et al.*, 2007). Rates of self-scratching during the approach of other individuals have been used as measures of Security (Castles *et al.*, 1999; Silk, 2002; Kutsukake, 2003). Fraser *et al.* (2008) and Silk (2002) however mentioned that these measures could provide valid assessments of relationship quality but choosing the best suitable behaviour to represent each component can be difficult.

An alternative and more accurate way of determining relationship quality is to implement all components of the model Cords and Aureli (2000) proposed. Several researchers already used this three-component model of relationship quality (Fraser *et al.*, 2008; Fraser & Bugnyar, 2010; Majolo *et al.*, 2010; Koski *et al.*, 2012; Morton *et al.*, 2015; Stevens *et al.*, 2015). Using Principle Component Analyses (PCA), a large number of behavioural variables can be reduced to just a few dimensions comparable to the 'Value', 'Compatibility' and 'Security' components of Cords and Aureli (2000). For every dyad, a PCA score for each component can be obtained.

1.2.2. Relationship quality in primates

The few studies which have tested the three-component model of relationship worked all but one (Fraser & Bugnyar on ravens: *Corvus* corax, (2010)) on primates: (chimpanzees, *Pan troglodytes* (Fraser *et al.*, 2008; Koski et al., 2012); Japanese macaques, *Macaca fuscata* (Majolo *et al.*, 2010), spider monkeys, *Ateles geoffroyi* (Rebecchini *et al.*, 2011), Barbary macaques, *Macaca Sylvanus* (McFarland & Majolo, 2011), Capuchin monkeys, *Cebus paella* (Morton *et al.*, 2015) and bonobos, *Pan paniscus* (Stevens *et al.*, 2015)). When studying different species, the use of different behavioural variables is inevitable. This resulted in slightly different outcomes. However, the first component of relationship quality always contained behaviours which indicate the importance of a relationship in terms of its direct benefits (Fraser *et al.*, 2008). The second component 'Compatibility' always represented tolerance and affiliation between individuals of a dyad but often contained slightly different behaviours. The

last component comprises behavioural variables which determine relationship stability or predictability and equality. This 'Security' component consisted of the most variable combinations of (species-specific) behavioural variables and could not be found in three previous studies (Rebecchini *et al.*, 2011; Morton *et al.*, 2015; Stevens *et al.*, 2015).

1.3. Friendship and personality

Often, non-dispositional factors like age difference, sex combination, rank difference and kinship have been used to explain the variability of relationships (Fraser *et al.*, 2008; Fraser & Bugnyar, 2010; Majolo *et al.*, 2010; Clutton-Brock & Hutchard, 2013; Stevens *et al.*, 2015). However, the influence of the non-dispositional factors is very inconsistent across studies. Therefore, other factors than these non-dispositional factors contribute to the variance in social relationships between animals. According to the 'similarity principle' of de Waal and Luttrel (1986), it would be more beneficial to maintain friendships of higher quality with individuals with similar phenotypic traits. Friendship takes investment of energy, time and trust. It is only beneficial to invest and maintain bonds that are more trustworthy. Similar personalities may increase this trust by facilitating reciprocity among these animals (Rivas, 2009). Similarity of phenotypic characteristics may therefore promote friendship in humans as well in nonhuman animals. In humans homophily is one of the most important factors which determine friendships of high quality. Homophily is defined as the phenomenon where contact between people with similar phenotypic traits occur more than among more different people (McPerson et al., 2001). Massen & Koski (2014) investigated whether similarity, or homophily, in personality traits predicted friendship in chimpanzees. They found four personality traits (Sociability, Grooming Equity, Anxiety, Boldness). Using contact sitting as the conventional index of friendship, they found only a negative correlation for the first dispositional (personality) trait, Sociability (Figure 1). Individuals with smaller differences in Sociability scores, spend more time sitting in contact than individuals with larger differences in Sociability. This negative correlation is indicative for homophily in the personality trait Sociability. However, no such effect was found for the three other personality traits (Figure 1). They also found a stronger negative correlation (stronger homophily in Sociability) for related individuals than for unrelated individuals (Solid line vs dashed line in Figure 1). Apart from maternal relatedness, they also included sex combination and age difference as non-dispositional factors in their model. None of these main predictors significantly influenced contact sitting between chimpanzees (Massen & Koski, 2014).

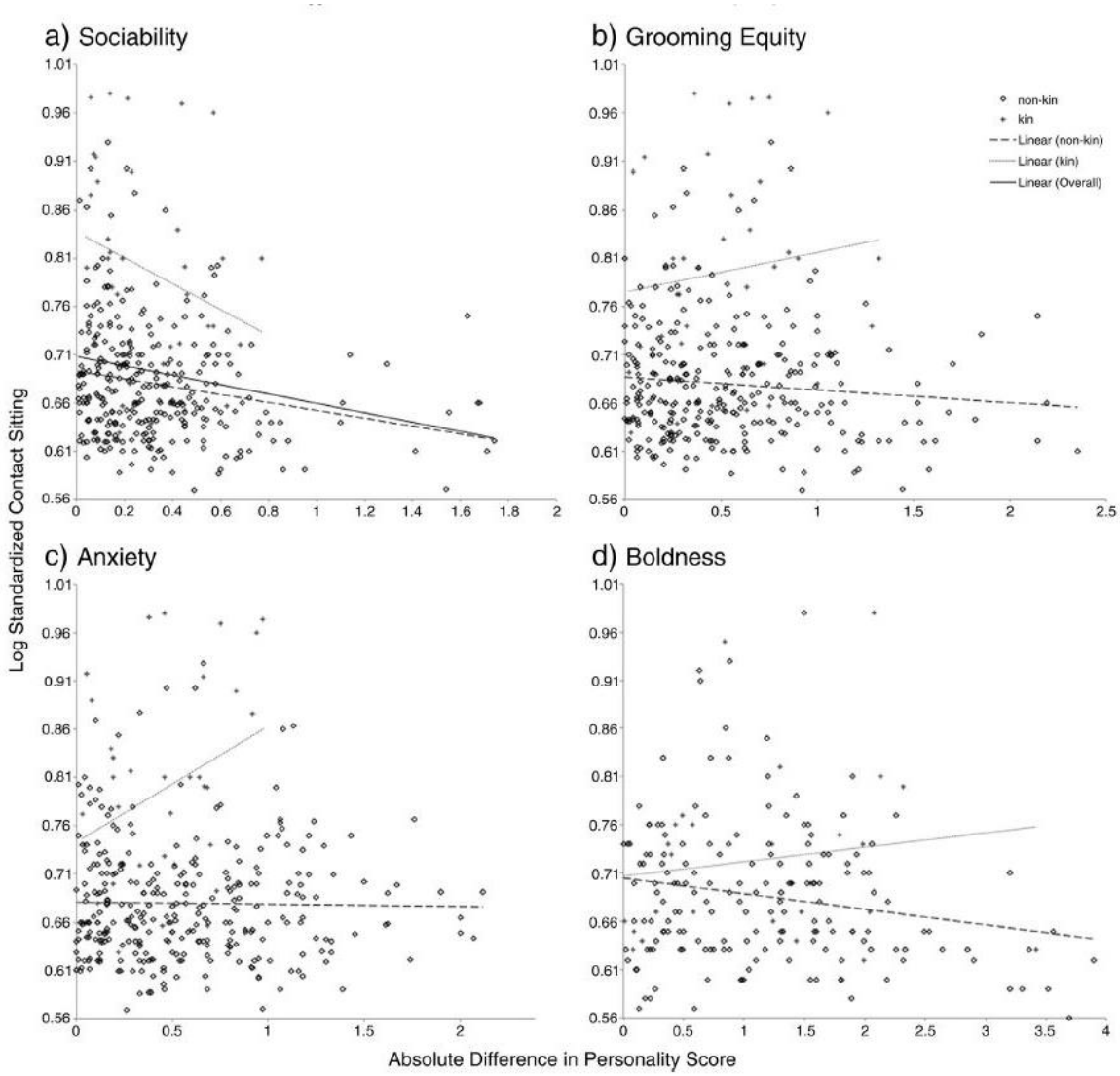

Figure 1: Relation between contact sitting and the absolute difference in four dyadic personality scores sitting for kin and non-kin in chimpanzees (Massen & Koski 2013). A significant negative correlation shows homophily.

1.4. Study species: bonobos

Bonobos, a primate species which is also closely related to humans, are much less studied than chimpanzees (Wildman *et al.*, 2003; Won & Hey, 2005; Stumpf, 2007). This is mainly due to their limited distribution in remote locations and the civil war in Congo which hampered research in the 1990s (Stumpf, 2007). Bonobos (*Pan paniscus*) are great apes endemic to the forests of the Demographic Republic of Congo and belong to the Hominidae family and the order Primates (Koop, 1989). In 1929, bonobos were considered to be a sub-species of chimpanzee (*Pan satyrus paniscus*) (Schwarz, 1929) until Coolidge (1933) eventually classified bonobos as a separate species *Pan paniscus*. Both species belong to the genus *Pan*

but are geographically isolated by the Congo River in Central-Africa (Coolidge, 1933; Badrian & Badrian, 1977; Fruth, 1999). Further morphological, behavioural and genetic studies confirmed this distinct species status and estimated the split between chimpanzees and bonobos at around 0.9 million years ago (Shea & Coolidge, 1988; Yu *et al.*, 2003; Won & Hey, 2005) Both species share approximately 98.4% of their genome with humans (Wildman *et al.*, 2003; Stumpf, 2007; Prufer *et al.*, 2012). Bonobos are also morphologically very similar to chimpanzees and can be distinguished from the latter by their slender body (Coolidge, 1933; Badrian & Badrian, 1977; Wrangham, 1985), their darker hair and face and their typical pinkish lips (de Waal, 1995). Bonobos and chimpanzees have retained several similar characteristics like size and degree of sexual dimorphism and male philopatry (Furuichi & Ihobe, 1994; Fruth *et al*., 1999; Parish, 1996), but research on captive and wild populations also revealed several behavioural differences. In contrast to chimpanzees, bonobos exhibit a large female-female and male-female association and low degree of male bonding, have greater group cohesion and less aggressive inter- and intra-group interactions (Wrangham, 1993; Furuichi & Ihobe, 1994).

1.4.1. Bonobo socioecology

The social organization of both chimpanzees and bonobos is characterized by fission-fusion of small temporary groups (parties) within larger and more stable multimale-multifemale groups (communities) where social interactions are highly present. (Kano, 1992; Van Elsacker *et al.*, 1995; Furuichi *et al.*, 1998). Adolescent females leave their natal group which results in male philopatry in both chimpanzees and bonobos, an exception to the common primate pattern (Hashimoto *et al.*, 1996). Male philopatric species normally consist of communities where closely related males form the strongest affiliation and cooperation. In chimpanzees indeed, males form strong cooperative bonds. Bonobos on the other hand show striking differences with chimpanzees and other male philopatric species. Females, which are distantly related to one another, are highly gregarious and form strong affiliations with other group members. Male-male interactions are often rare and weak whereas male-female alliances are stronger (Parish, 1994). However Stevens *et al.* (2006) found that in captive bonobo groups, bonds between female-female dyads were on the whole not significantly stronger than male-female dyads. Therefore, female-female bonds can be strong but can also be equally strong as bonds between unrelated males and females. These findings are similar to the findings of Fruth *et al.* (1999) and Hohmann *et al.* (1999) on wild bonobos in Lomako. Adult males stay in their natal group and maintain strong bonds with their mother, which has a positive effect on their dominance rank (Kano, 1992; Furuichi, 1997).

The strong bonds between unrelated female bonobos are often seen as the underlying force for their higher dominance status (Furuichi, 2009). Males on the other hand lack such interactions between one another and can therefore be dominated by female alliances (Parish, 1994; Vervaecke *et al.*, 1999; Stevens *et al.*, 2007). Although Vervaecke *et al.* (2000) and Stevens *et al.* (2007) found that in several groups males dominated some females.

Initially bonobos were seen as the gentle and tolerant alternative of chimpanzees. Several studies suggested that behavioural aspects like dominance, aggression, sexual behaviour and intercommunity interactions differed significantly from that of chimpanzees (de Waal, 1995; Fruth *et al.*, 1999). Although more research on both species revealed that they don't differ as much as people thought and that even within species large differences exist, for example due to different ecological conditions (Stanford, 1998; Yamakoshi, 2004; Stumpf, 2007).

1.4.2. Personality in bonobos

Personality studies on bonobos are rare. They have been included in several studies on great ape personalities in general (e.g; Uher *et al.*, 2007; Uher & Asendorpf, 2008) but no publications focused solely on bonobo personalities yet. However, some data are available as students of Nicky Staes (Sanne Roelofs, 2014; Martina Wildenburg, 2014) did their master thesis on personalities of bonobos. Both wanted to assess personality traits in this ape-species. Roelofs (2014) used group observations and group experiments to capture inter-individual differences in behaviour. The observational data resulted in five separate personality factors: Sociability, Dominance, Playfulness, Positive Affect and Anxiety. Out of the factor analysis on experimental data came three personality traits: Boldness, Exploration and Persistence. Further, she tested whether correlations were present between factors from the observational and experimental data. Sociability was found to be positively correlated with Persistence. Playfulness also correlated positively with the exploration factor. Lastly, Positive Affect an boldness were also positively related. Roelofs (2014) concluded that all personality traits that she found were comparable to chimpanzee personality traits. However she also recommended further research on bonobo personalities to confirm her findings.

Wildenburg (2014) on the other hand compared personalities between bonobos and chimpanzees. She found similar personality traits as Roelofs (2014). However, she only included observational data and therefore found following four personality traits: Sociability, Positive Affect, Anxiety, Autogrooming.

1.4.3. Relationship quality in bonobos

While two studies have focused on the three-components model of relationship quality on chimpanzees (Fraser et al., 2008; Koski et al., 2012), few has been done on bonobos. Stevens *et al.* (2015) were the first to apply the three-component model of Cords and Aureli (2000) on bonobos. They aimed to describe these three factors of relationship quality, using PCA and compare them to those found in chimpanzees. Quantifying relationship quality on both species could shed light on the debate about the differences between both species (Stevens *et al.*, 2015). Their findings were in line with earlier results on chimpanzees, however some differences were present. Three components of relationship quality could be extracted using traditional methods and were labelled: Value, Compatibility and Security. However, using Parallel Analysis, a more reliable method to determine the number of extracted components (O'Connor, 2000), they could only retain the two first components. The Value component was very consistent across taxa while the Compatibility factor showed some slight differences with other findings. However, the Security component was not statistically valid and could be the least consistent component across studies and taxa. Validation of this three-component model was therefore needed.

Contrary to the psychological notion that 'opposites attract', friendships between individuals with similar personalities are stronger and more affiliative than between other dyads. Moreover, these findings have been reported across a range of phylogenetically distant taxa including humans (human, *Homo sapiens,* McPherson *et al*., 2001; zebra finches, *Taeniopygia guttata* (Schuett *et al.*, 2011); chimpanzees, *Pan troglodytes* (Massen & Koski, 2014); capuchin monkeys, *Cebus apella* (Morton *et al.*, 2015) and chacma baboons, *Papio ursinus* (Carter *et al.*, 2015)). Therefore, a study linking differences in personality to components of relationship quality in bonobos can help us understand why or how friendships form in this ape species.

2. Aims of this study

In this study, we aim to determine whether similarities in personality factors influence friendships in captive bonobos.

- First, we aim to **analyse the personality structure** of captive bonobos, based on behavioural coding.
    - We predict that we will find a similar personality structure as found by Roelofs (2014) and Wildenburg (2014) because we use the same data as they did except for the data of the Wilhelma zoo (15 individuals) which I collected myself.

  We will use these individual personality scores to calculate absolute differences in personality scores for each dyad.

- Second, we will explore which of the following **factors influence similarity in personality** scores between individuals: sex combination, age difference, tenure, rank difference. For some of these variables we expect following effects on personality similarity:
    - Age difference may have more influence on some personality traits as several behaviours like for example play are age related. Therefore, two individuals of a similar age may show similar behaviours, hence more similar personalities.
    - We expect the absolute difference in Positive Affect and tenure to be negative correlated as in older individuals play levels decrease with age (Palagi & Paoli, 2007).

  For other effects there is no theoretical reason to assume an effect on personality but I will test for them anyway, because these variables will be included in the later analyses of friendship. By investigating the relationship between these variables and personality similarity, later interaction effects can be better interpreted.

- Third, we will study two measures of friendship
    - **A conventional measure** of friendship: contact sitting.
    - **Relationship quality** as a composite measure. Using an entirely different dataset but the same behavioural variables, we will try to replicate the study by Stevens et al (2015) and look for components of relationship quality. Because we use the same behavioural variables, we predict to find the components Relationship Value and Relationship Compatibility.

- Finally, we will look for the **influence of dispositional factors** (absolute differences in personality scores) **on** these measures of **friendship**. Non-dispositional measures (age difference; rank difference; tenure; sex combination) will also be examined, but only mentioned briefly as they are not the topic of my study.
    - We predict that we will find similar results in bonobos as earlier studies on chimpanzees (Massen & Koski, 2014). Moreover, this would suggest that friendships between these close relatives are partially based on the same elements.

    - We predict that for contact sitting and relationship quality, there will be a negative correlation (homophily) for Sociability. Individuals might benefit of Valuable relationships with individuals of similar personalities as investment in these friendships would be more reciprocal.

3. Methods

3.1. Study species and housing

Six captive groups of bonobos are included in this study. Data were collected by seven students, including me, for the PhD Project of Nicky Staes in 2011-2014 in six different zoos. The demographic composition of some groups varied across the different years due to births, deaths and replacement of individuals for the breeding program. Apenheul and Frankfurt zoo implemented artificial fission fusion in their bonobo groups. This management involves the daily change of group composition. Individuals were allowed to gather and to separate themselves in two separate groups which remained the same for at least a few hours. No social interactions occur before feeding moments in the morning and after nest building (Stevens *et al.*, 2008), therefore all bonobos were observed from about 9:00 am until 17:00 pm.

The bonobo group of Apenheul (AP) in Apeldoorn, The Netherlands, was observed in 2012 (128h) and in 2013 (139h). It contained 2-3 adult or adolescent males, 4 adult or adolescent females and 3 juveniles. Seven individuals were born in captivity; 2 in the wild and 1 animal was brought up by hand. This group composition was very variable.

Zoo Frankfurt (FR), Germany had, in 2012 (122h) and 2014 (201h) had 2-3 adult or adolescent males, 6-7 adult or adolescent females and 7 juveniles. All individuals were born in captivity except for two individuals that were born in the wild and one which was brought up by humans. The group composition of Frankfurt changed regularly.

The group of Planckendael (PL) in Muizen, Belgium, observed in 2012 (395h) consisted of three adult or adolescent males, 2-3 adult or adolescent females and 2-3 juveniles. All individuals were born in captivity and raised by their parents.

The bonobo group of Twycross (TW) in North Warwickshire, United Kingdom, was observed in 2012 (135h) and 2013 (156h). During this period, the bonobo group was permanently separated in two smaller groups. The first group consisted of 3 adult females, 2 adult or adolescent males and 2 juveniles. The second group contained 2 adolescent or adult females, 1 adolescent male and 1 juvenile. Three of all 13 bonobos were raised by hand, whereas all others were raised by their own parents.

Wuppertal oo (WU) in Wuppertal, Germany, housed 7-9 animals in 2012 (100h) and 2013 (184h). The group consisted of 3 and 2-3 adult or adolescent males and females respectively and 2-3 juveniles. All animals were housed together during the study period and all but one, which was raised by humans, grew up nearby their own mother.

Three adult males, 7 adult or adolescent females and 3-6 juveniles were present in the bonobo group of Wilhelma Zoo (WI) in Stuttgart, Germany in 2013 (260h) and in 2014 (193h) which I collected myself. Six individuals were born in the wild, only one was raised by hand and all others were born in captivity. These animals were housed in two separated groups. In 2013, group composition changed regularly while in 2014 both group compositions were fixed.
One or more infants or juveniles, younger than 7 years (Furuichi, 1998; Stevens *et al.*, 2008), were present in several groups. They were not included in the analyses as their behaviour resembles their mother's. The age classes we used are based on Kano's book 'The Last Ape' (1992, Table 1).

Table 1. Bonobo age classes (Based on Table 8 in The Last Ape (Kano, 1992)).

Age class		**Age (years)**
Infant		0-1
Juvenile	Early	2-4
	Late	5-6
Adolescent	Early	7-8
	Middle	9-12
	Late	13-14
Adult	Early	15-19
	Middle	20-30
	Late	31-…

Appendix A gives an overview of the sex, studbook number, date of birth, the origin and parents of the animals and the observer in every period of observation. Several males and females of different life-stages were present in each group, which resembles the natural composition of bonobo groups in the wild (Kuroda, 1979; Lacambra *et al.*, 2005; Vigilant, 2007). All enclosures consisted of an inside and outside enclosure (except for Wuppertal zoo which had no outside enclosure during the study period) with various enrichment items like nets, hay, balls and climbing facilities. The animals were fed several times a day with a mixture of fruit, vegetables, nuts, bread and seeds and had ad libitum access to water.

3.2. Behavioural Observations

As mentioned before, data were collected by several people, including me, during different periods (Appendix A). Before starting the data collection, each observer was trained for at least two weeks. A standardized ethogram was used for all observations.

A combination of continuous focal sampling, continuous group sampling and group scan sampling (Altmann, 1974) were used for recording. During continuous sampling all activities of one or more individuals are recorded. This sampling method gives an accurate estimate of frequency and duration of behaviours.

All occurrences of specific behaviours of one typical individual are recorded during focal sampling. Each focal session lasted for 10 minutes and individuals were chosen randomly. The advantage of this sampling method is that all actions can be recorded and even subtle behaviours won't be missed. The disadvantage is that only one individual can be observed during that time interval. All aggressions and sexual actions were recorded ad libitum even when the focal individual wasn't involved.

Continuous group sampling was used during feeding sessions. These are periods with a high prevalence of interactions like aggressions and sex. This method doesn't yield homogeneous measures of behaviours and tends to overestimate common or conspicuous actions but the biggest advantage is that all animals can be observed at once.

Scan observations were implemented before each focal sample. Every state of behaviour displayed by each individual at the moment they are observed together with its proximity with all other individuals in the group was recorded. Theoretically, the data are considered to be sampled at a precise slice in time. Practically, it takes a few seconds to complete the whole observation.

All observations were collected using a voice recording program and later entered in the Observer® software (version 11; Noldus Information Technology, Wageningen, The Netherlands), or directly entered in the Observer.

3.3. Data Analysis

3.3.1. Factors influencing personality similarity

3.3.1.1. Determining personality

The selection of relevant behaviours to determine personality, determination of the behavioural variables and factor analysis were based on Koski's (2011) work and were implemented by Sanne Roelofs (2014). We give a brief summary of the procedures she used and which calculations we performed. The personalities of the individuals of the Wilhelma zoo in Stuttgart were determined based on data of 2013 and data collected in 2014. All other personalities were determined based on data which were collected in several years (Appendix A).

a) Selecting relevant behaviours

From the observational data, individual scores of behavioural variables were extracted (Table 2). These variables are based on Koski's (2011) work and are potential personality behaviours. Several modifications have been made to make it suitable for studies on bonobos. For example behaviours which were not included in Koski's work but are important in bonobo societies, like socio-sexual behaviours (Blount, 1990; Lacambra, 2005), were included in this study. Behaviours that were not observed adequately to use in the statistical analyses were excluded from Koski's (2011) list or merged with other behavioural variables in one single variable. Juveniles, as mentioned before, don't act independently of their mother. Behaviours involving juveniles were excluded from the statistical tests to avoid bias towards mother-infant interactions.

b) Behavioural variables

Behavioural variables based on durations of behaviours like activity, grooming given, grooming received, individual play, social play, auto-scratching and auto-grooming were calculated as proportions of time performing that behaviour and corrected for the focal observation time. The behavioural variables where the frequency of behaviours is important (submission, aggression given, aggression received, point affinitive behaviours, socio-sexual behaviours and nose wipes) were calculated as frequencies per hour and again corrected for individual total observation times.

Table 2. Behavioural variables used to determine personality.

Behavioural variable	Definition	Calculated as
Activity	Time spent not resting, sleeping, sitting or autogrooming	Focal observation time minus time spent resting, sleeping, sitting or autogrooming, divided by focal observation time (F)
Submission	Frequency of submissive behaviours	Frequency per hour of flee, flinch and crouch behaviours (F+AO)
Aggression given	Frequency of performed aggressive behaviours	Frequency per hour of aggressive intentions, long charges, short charges, direct displays, mutual displays and parallel displays (F+AO)
Aggression received	Frequency of received aggressive behaviours	Frequency per hour of received aggressive intentions, long charge, short charges, direct displays, mutual displays and parallel displays (F+AO)
Sit alone	Percentage of time spent being alone (without group members within 2 meters of subject)	Number of scans recorded as 'sit alone' divided by the total number of scans (S)
Number of neighbours	Average number of group members in proximity to subject	Average number of group members in subject's proximity in scans recorded as 'sit with' (S)
Proximity maintenance	Responsibility for maintaining proximity with group members	Mean Hinde's index for proximity (see text for formula) (F)
Grooming density	Number of group members groomed by subject	Number of individuals the subject gives grooming to divided by total available grooming partners (F)
Grooming diversity	Equality of grooming effort given to different grooming partners	Shannon-Wiener diversity index corrected for group size effect (see text for formula) (F)
Grooming given	Time spent grooming others	Time spent grooming divided by focal observation time (F)
Grooming received	Time spent being groomed by others	Time spent grooming divided by focal observation time (F)
Point affinitive behaviours	Frequency of short-duration affinitive behaviours	Frequency per hour of affiliative touch, embrace, buddywalk and mountwalk behaviours (F+AO)
Play	Time spent playing individually and with others	Total duration of play divided by focal observation time (F)
Autoscratching	Time spent self-scratching, both gentle and rough	Total duration of rough and gentle autoscratching behaviours divided by focal observation time (F)
Autogrooming	Time spent self-grooming	Total duration of autogrooming divided by focal observation time (F)
Socio-sexual behaviours	Frequency of sexual behaviours performed in social context	Frequency per hour of copulations and non-copulatory mounts divided by the total observation time (F+AO)
Nose wipes	Frequency of nose wipes	Frequency per hour of nose wipes divided by focal observation time (F)

All frequencies and duration measures are corrected for individual observation times.
(F): Behaviours based on focal animal sampling data. (F + AO): Behaviours based on focal animal sampling and all occurrence observations. (S): Based on scan sampling data

The behavioural variable "sit alone" is the proportion of all scans that an individual spent being alone. The number of neighbours was measured as the average number of individuals being within 2 meter of the subject. Proximity maintenance was calculated using Hinde's index for proximity:

$$Proximity\ index = \frac{Ap_s}{Ap_s + Ap_p} - \frac{L_s}{L_s + L_p}$$

Ap_s and Ap_p are the number of approaches made by the subject and by the partner respectively. L_s and L_p are the number of times the subject and partner leaved. The proximity of all possible dyads for the subject was calculated with this index. A proximity value of -1 indicates that the partner is entirely responsible for maintaining proximity. A value of +1 on the other hand suggests that the subject is completely responsible for the maintenance of the proximity. The indices, which ranged from -1 to +1, of each subject were averaged to calculate the individual scores for proximity maintenance. Grooming density was calculated as the proportion of available grooming partners that effectively were groomed by the subject individual. After correcting for group size effects, grooming diversity was calculated with the Shannon-Wiener diversity index (Koski, 2011):

$$Grooming\ diversity\ index\ (GDI) = \frac{H}{H_{max}}$$

$$H = -\sum(p_i \,.\ln(p_i))$$

in which p_i is the proportion of the grooming effort of the subject to the *i*th individual.

$$H_{max} = \ln(N - 1)$$

N is the number of individuals in the subject's group. The GDI value becomes 0 when all of the grooming effort of the subject is directed towards one individual. If the subject divides its grooming effort between all group members, the GDI will be 1.

Data which were collected during all years (Appendix A) were used for determining personality of each individual to enlarge the sample size.

c) Factor analysis

All processing and statistical tests were done with RStudio, SAS, and IBM SPSS Statistics 20. Factor analysis was chosen to reduce the amount of dimensions in this study, since it is the most appropriate statistical method to detect unobservable constructs like personality traits (Budaev, 2010). Suitability for factor analysis was tested before implementation by producing a correlation matrix with significance values for each correlation. Factor analysis results in factors based on inter-variable correlations so non correlated variables are not suited for this method (Field, 2005). The values of the determinant of the correlation matrix, the Bartlett sphericity test and the Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy are other measures of suitability (Field, 2005; Budaev, 2010). These tests were applied on the final correlation matrix after removal of the unsuitable variables.

Principle axis factoring based on the correlation matrix was used as factor analysis. All factors were extracted based on the comparison of the eigenvalues (Value > 1) and the corresponding scree plot. First the solution was orthogonally rotated (using the Varimax with Kaiser normalization) and then the analysis was repeated with an oblique rotation (Oblimin with Kaiser normalization) to check for correlations between the factors. Factor loadings could be interpreted when they were between 0,5 and -0,5 or equal to 0,5 (Budaev, 2010). As the definition of personality requires that the behavioural variables used for personality analysis are stable across time, these were tested for temporal consistency by Staes *et al.* (in preparation). In this study, only those variables that were significantly repeatable when tested again one year later were retained in the analysis.

3.3.1.2. Factors influencing personality similarity per dyad

We used Linear Mixed Models to determine which factors influenced similarity in personality. For each personality trait, similarity in personality scores were obtained by taking the absolute difference in personality score of the two individuals of a dyad. Then these scores were used as response variable to determine the effect of maternal kinship, tenure, sex combination, age and rank difference. Therefore, we ran different models for each personality trait. We didn't include two-way interactions as for further analysis two way interactions between these non-dispositional factors and the dispositional factors will be included. The studbook of Pereboom

et al. (2011) was used to become kinship information. Individuals with maternal relatedness coefficients larger than 0.125 were treated as kin (lower Values were said to be non-kin). This resulted in a binary variable (kin vs non-kin), with kin dyads including one mother-daughter dyad, three maternal brother dyads and seven mother-son dyads. Relationship tenure, the amount of years two individuals spent together, was also calculated from the studbook (with an error margin of 0.5 years; minimum 1, maximum 44 years). Age difference between two individuals of a dyad was calculated by taking the difference of years of birth (Pereboom *et al.*, 2011). Rank difference was calculated using David's scores (David 1987). Gammell *et al.* (2003) showed that these scores give the most suitable values for individual overall success as it takes the relative strengths of the other individuals into account. Bonobo identity and group were entered as random variables. *F*-tests and backward selection were used to construct a final model that contains variables with only significant effects. For categorical variables, post-hoc pairwise comparisons were performed, using Tukey tests for multiple comparisons of means.

3.3.2. Factors influencing friendship: a conventional measure

Similar to what Massen and Koski (2014) did on chimpanzees, we first used contact-sitting as a conventional measure of friendship to assess whether similarity in personality together with other factors influence friendships. A Linear Mixed Model was used to determine which influence maternal kinship, tenure, sex combination, both age and rank difference and similarity in personality have on the contact sitting score for each dyad.

Therefore, we ran one model with contact sitting as response variable. The raw contact sitting data were standardised into z-scores per zoo before pooling all data of the different zoos. Furthermore, we added 5 to each z-score to obtain positive values per dyad and log transformed these data to create a normal distribution. Values for maternal kinship, tenure, sex combination and age and rank difference were the same as those used to determine the influence on similarity in personality (See previous section). Here, bonobo identity and group were also entered as random variables.

Further, F-tests and backward selection were used to construct a final model which only contained variables with significant effects. For categorical variables, post-hoc pairwise comparisons were performed, using Tukey tests for multiple comparisons of means. Also for interaction effects, post-hoc pairwise comparisons were performed to become the separate slopes for each quartile.

3.3.3. Factors influencing friendship: a composite measure

3.3.3.1. Determining relationship quality

The determination of all components of relationship quality is based on the work of Fraser *et al.* (2008) and Stevens *et al.* (2015).

a) Behavioural variables

Dyadic scores of several behavioural variables were extracted from the observational data (Table 3). For aggression, and coalitionary support, all occurrence observation was used.
For each grooming bout, the participation of each individual was only scored once and switches between the active and passive role were not counted as separated bouts (Vervaecke *et al.*, 2000). Proximity was scored using group scan sampling, noting which individuals were within arm's reach, meaning less than one meter, from each other.

Table 3. Behavioural variables used to determine relationship quality.

Behavioural variable	Definition
Aggression frequency	Frequency of all aggressive interactions within a dyad
Aggression symmetry	Symmetry of aggression within a dyad (see text) (F+ AO)
Counter-intervention	Index of counter-intervention (frequency of counter-intervention/ opportunity to intervene)
Grooming frequency	Number of grooming bouts exchanged within a dyad (i.e. the sum of all bouts from A to B and from B to A)
Grooming symmetry	Symmetry of grooming within a dyad (see text)
Peering	Frequency of peering
Proximity	Proportion of scans spent within arm's reach
Support	Index of agonistic support (frequency of support/opportunity to support)

The total number of samples per dyad was divided by the total number of samples taken per group to calculate a proportional value. Grooming and aggression frequency were calculated as the total number of aggressions and grooming bouts from A to B and vice versa and divided by the total group observation time. Grooming symmetry was calculated using: A grooms B/ (A grooms B + B grooms A). The lowest of both results when reversing A's and B's role was chosen so grooming symmetry varied between 0 to 0.5 (Stevens *et al.*, 2015). Aggression symmetry was calculated in a comparable way. Peering, the behaviour were an actor stares at a

receiver's face from very close distance (Kano, 1992), was used as a measure for tolerance (Stevens *et al.*, 2005). Support was defined as all situations where an individual A intervenes with an aggressive behaviour within 30 s in an agonistic confrontation between two other individuals B and C to aid one of these actors (de Waal, 1978). Only triadic interactions were studied because in polyadic interventions, more than 3 individuals involved, it is unclear which individual supported who. To correct for the opportunity for individual A to support B in a conflict against C, we divided the total number of support between A and B by the total number of conflicts that individuals A and B encountered with other group members, excluding the conflicts they had with each other and then multiplied this with 100 (Stevens *et al.*, 2006; Stevens *et al.*, 2015). Supporting one individual automatically implies contra support against the opponent during the interaction (de Waal, 1978; Stevens *et al.*, 2015).

Observation times differed between groups and therefore we transformed all behaviours to frequencies, dividing by the number of group observation hours, or to proportions.

While for every individual personality scores could be calculated, 102 dyads of captive bonobos were studied. The bonobo group of Apenheul was excluded for further analyses since the group composition was too variable for determining relationship quality.

b) Principle component Analysis

Principle component analysis (PCA) was used to obtain measures of relationship quality. PCA is a statistical technique that can be used to reveal underlying factors, principle components, which explain correlations within sets of variables. This mathematical procedure uses an orthogonal transformation to convert a set of observations of correlated variables into a set of uncorrelated variables. Eventually, the number of principle components is less than or equal to the number of original variables (Van Dongen, 2013). The output of the PCA analysis consists of coefficients of correlation between each behavioural variable and each extracted component and provides relative scores for each dyad and each component.

For each dyad, eight behavioural variables were included in the PCA (Table 2) with varimax rotation and Kaiser normalization. All frequency data were transformed using square root transformation to improve normality. According to Kaiser's rule all components with an eigenvalue greater than 1 were accepted (Kaiser, 1960). Coefficients of correlation greater than 0.5 or less than -0.5 were considered to be high. O'Connor (2000) and Stevens *et al.*, (2015) suggest to use Parallel analysis to determine the number of extracted components because Kaiser's procedure may lead to an overestimation of the number of factors. Zwick and Velicer

(1986) define this Parallel Analysis as ‘a sample based adaptation of the population based Kaiser’s rule’ and therefore allows us to determine the statistical significance of the PCA components. The components of whom the eigenvalues from PCA are larger than the corresponding eigenvalues from Parallel Analysis should be considered as true components.

c) Factors influencing the composite measure of friendship

Linear Mixed Models were used to determine which influence maternal kinship, tenure, sex combination, age and rank difference and similarity in relationship have on the extracted scores from the PCA. Therefore, we ran different models with each component of relationship quality as response variable. Values for maternal kinship, tenure, sex combination and age and rank difference were exactly the same as those used to determine the influence of the these factors on similarity in personality (See previous section). Here, bonobo identity and group were also entered as random variables and F-tests and backward selection were used to construct a final model which only contained variables with significant effects. For categorical variables, post-hoc pairwise comparisons were performed, using Tukey tests for multiple comparisons of means.

4. Results

4.1. Factors influencing personality similarity

4.1.1. Personality Structure

From the factor analysis, three components had eigenvalues larger than one. Parallel analyses showed that all three personality factors could be retained (Table 4). The first factor explained 30.5% of the total variance. It included strong loadings of the number of individuals in close proximity, grooming given and received and the frequency of being approached. Autogrooming had a high negative loading on this first factor. These behaviours reflect relationship maintenance and Sociability and therefore we labelled this personality factor 'Sociability' (Koksi, 2011). The second personality factor explained 14.23% of the variance. The frequency of approaching others, frequency of play and frequency of received aggressions loaded on this factor. We therefore labelled this factor as 'Positive Affect'. The third factor explained 13.87% of the total variance and had high positive loadings from the self-directed behaviour autoscratch, both grooming density given and received and high negative loadings for activity. As this self-directed behaviour and a lower activity can be considered as indicators of Anxiety (Schino *et al.*, 1996), we labelled this factor 'Anxiety'.

Table 4. Varimax rotated solution of the factor analysis on variables in the personality model. An asterisk indicates high loadings: >0.5 or <-0.5.

	Sociability	Positive Affect	Anxiety
Grooming Given	**0.77***	-0.01	-0.10
Grooming Received	**0.83***	-0.20	-0.09
No. Neighbours	**0.89***	0.33	-0.33
Being Approached	**0.59***	0.04	0.29
Autogrooming	**-0.53***	-0.13	-0.11
Approach	0.28	**0.84***	0.03
Play	0.04	**0.60***	-0.07
Aggression Received	-0.18	**0.58***	0.10
Scratch	-0.08	0.03	**0.85***
Groom Density Given	0.48	0.44	**0.57***
Groom Density Received	0.43	-0.34	**0.56***
Activity	0.33	0.46	**-0.51***
% variance explained	30.54	14.23	**13.87**
Eigenvalue	4.02	2.15	**2.01**

4.1.2. Factors influencing personality similarity

For both Sociability and Anxiety, no significant predictor effects were found (Table 5).

Table 5. Predictor variables for all personality traits, assessed with a Linear Mixed Model (LMM). An asterisk indicates a significant effect: p-value <0.05.

	Effect	Num df	Denom df	F-Value	P-Value
Sociability	Sex combination	2	59.4	1.80	0.18
	Rank difference	1	82.6	0.14	0.71
	Age difference	1	87.4	1.88	0.17
	Maternal Kinship	1	81.6	0.00	0.98
	Tenure	1	68.6	1.28	0.26
Positive Affect	Sex combination	2	84.2	1.92	0.15
	Rank difference	1	84.9	0.09	0.77
	Age difference	**1**	**80.1**	**8.29**	**<0.01***
	Maternal Kinship	**1**	**80.7**	**17.11**	**<0.01***
	Tenure	**1**	**83.2**	**19.64**	**<0.01***
Anxiety	Sex combination	2	52.1	2.48	0.09
	Rank difference	1	85.2	0.85	0.36
	Age difference	1	74.6	1.49	0.23
	Maternal Kinship	1	72.1	2.58	0.11
	Tenure	1	77.1	2.01	0.16

However, the absolute difference in Positive Affect between individuals was significantly influenced by age difference, maternal kinship and tenure (Table 5). Dyads consisting of individuals with more similar ages have more similar Positive Affect scores (Figure 2).

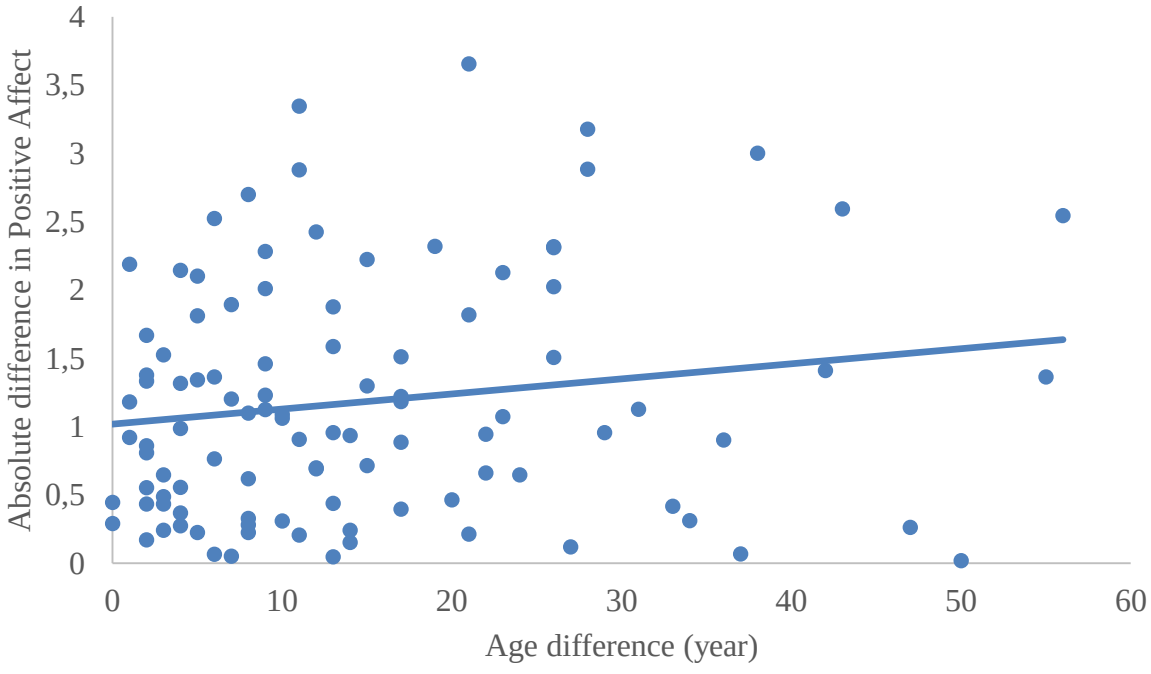

Figure 2. Relation between the absolute difference in Positive Affect and age difference.

Related dyads had significantly higher differences in Positive Affect scores (Figure 3). Finally, the absolute differences in Positive Affect became smaller with longer relationship tenure (Figure 4).

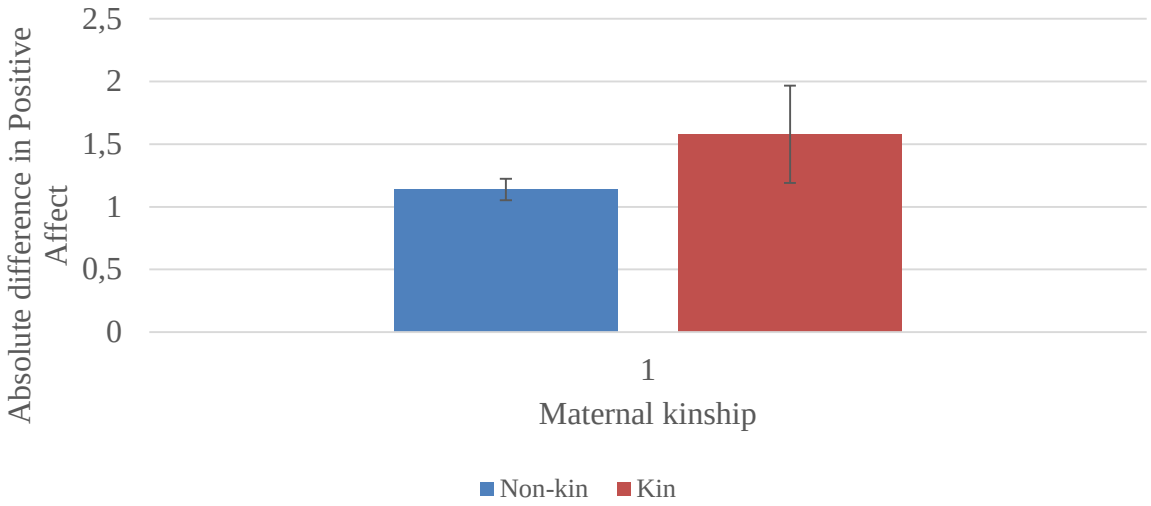

Figure 3. Relation between the absolute difference in Positive Affect and maternal kinship.

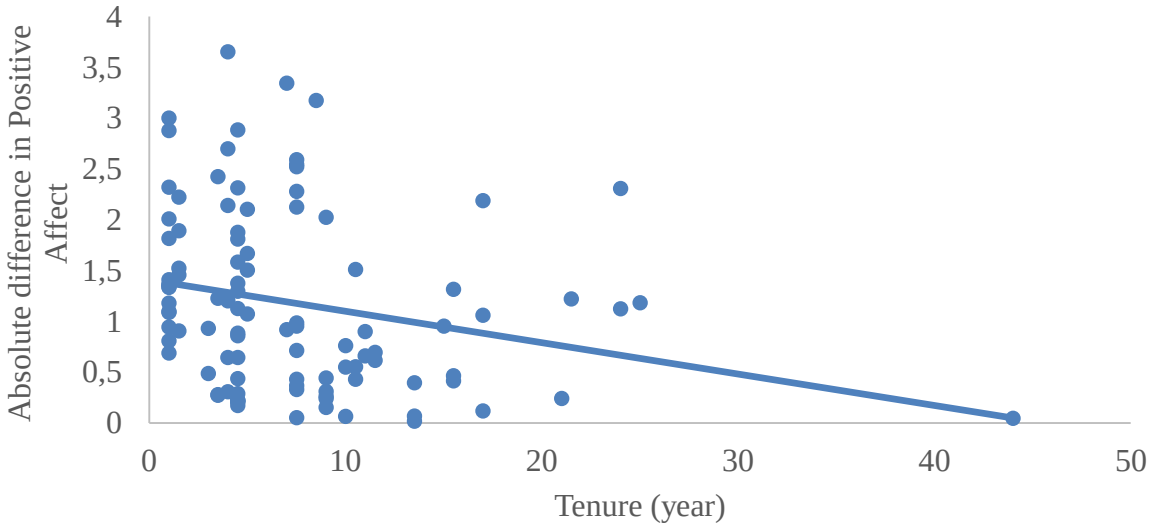

Figure 4. Relation between the absolute difference in Positive Affect and tenure.

4.2. Factors influencing friendship

4.2.1. Contact sitting as a conventional measure of friendship

For the model with contact-sitting as response variable, all five non-dispositional variables (i.e. variables that are not directly related to personality differences: sex combination, rank

difference, age difference, maternal kinship and tenure) were significant. For further interpretations of these non-dispositional variables and all factors with corresponding F and P-Values (see appendix B).

Here, we will focus on the significant dispositional (personality) variables and interaction effects (Table 6).

Table 6. All main effects and the significant dispositional interaction effects on contact sitting, assessed with a Linear Mixed Model (LMM). An asterisk indicates a significant effect: p-value <0.05.

	Effect	Num df	Denom df	F Value	P-Value
Non-dispositional	**Sex combination**	**2**	**82.1**	**10.24**	**<0.01***
	Rank difference	**1**	**79.7**	**10.24**	**<0.01***
	Age difference	**1**	**89.0**	**9.44**	**<0.01***
	Maternal kinship	**1**	**89.0**	**12.67**	**<0.01***
	Tenure	**1**	**84.4**	**15.31**	**<0.01***
Dispositional	**Abs. difference in Sociability**	**1**	**81.5**	**4.26**	**0.04***
	Abs. difference in Positive Affect	1	77.3	1.04	0.31
	Abs. difference in Anxiety	1	88.0	2.24	0.14
Significant interactions	**Sociability*Age difference**	**1**	**85.8**	**5.44**	**0.02***
	Anxiety*Tenure	**1**	**68.9**	**4.40**	**0.04***
	Sex combination*Maternal kinship	**2**	**88.7**	**7.12**	**<0.01***
	Rank difference*Tenure	**1**	**83.2**	**7.38**	**<0.01***

For presentation of the non-dispositional variables see Appendix B

The only significant dispositional main effect was the absolute difference in Sociability which had a weak significant negative effect on contact sitting, i.e. there is weak homophily in Sociability. The more similar two individuals were with regard to the Sociability trait, the more often they sat together in contact with each other (Figure 5).

We found a significant interaction effect between absolute difference in Sociability and age difference ($F_{1,85.5} = 5.44$, $p = 0.02$) meaning that the slopes for the different age classes significantly differ from each other. However, post-hoc testing showed that for none of the four age quartiles, a significant correlation was found: $t_{0\leq\leq5} = 0.33$, $p = 0.74$; $t_{6\leq\leq11} = -0.33$, $p = 0.74$; $t_{12\leq\leq22} = 0.15$, $p = 0.88$; $t_{\geq23} = -0.57$, $p = 0.57$ (Figure 6).

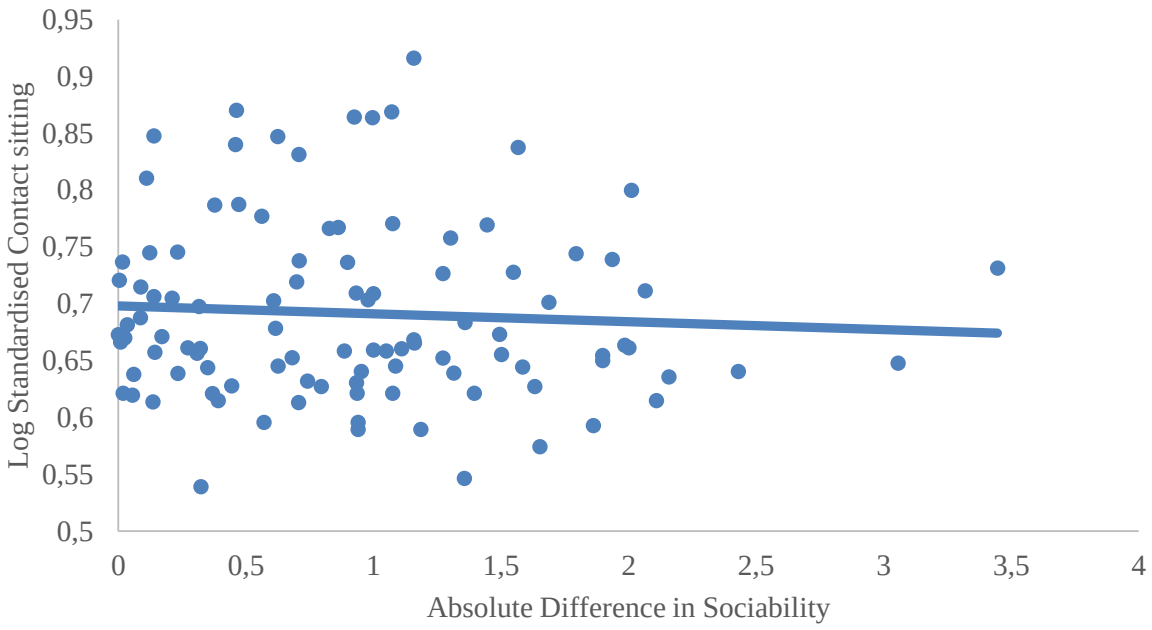

Figure 5. Relation between contact-sitting (log of standardised Values) and the absolute difference in dyadic personality scores of Sociability.

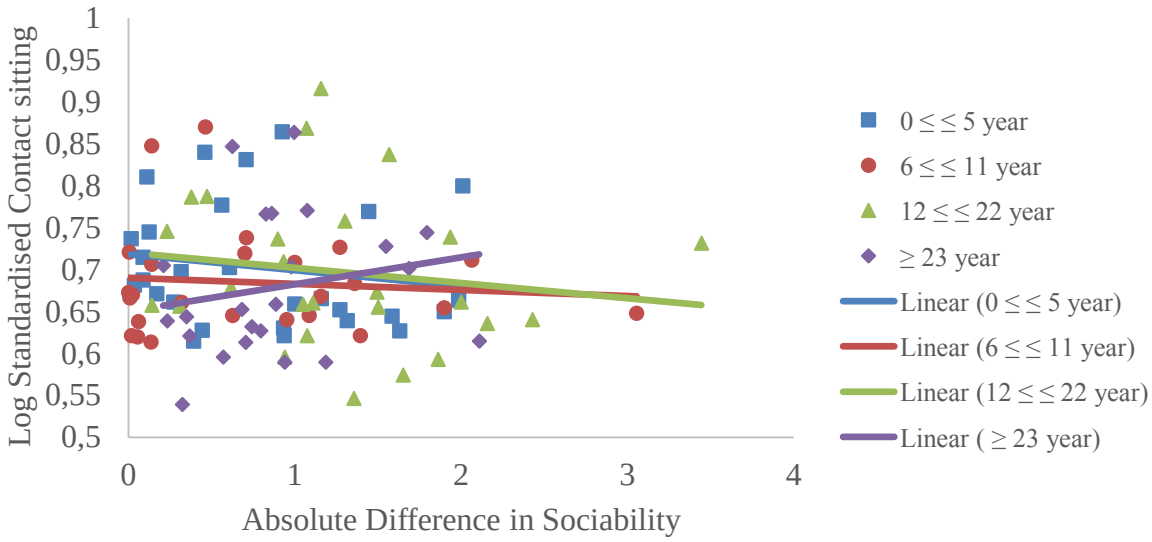

Figure 6. Relation between contact-sitting (log of standardised Values) and the interaction between the absolute difference in dyadic personality scores of Sociability and age difference.

Although the main effect of Anxiety difference was not significant, we found a significant interaction effect between the absolute difference in Anxiety and tenure on contact-sitting. This indicates a significantly difference in the slope for the different tenure quartiles. The correlation was mildly negative but not significant ($t_{0<4}$ = -0.99, p = 0.32) (indicative for weak homophily in Anxiety) for individuals that resided for less than 4 years together and strongly negative but not significant ($t_{\geq 10}$ = -1.59, p = 0.11) (indicative for stronger homophily in Anxiety) for

individuals which resided for more than 10 years (Figure 7). For intermedium tenures, no significant slopes could be found either ($t_{4\leq\leq5}$ = -0.17, p = 0.86; $t_{5<<10}$ = -0.83, p = 0.4088).

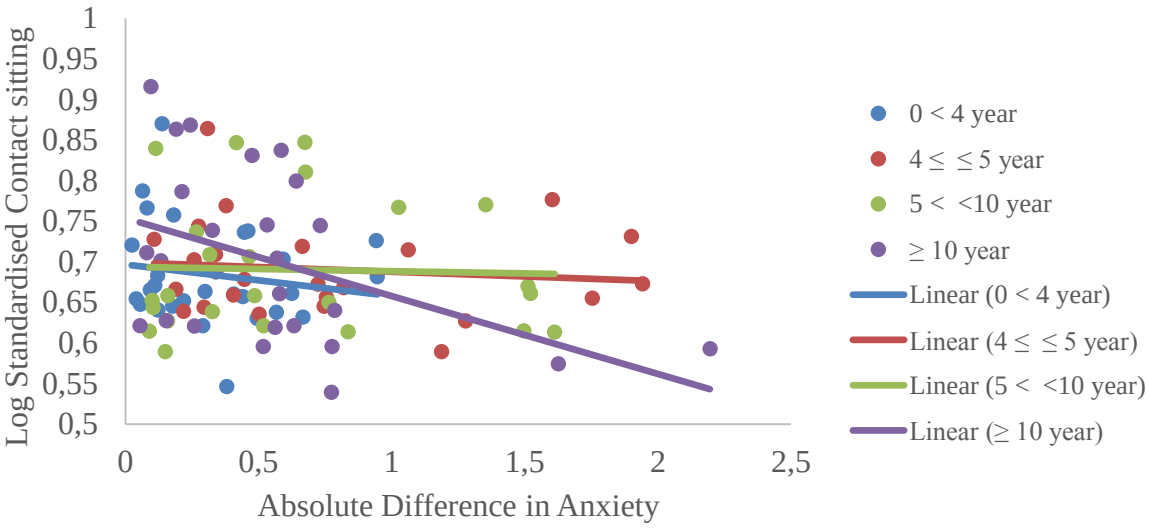

Figure 7. Relation between contact-sitting (log of standardised Values) and the interaction between the absolute difference in dyadic personality scores of Anxiety and tenure.

4.2.2. Relationship quality: a composite measure of friendship

4.2.2.1. Determining components of relationship Quality

Based on Kaiser's criterion, two components were extracted from the principle component analysis. Based on Parallel Analysis, these two components could be retained for further analysis. The first component had high positive loadings for grooming frequency, grooming symmetry, peering, proximity and support. These variables are comparable to earlier findings of the relationship Value component (Cords &Aureli, 2000; Fraser *et al.*, 2008; Stevens et al., 2015) and therefore we labelled it 'Value'. The second principle component had high positive loadings for aggression frequency and symmetry and counter-intervention. These variables resemble variables belonging to the 'Incompatibility' component as suggested by Fraser *et al.*, (2008). Therefore, we reversed the signs for all scores obtained for each dyad for that component for further analyses so that the values represented the degree of Compatibility (cf. Fraser *et al.*, 2008; Stevens *et al.*, 2015). Table 7 shows all factor loadings for component one and two resulting from the PCA. In this model, the first component explained 36,42% and the second 17,67% of the total variance.

Table 7. The varimax rotated matrix of the Principle Component Analyses for the dyadic scores for all 8 variables, assessed with a Linear Mixed Model (LMM). An asterisk indicates high loadings: >0.5 or <-0.5.

Variable	Value	(in)Compatibility
Proximity	**0.91***	-0.06
Groom frequency	**0.89***	0.08
Groom symmetry	**0.68***	0.12
Support	**0.64***	0.10
Peering	**0.61***	-0.12
Aggression frequency	-0.04	**0.83***
Aggression symmetry	-0.05	**0.64***
Counter-intervention	0.13	**0.53***
% of variation explained	36.42	17.67
Eigenvalue	2.91	1.41

4.2.2.2. Relationship Value

Table 8. All main effects and the significant dispositional interactions effects on relationship Value, assessed with a Linear Mixed Model (LMM). An asterisk indicates a significant effect: p-value <0.05.

	Effect	Num df	Denom df	F Value	P-Value
Non-dispositional	**Sex combination**	**2**	**75.3**	**8.54**	**<0.01***
	Rank difference	1	68.3	3.50	0.07
	Age difference	**1**	**62.0**	**19.23**	**<0.01***
	Maternal kinship	**1**	**75.3**	**6.00**	**0.02***
	Tenure	**1**	**75.3**	**4.63**	**0.01***
Dispositional	**Abs. difference in Sociability**	**1**	**70.9**	**11.01**	**<0.01***
	Abs. difference in Positive Affect	1	73.2	3.25	0.08
	Abs. difference in Anxiety	1	72.3	0.02	0.88
Significant interactions	**Sociability*Maternal kinship**	**1**	**69.8**	**16.2**	**<0.01***
	Positive Affect*Maternal kinship	**1**	**72.0**	**5.42**	**0.02***
	Anxiety*Maternal kinship	**1**	**76.0**	**5.10**	**0.03***
	Anxiety*Rank difference	**1**	**63.3**	**4.07**	**0.05***
	Anxiety*Tenure	**1**	**76.1**	**5.06**	**0.03***

For presentation of the non-dispositional variables see Appendix C

Relationship Value was significantly influenced by four of the non-dispositional main effects sex combination, age difference, maternal kinship and tenure, as well as by the dispositional main effect "absolute difference in Sociability" (Table 8). In the scope of this study we will focus on the dispositional effects and the significant interaction effects. For interpretations and results of the non-dispositional effects, see appendix C. Individuals with more similar Sociability scores exhibit relationships of higher Values (Figure 8). Furthermore, we found a

significant interaction ($F_{1,69.8}$ = 16.20, p = 0.0001) between the absolute difference in Sociability and maternal kinship, indicating that the slope for related individuals significantly differs from the slope of non-related individuals (Figure 9). However, post-hoc testing shows that within both unrelated ($t_{non\text{-}kin}$ = -1.67, p = 0.10) and related dyads (t_{kin} = 1.83, p = 0.08) no significant correlation could be found.

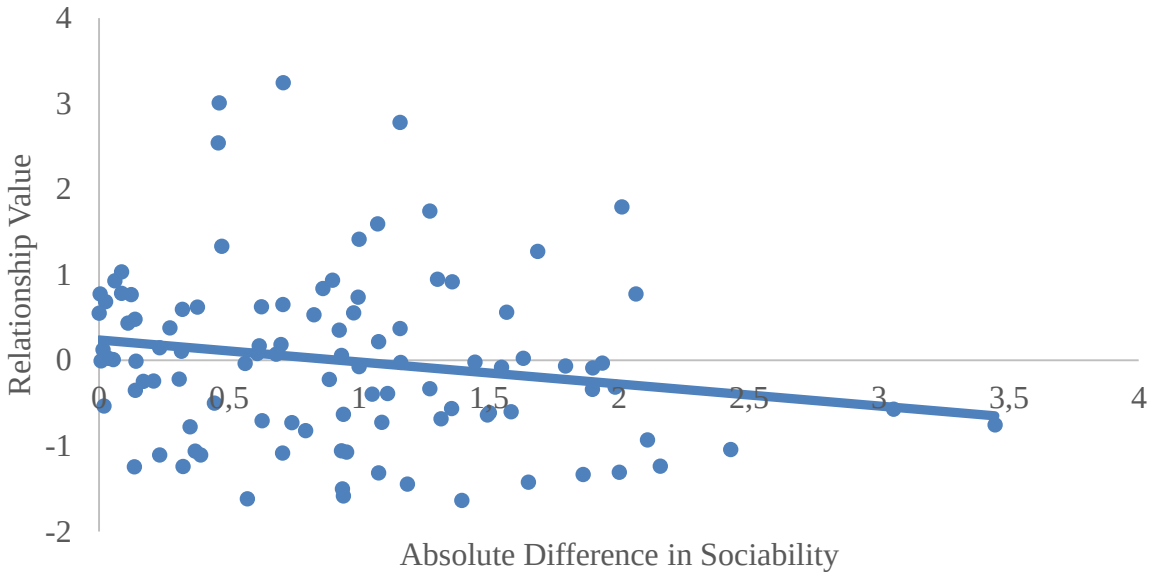

Figure 8. Relation between relationship Value and the absolute difference in dyadic personality scores of Sociability.

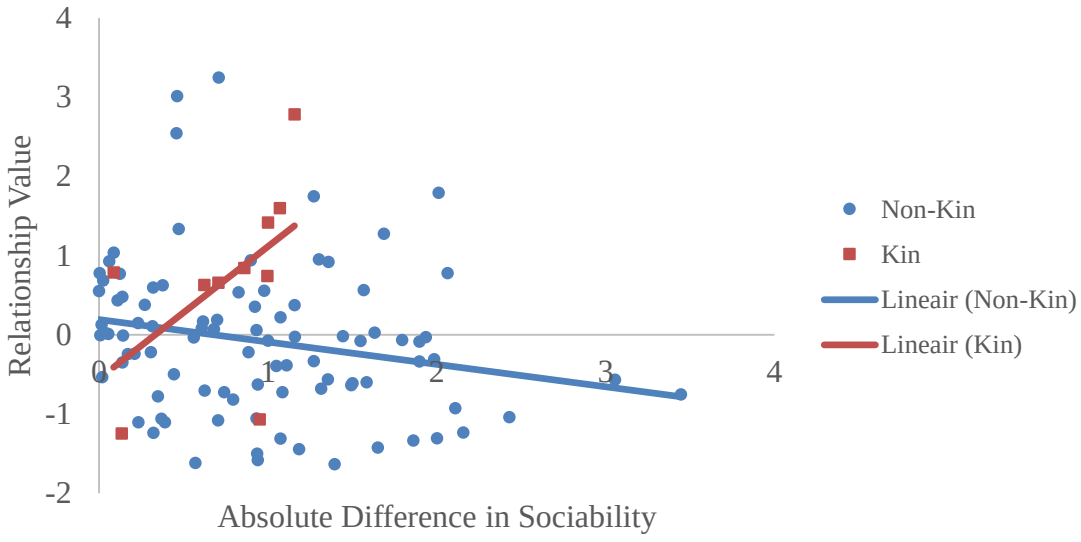

Figure 9. Relation between relationship Value and the interaction between the absolute difference in Sociability and maternal kinship.

Although there was no significant main effect of difference in Positive Affect and or difference in Anxiety, a significant interaction between maternal kinships and both Positive Affect ($F_{1,72.0}$ = 5.42, p = 0.02) and Anxiety ($F_{1,76.0}$ = 5.10, p = 0.03) was found (Figure 10 and 11). This shows that for both personality dimensions, the slopes for related individuals and unrelated individuals significantly differs. However, post-hoc analysis showed that the correlation within both kin (t_{kin} = -0.69, p = 0.80) and non-kin ($t_{non\text{-}kin}$ = -0.25, p = 0.80) was not significant for the absolute difference in Positive Affect. For the absolute difference in Anxiety, no significant correlation within unrelated individuals ($t_{non\text{-}kin}$ = 0.44, p = 0.66) could be found, while for related dyads relationship Value became significantly lower (t_{kin} = -2.09, p = 0.04) with larger absolute differences in Anxiety.

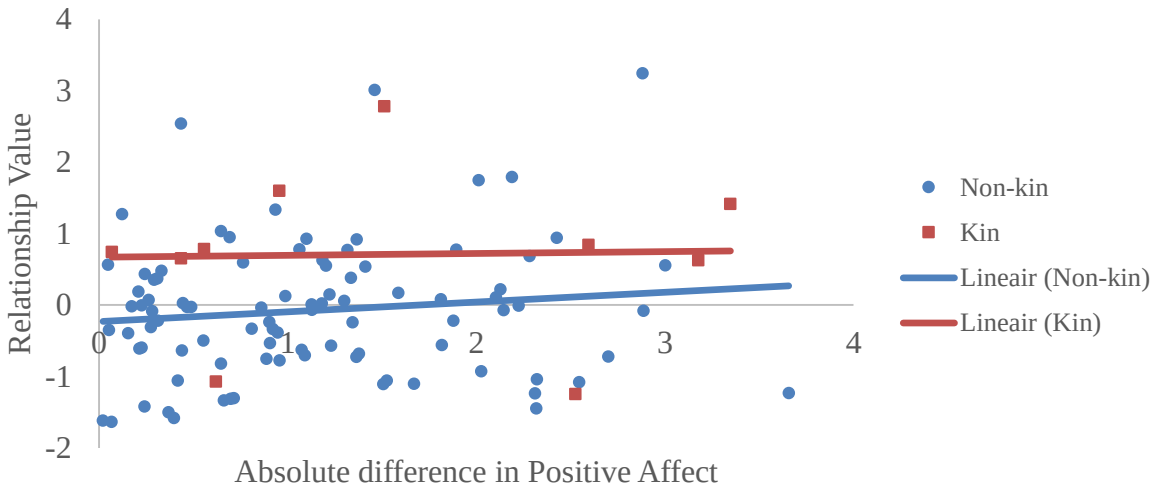

Figure 10. Relation between relationship Value and the interaction between the absolute difference in Positive Affect and maternal kinship.

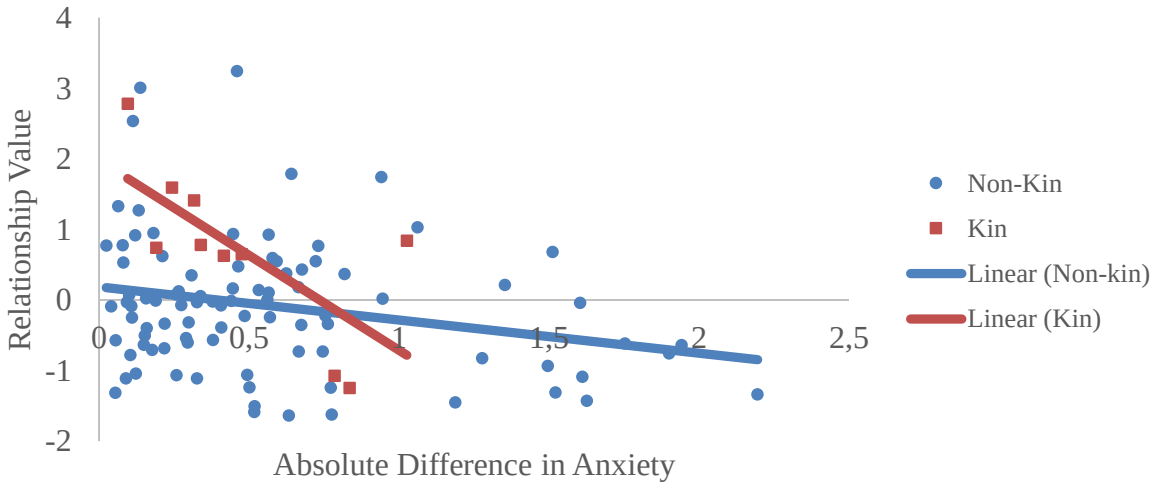

Figure 11. Relation between relationship Value and the interaction between the absolute difference in Anxiety and maternal kinship.

We found that the interaction between the absolute difference in Anxiety and rank difference had a significant influence on relationship Value ($F_{1,63.3} = 4.07$, $p = 0.05$). This indicates that the slopes for all classes of rank differences significantly differ. When breaking up the data in four quartiles, we found a weaker but not significant negative correlation (weaker homophily in Anxiety) for dyads with either the same rank (rank difference of zero) ($t_0 = 0.15$, $p = 0.88$) or individuals with relatively high rank distances (between 0.4 and 1.3) ($t_{\geq 1.3} = 0.83$, $p = 0.41$) and a stronger (not-significant: $t_{0< <0.4} = -0.47$, $p = 0.64$; $t_{0.4< <1.3} = -0.01$, $p = 0.99$) negative correlation (stronger homophily Anxiety) for dyads with rank differences between 0 and 0.4, as well as for dyads with rank differences larger than 1.3 (Figure 12).

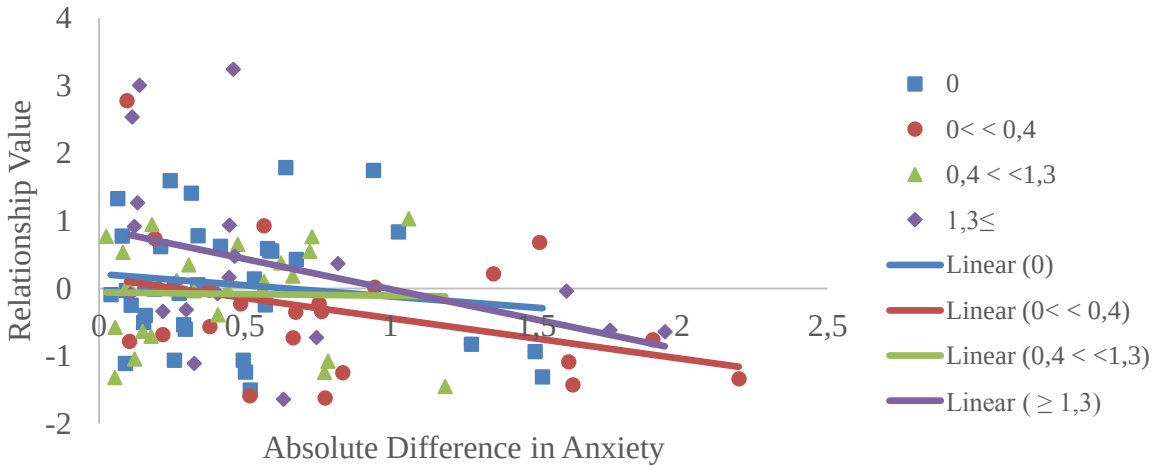

Figure 12. Relation between relationship Value and the interaction between the absolute difference in Anxiety and rank difference expressed in David's scores.

The significant interaction between the absolute difference in Anxiety and tenure ($F_{1,76.1} = 5.06$, $p = 0.03$), indicating significant slope differences between the tenure classes, is most explicit between individuals which lived together for more than 10 years (Figure 13). However, post-hoc analysis showed that the correlations within all classes of rank differences for the absolute difference in Anxiety were not significant ($t_0 = -0.13$, $p = 0.90$; $t_{0< <0.4} = -0.25$, $p = 0.80$; $t_{0.4< <1.3} = -0.49$, $p = 0.62$; $t_{\geq 1.3} = -0.61$, $p = 0.5480$). In dyads which lived together for more than 10 years relationship Value is higher between individuals with a low difference in Anxiety (homophily in Anxiety is present). This homophily effect in Anxiety was lower, but still present in dyads which resided for an intermedium period (4-10 years). Between individuals which knew each other for less than 4 years, relationship Value was higher when individuals were less similar according to Anxiety (no homophily in Anxiety).

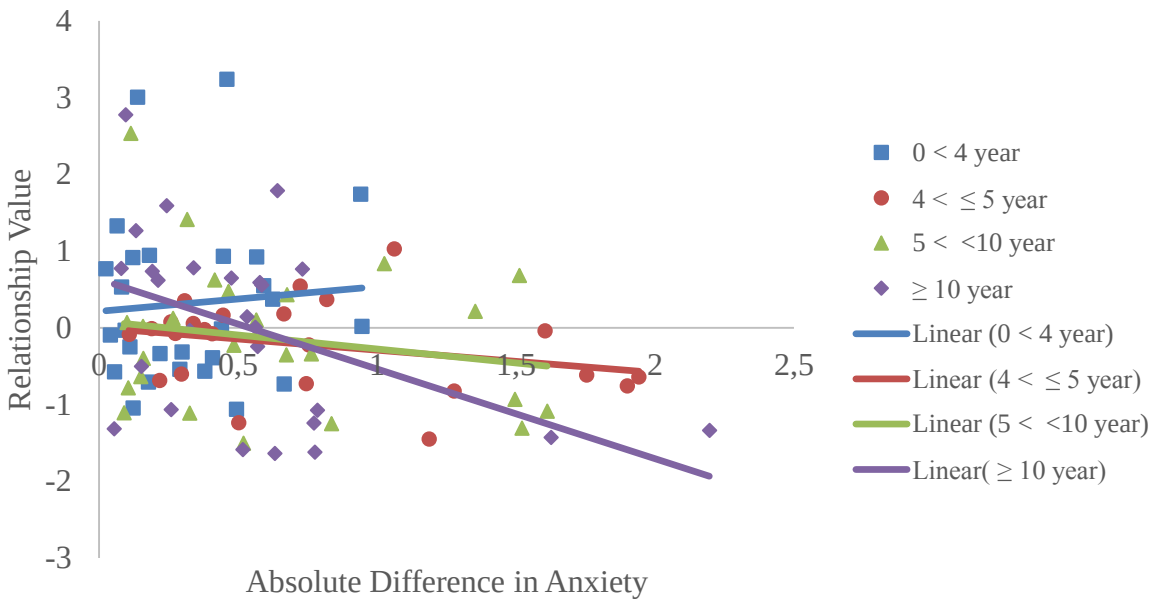

Figure 13. Relation between relationship Value and the interaction between the absolute difference in Anxiety and tenure.

4.2.2.3. Relationship Compatibility

Relationship Compatibility was significantly influenced by all non-dispositional main effects: sex combination, rank difference, age difference, maternal kinship and tenure. However, for further results on these factors see appendix D. Here, we only present all main effects and the significant dispositional interaction effects (Table 9).

Table 9. All main effects and the significant interactions effects on relationship Compatibility, assessed with a Linear Mixed Model (LMM). An asterisk indicates a significant effect: p-value <0.05.

	Effect	Num df	Denom df	F Value	P-Value
Non-dispositional	**Sex combination**	**2**	**83.0**	**6.67**	**<0.01***
	Rank difference	**1**	**86.4**	**4.86**	**0.03***
	Age difference	**1**	**64.8**	**8.94**	**<0.01***
	Maternal kinship	**1**	**73.5**	**7.08**	**0.01***
	Tenure	**1**	**74.5**	**9.99**	**<0.01***
Dispositional	Abs. difference in Sociability	1	75.7	1.51	0.22
	Abs. difference in Positive Affect	1	82.1	0.1	0.75
	Abs. difference in Anxiety	1	86.9	3.49	0.07
Significant interactions	**Positive Affect*Age difference**	**1**	**84.6**	**5.63**	**0.02***
	Anxiety*Sex combination	**2**	**83.9**	**3.39**	**0.04***
	Anxiety*Rank difference	**1**	**82.0**	**9.38**	**<0.01***
	Anxiety*Tenure	**1**	**81.5**	**11.43**	**<0.01***

For presentation of the non-dispositional variables see Appendix D

Relationship Compatibility was not significantly influenced by any of the dispositional main effects. Thus absolute differences in personality scores did not directly influence relationship Compatibility. A significant interaction effect ($F_{1,84.6}$ = 5.63, p = 0.02) between the absolute difference in Positive Affect and age difference was found. This indicates that the slopes between the different age classes and the absolute difference in Positive Affect significantly differ from each other. We found a steeper but not significant ($t_{0\leq <6}$ =-1.15, p = 0.26; $t_{6\leq \leq 11}$ =-0.30, p = 0.76; $t_{11< <23}$ =-0.50, p = 0.62) negative correlation (stronger homophily) for Anxiety in individuals with large age differences (more than 6 years). Figure 14 shows that for dyads with small age differences (between 0-6 year differences), relationship Compatibility is higher between individuals with large differences in Positive Affect. However, post-hoc analysis showed that the correlation within this age class is not significant ($t_{\geq 23}$ =-1.33, p = 0.19 (Figure 14).

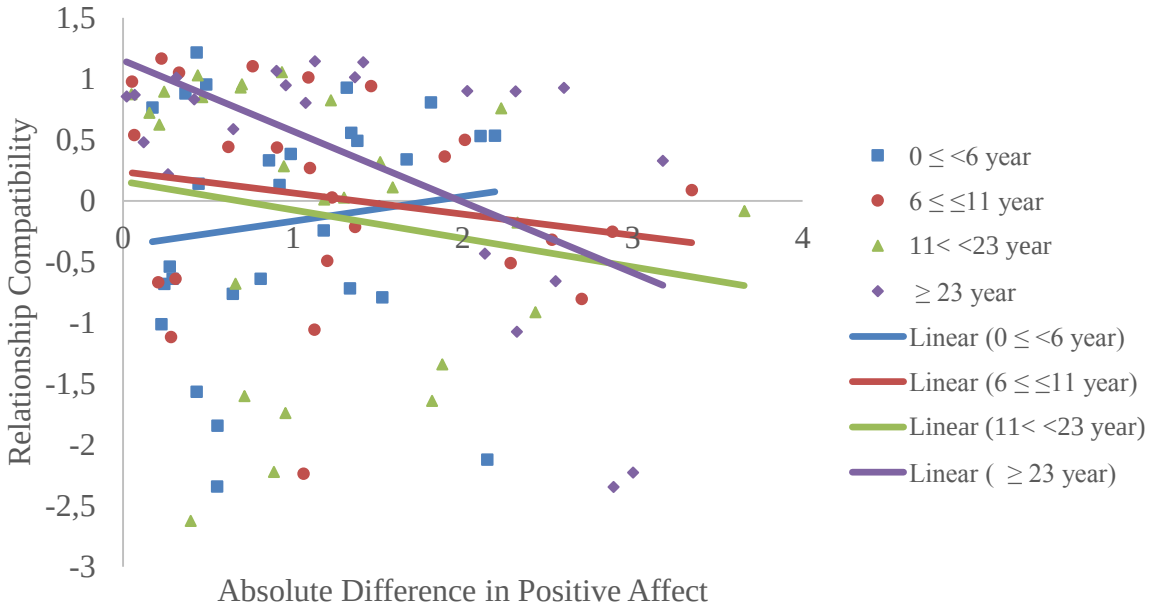

Figure 14. Relation between relationship Compatibility and the interaction between the absolute difference in Positive Affect and age difference.

We also found interaction effects on relationship Compatibility between absolute difference in Anxiety and sex combination ($F_{2,83.9}$ = 3.39, p = 0.04), rank difference ($F_{1,82.0}$ = 9,38 p = <0.01) and tenure ($F_{1,81.5}$ = 11.43, p = <0.01).

For female-female dyads, the difference in Anxiety did not affect relationship Compatibility (t_{FF} = 0.37, p = 0.71). For male-male dyads, relationship Compatibility is much higher between

individuals with greater Anxiety differences (no homophily in Anxiety) while between males and females a slightly negative relation is found (homophily effect in Anxiety. Male-female dyads with large Anxiety differences will have lower relationship Compatibility (Figure 15). However post-hoc testing showed that also for male-female (t_{MF} = -0.40, p = 0.69) and male-male (t_{MM} = 1.73, p = 0.09) dyads, no significant correlation could be found.

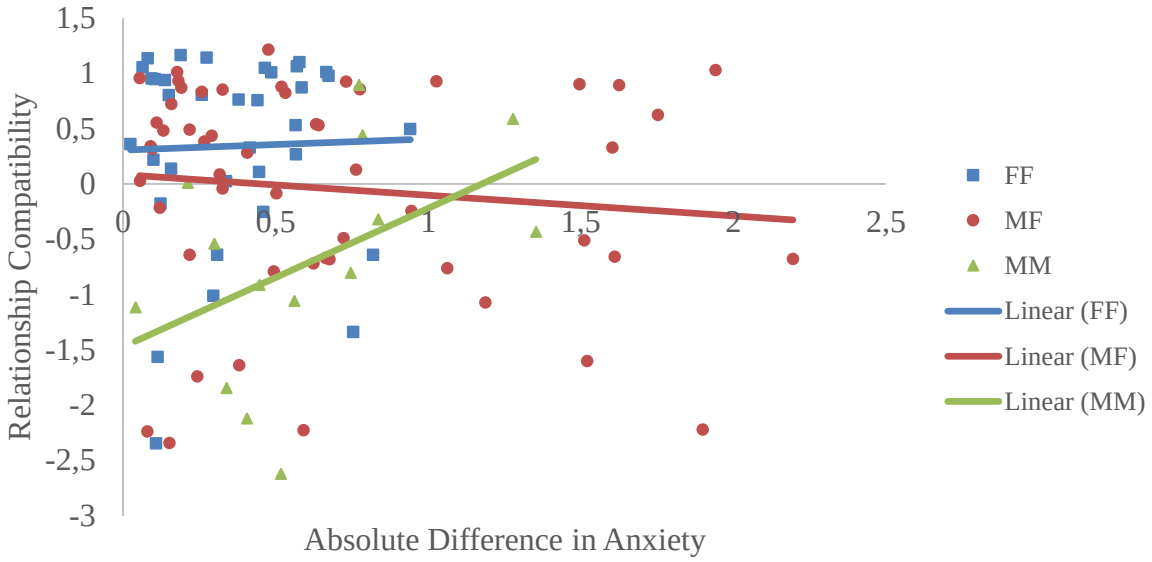

Figure 15. Relation between relationship Compatibility and the interaction between the absolute difference in Anxiety and sex combination (FF: female-female dyads; MF: male-female dyads; MM: male-male dyads).

For dyads consisting of individuals with no difference in rank or with very large differences in rank, relationship Compatibility is higher when the absolute difference in Anxiety is larger and the other way around (no homophily in Anxiety). For intermedium values of rank difference, relationship Compatibility between individuals is higher with smaller differences in Anxiety (homophily in Anxiety is present) (Figure 16). However, post-hoc analysis showed that none of the correlations within the classes of rank difference were significant (t_0 =0.43, p = 0.67; $t_{0<\ <0.4}$ = -0.93, p = 0.36; $t_{0.4<\ <1.3}$ = 0.16, p = 0.87; $t_{\geq 1.3}$ = 1.37, p = 0.18).

For dyads which already resided for more than 10 years, relationship Compatibility is higher between individuals with a larger difference in Anxiety. Individuals which only lived together for less than 4years or between 5 and 10 years, relationship Compatibility is lower when the difference in Anxiety is larger. For dyads which resided for more than 4 but less or equal to 5 years, there is no effect of difference in Anxiety on the relationship Compatibility (Figure 17). Post-hoc analysis, however, showed no significant correlation within any of the tenure classes ($t_{0<\ <4}$ = -0.93, p = 0.36; $t_{4<\leq 5}$ = -0.67, p = 0.51; $t_{5<\ <10}$ = 1.45, p = 0.16; $t_{\geq 10}$ = 1.46, p = 0.16).

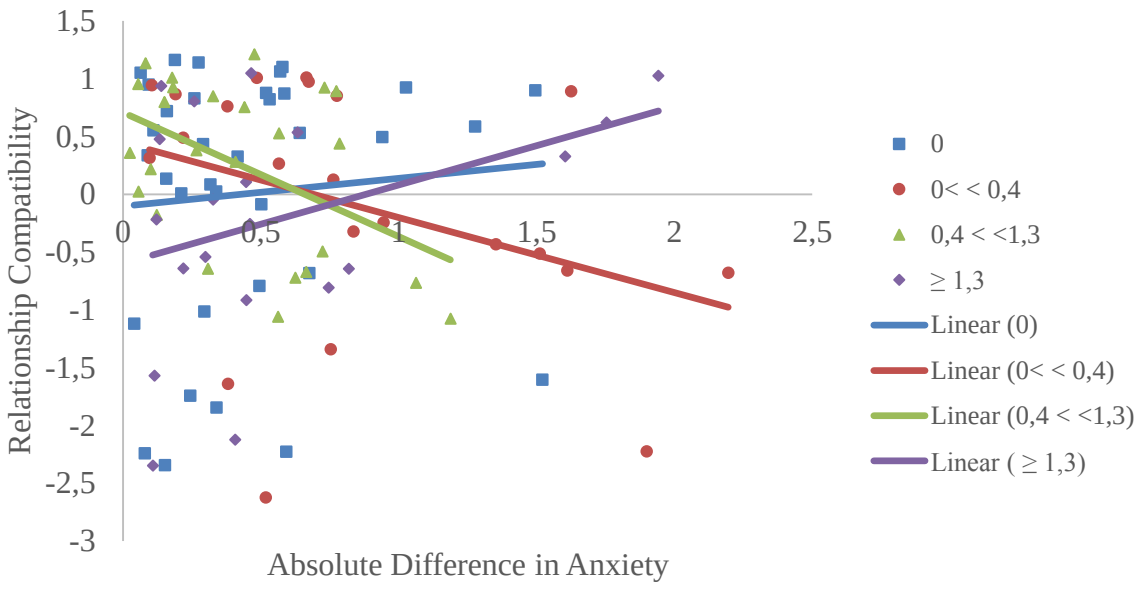

Figure 16. Relation between relationship Compatibility and the interaction between the absolute difference in Anxiety and rank difference (expressed in David's scores).

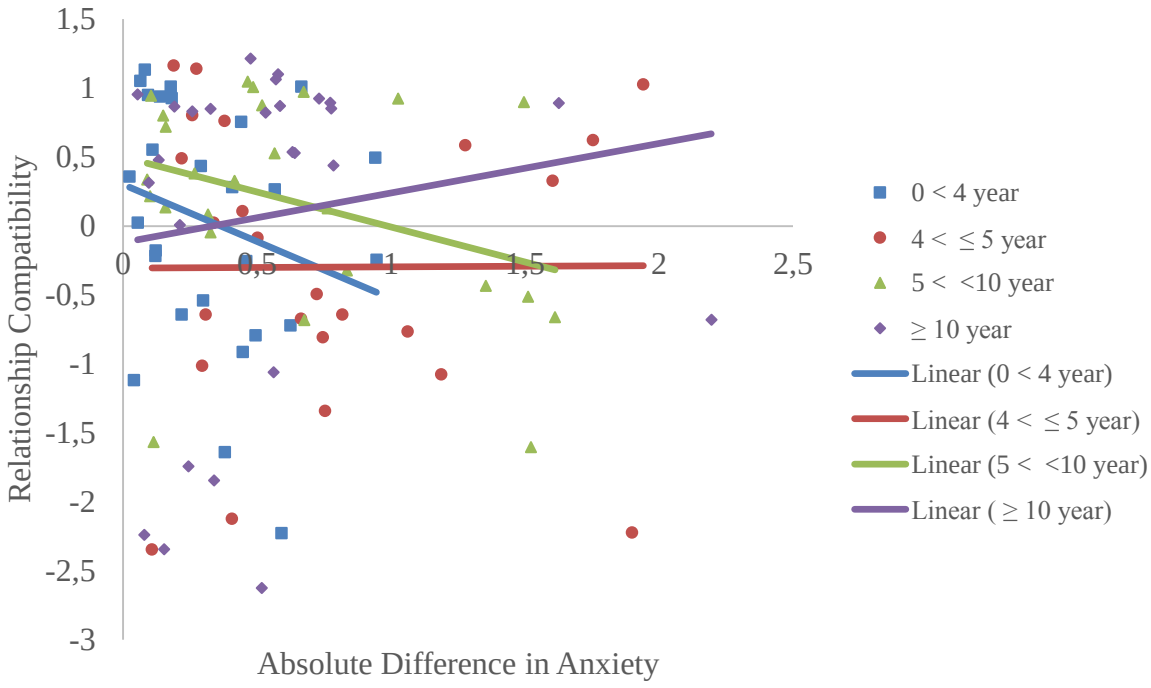

Figure 17. Relation between relationship Compatibility and the interaction between the absolute difference in Anxiety and tenure.

5. Discussion

During this study we aimed to see whether differences in personality scores between individuals influenced their friendship. We used behavioural observations to calculate personality scores and correlated these with a conventional measure of friendship based on the outcomes of PCA. We expected to find a similar personality model as in previous bonobo studies, and like in studies on chimpanzees we expected that individuals with small differences in personality scores would have stronger friendships.

5.1. Factors influencing personality similarity

5.1.1. The personality model

The first aim of this study was to become personality traits in captive bonobos. To enlarge the sample size, only observational data of naturalistic conditions were used as some individuals were not included in previous experimental studies. Based on these data, three personality traits were found, similar to previous studies on bonobo personality that have used partially the same dataset (Roelofs, 2014; Wildenburg, 2014). Koski (2011) found for chimpanzees a more complex model with five different behavioural traits.

The first factor included positive loadings for grooming frequencies, proximity with other group members and a negative loading for autogrooming. These behaviours reflect components of relationship maintenance in bonobos (Sakamaki, 2013; Vervaecke *et al.*, 2000b) and therefore we labelled it 'Sociability'. More sociable individuals showed higher frequencies of grooming interactions and had a higher number of neighbours sitting in close proximity, which indicates higher investment of time and energy in their social relationships. On the other hand, individuals scoring low on this factor will show higher frequencies of autogrooming. In Koski's study (2011), autogrooming had high positive loadings on the personality trait 'Anxiety'. However, in the unpublished work of Wildenburg (2014), autogrooming also loaded negatively on Sociability. It is possible that the function of autogrooming differs in bonobos and chimpanzees. A study that investigates the stress reducing effects of autogrooming by examining cortisol levels in bonobos for example could help to resolve this puzzle.

For now, we conclude that more sociable bonobos showed lower autogroom frequencies, spend more time grooming others and were more in proximity of larger amount of neighbours, which indicates higher investment in time and energy to maintain social bonds.

The second personality trait included the tendency to approach others, play activity and received aggressions which are all, except for the latter, affiliative behaviours. Therefore we labelled it 'Positive Affect', similar to what Koski (2011) found in her study on chimpanzees. Aggression received was not included in Koski's analyses, because it was not replicable. In the study of Wildenburg (2014), play also loaded on Positive affect. In the study of Roelofs (2014) aggression received loaded, together with submission, on Dominance. However, submission was not a repeatable variable in our personality model (Staes *et al.*, in preparation).

A possible explanation for the presence of received aggression and play in the same personality trait in bonobos may be that play could be used as a tension reduction tactic (Palagi & Paoli, 2008). Therefore, individuals which receive most aggressions would have higher play frequencies to lower the tension in active periods like pre-feeding for example.

The last trait we found was based on the self-directed behaviour auto-scratching, grooming density given and received and a negative loading for activity. The composition of this personality trait is uncommon as higher grooming densities do not indicate Anxiety. Further, Wildenburg (2014) found a negative loading of grooming density given on Anxiety. However, we labelled this personality factor Anxiety because of the high loading of scratch and activity, which are considered to be indicators of Anxiety (Baker & Aureli, 1997; Schino *et al.*, 1996). In the chimpanzee study (Koski, 2011), Activity was a separate component, together with aggression given (which was not repeatable in our personality model).

Despite the fact that Roelofs (2014), Wildenburg (2014) and we used data on the same bonobo groups, some different results were found. The variable group compositions and the use of the new data which we collected ourselves may be possible explanations. As zoo managements want to reduce stressful interactions between bonobos, less but more variable aggressions may be present. Using these behaviours in personality analysis may therefore change the personality structure. Longer observational periods, less variable group compositions and especially larger captive groups could reduce this variability.

As with all personality studies, labelling of the traits is subjective, and care should be undertaken not to identify the label of the trait too strongly with its subjective name. The three personality factors in this study have similar names to the ones in the chimpanzee studies by Koksi (2011) and Massen & Koski (2014) but are not entirely similar. However, as both species differ in several socioecological aspects and behaviours may have different functions, differences in personality factors may be expected.

5.1.2. Factors influencing homophily in personality

Second, I aimed to determine whether the non-dispositional effects sex combination, degree of kinship, age difference, rank difference and tenure influence personality differences between dyads. For the majority of these factors we did not have specific predictions.

The absolute difference in Sociability and Anxiety between individuals of a dyad were not significantly influenced by any of the predictor variables included in this study.

However, differences in Positive Affect were larger between individuals with large age differences, between related individuals and between individuals which only reside together for a relatively short period. According to the similarity principle of de Waal and Luttrell (1986), individuals with similar ages and similar social background would form stronger bonds, which confirms our findings. The stronger correlation for related individuals may be biased as we only included one mother-daughter dyad, three maternal brother dyads and seven mother-son dyads. Like we expected, a negative correlation between the absolute difference in Positive Affect and tenure was found. Namely, longer tenures were only present between older individuals and play levels decrease with age (Palagi & Paoli, 2007).

5.2. Factors influencing friendship

We found that in bonobos homophily of some personality traits is related to dyadic friendship, as assessed with both the conventional measure of contact-sitting and the composite measure of relationship quality. In broad terms individuals with similar Sociability scores had stronger friendships based on contact sitting, on relationship value but not on relationship compatibility.

5.2.1. Components of relationship Quality

We aimed to find the different components of relationship quality as suggested by Cords and Aureli (2000) and to determine the effect of similarity in personality together with sex combination, degree of kinship, age difference, rank difference and tenure on these components.

As predicted, combining principle component analysis and Parallel analysis, only two components of relationship quality could be found. Using different data, our findings, including the factor loadings on the PCA, are almost identical to those of Stevens *et al.* (2014). The third component 'Security' could not be found in our study either. Stevens *et al.*, (2015) mention that this component is least consistent across studies as it contains the most species-specific

behaviours. Another possible explanation may be the length of the observation period. Security is defined as ' the predictability of the partner's response to social interactions' (Cords & Aureli, 2000). The term 'predictability' immediately implicates multiple and long term interactions between individuals so longer observational intervals may be needed to find this third component in bonobos. Overall it is striking that using a totally different dataset but with the same behavioural variables and statistical analyses, the same two factors are found. This suggests that the factors are replicable across (captive) studies and may be a promising tool to objectively describe friendships between bonobos.

5.2.2. Non-dispositional factors influencing friendships

The **non-dispositional effects** tell us something about social relationships outside of the context of personality differences. Moreover, controlling for these effects allows us to determine whether other effects than those reflected by these non-dispositional effects contribute to variation in friendships. Some personality traits like boldness for example are heritable (van Oers *et al*., 2003). Dyadic similarity in these personalities may therefore be a proxy for the degree of relatedness in these dyads.

5.2.2.1. A conventional measure of friendship: contact sitting

In bonobos, stronger friendships were found for both **female-female and male-female dyads** which is in line with findings in macaques (Majolo *et al.*, 2010) and bonobos (Stevens *et al.*, 2015) but contrary to the results on chimpanzees (Fraser *et al.*, 2008, Massen & Koski, 2014). This can be explained by the socioecological difference between chimpanzees and bonobos. Chimpanzee males form strong cooperative bonds while in bonobos strong bonds are formed between both (un)related females and between males and females (Parish, 1994; Stevens *et al.*, 2006; Stevens et al., 2015), therefore we expected female-female dyads to have the most valuable friendships. Dyads with large **rank differences** also sat more in contact. Individuals with similar rank groomed more reciprocally but not more frequently (Vervaecke *et al.*, 2000b) and therefore most intentions to sit in contact may come from the low ranked individual.

Dyads with small **age differences** sat also more in contact. According to the similarity principle of de Waal and Luttrel (1986), individuals will form bonds with others whom they most resemble. For **maternally related** bonobos, higher contact sitting scores were found. These findings are in line with our expectations resulting from studies on the inclusive fitness between

kin (Silk, 2002). Finally, higher contact sitting scores were found for dyads with longer **relationship tenure**. These findings may indicate that friendships need time to get formed.

5.2.2.2. A composite measure of friendship: relationship quality

Our results concerning the influencing non-dispositional factors on the composite measure for friendship **confirm** earlier findings by **Stevens *et al.* (2015)**, in that we found higher relationship Value in female-female dyads compared to female-male and male-male dyads and for maternal related bonobos. For related dyads and in male-female dyads, relationships became also more Valuable with longer tenure. Relationship Compatibility was also higher for related individuals and both female-female and male-female dyads, while for large rank differences relationship Compatibility was lower.

In spite of the similar findings, some **different results** were found. Dyads with small age differences had higher relationship Value, while Compatibility was higher between individuals with large age differences. However, Stevens *et al.* (2015) found no effect of age difference on either of the relationship quality components.

Further no effect of rank difference on relationship Value was found in the previous study (Stevens *et al.*, 2015), while in this study higher relationship Value was found between female-female dyads with large rank differences. Asymmetry in relationships was more explicit in female-female dyads than in male-male dyads (Majolo *et al*., 2010). Therefore, friendships in female-female dyads may be more valuable but very asymmetrical.

More Compatible relationships were found for related dyads and for dyads with longer relationship tenure, while Stevens *et al.*, (2015) did not find an effect of both maternal relatedness or tenure on Compatibility.

Concluding, both similar and differing results are found compared to the findings of Stevens *et al.* (2015). Several individuals were transferred among zoos during the period between the two studies and both the bonobo group of Wilhelma and Frankfurt zoo were not included in the study of Stevens *et al.* (2015). These differences may explain the almost identical results for the PCA analysis, while some different influencing non-dispositional factors on relationship quality were found.

5.2.3. Dispositional factors influencing friendships

Using the conventional measure of friendship, homophily in Sociability was found. Similar Sociability scores resulted in slightly, but significantly more contact sitting and therefore in stronger friendships. Higher relationship Values were also found in dyads with similar Sociability scores. Therefore, **homophily in Sociability** is found for both **the conventional measure and relationship Value**. For relationship Compatibility, however, no such homophily effect was found.

Further, several **interaction effects** between dispositional and non-dispositional factors were found. However, due to the small sample size interpreting these results have to be done cautiously.

Only for relationship Compatibility, a significant interaction effect including **sex combination** was found. A small homophily effect in Anxiety was found for male-female dyads while for same-sexed dyads, a heterophily effect was found. Dyads between same-sexed individuals with large differences in Anxiety scores consist of an individual with a high frequency of autoscratching and grooming density and a low activity level on one side and on the other side an individual with the opposite characteristics. Furthermore, compatible relationships are characterised by low frequencies of less reciprocal aggressions and few counter-interventions. Consequently, the few aggressive interactions are mostly performed towards the individual with higher Anxiety score.

For both relationship Value and relationship Compatibility, a significant interaction effect between the absolute difference in Anxiety and **rank difference** was found. For all classes of rank differences, dyads with larger absolute differences in Anxiety had less valuable relationships. However, for relationship Compatibility, this homophily effect in Anxiety was only present in dyads with intermediate rank differences ($0< <1.3$).

Further, only for relationship Value, significant interaction effects were found between similarity in personality and **maternal kinship**. For related dyads, homophily in Positive affect and Anxiety was found, while for Sociability, a heterophily effect was found. However, the number of related dyads in our sample was small (N=11) and this category included only one mother-daughter dyad, three maternal brother dyads and seven mother-son dyads (see Appendix E). Ideally, separated conclusions should be made for these different types of related dyads and further research is needed, including more related dyads, to confirm our findings.

Finally, a significant interaction effect between the absolute difference in Anxiety and relationship **tenure** was found on contact sitting, relationship Value and relationship Compatibility. For both contact sitting and relationship Value, homophily in Anxiety was

present for all relationship tenure classes and became stronger with longer tenures. Only for dyads with relationship tenure shorter than 5 year, a weak heterophily effect was found. However, for relationship Compatibility, homophily in Anxiety was present for all dyads with relationship tenures shorter than 10 year.

The significant interaction effects influencing relationship Value and contact sitting indicate that, apart from the main effect of Sociability, for specific dyads, homophily in Anxiety also results in more valuable relationships. However, for relationship Compatibility more variable results were found. Therefore, our findings indicate that the benefits resulting from relationships (relationship Value) may be more dependent of similarity in personality, more specific in Sociability and in some cases also Anxiety, between individuals, while the tolerance between friends (relationship Compatibility) may be more independent of similarity in personality. Dividing the relatively small sample size in even smaller classes for each interaction effect, may result in biased results. Therefore, the same interactions need to be verified in further research.

In general, our findings concerning the **conventional measure of friendship** are comparable to the findings of Massen and Koski (2014), in that we both found homophily in Sociability for contact sitting. Our sample size of maternal related individuals did not permit us to make correct conclusions, while for chimpanzees a significant effect of maternal relatedness was found (Massen & Koski, 2014). However, Massen and Koski (2011) also included few mother-offspring dyads but made some interpretations after all. Further, in their study on chimpanzees, relationship tenure was not included as a possible predictor variable. In our study on bonobos, the interaction between relationship tenure and Anxiety significantly influenced contact sitting. Including relationship tenure in a new study on chimpanzees is therefore recommended to become a better understanding of the influencing factors on friendships in these closely related species.

Contact sitting only measures one behavioural aspect of friendship. However, using a single measure for friendship runs the risk of interpreting relationship quality from the observer's perspective rather than from the animal's perspective (Fraser *et al.*, 2008). Furthermore, Massen and Koski (2014) considered contact sitting to be an active choice of affiliation, as it can easily be refused or broken by a partner. However, the fact that two individuals sit in contact does not automatically imply that both deliberately want to sit in contact. Both partners may also be

attracted to other elements like for example a third party (Silk, 2002). Therefore, in such contexts, sitting in contact may even be a proxy for tolerance as both individuals do not want to sit in contact but both tolerate each other's presence. Using a composite measure may therefore give a more correct and comprehensive representation of the real relationship quality (Fraser *et al.*, 2008).

Using the **composite measure of friendship**, we found a significant influence of homophily in Sociability on relationship Value. Indicating that Similarity in personality is important for the direct benefits resulting from relationship. Sociability in both our study and the study of Massen and Koski (2014) contains the tendency of being in close proximity to others and to approach others which is similar to the human personality trait 'Extraversion' (McCrae & John, 1992). In humans, friends prefer similarity in extraversion (Nelson *et al.*, 2011) which is also called Sociability (McCrae & John, 1992). Therefore, apparently similarity in Sociability results in stronger friendships in humans, chimpanzees and bonobos.

Beside the Value also the Compatibility of a relationship is determined using the composite measure. However, in the conventional measure of friendship no such component is present. Therefore, using a composite measure allowed us to determine both the Value, including the immediate benefits resulting from relationships, and Compatibility, the tolerance and affiliation between friends, which gives a more complete representation of the relationship quality.

6. Conclusion

In conclusion, the personality traits found in this study are comparable to previous findings on both chimpanzees and bonobos. Further, similarity in Sociability and Anxiety between dyads were not influenced by any non-dispositional effect while for similarity in Positive Affect different predictor variables were found.

Using contact-sitting as a measure for friendship, we found that friendships in bonobos are influenced by homophily in Sociability and Anxiety. As mentioned before, similarity in these traits may enhance reliability between dyads in cooperation. Our findings suggest that homophily in friendships is an evolutionary conserved feature present in both humans and their closest living relatives.

However, as the three-component of Cords & Aureli (2000) has been suggested to give a better representation of real friendships, the effect of homophily on tis composite measure of relationship quality was examined. We conclude that the 'Value' and 'Compatibility' component are very consistent measures of relationship quality. Using these components as a composite measure for friendship, we found that similarity in personality determines friendships in bonobos.

Furthermore, for both measures of friendship, homophily in Sociability and, for some specific dyads, Anxiety results in stronger relationships. This indicates that relationships between more similar individuals indeed may be more beneficial as de Waal and Luttrel (1986) suggested. Investments in these relationships will me more reciprocal and therefore benefits coming from these social relations are available for both partners. Therefore, the fitness of individuals involved in these valuable relationships will be higher.

However, Compatibility between individuals may be less dependent of similarity in Sociability. Relationship Compatibility measures the tolerance and affiliation between subjects based on previous interactions and is therefore important as it influences accessibility of the social partner. Dyads consisting of two unsociable or two sociable individuals may both have high Compatibility scores.

7. Perspectives for future research

As this is the first study on influences of personality on relationships between captive bonobos using behavioural coding and two different measures of friendships, further research is needed to confirm our findings. However, several recommendations can be made based on this study.

- Captive animals are often used as a representation for wild populations and therefore captive conditions should match wild conditions as much as possible. However, wild bonobo groups contain 20 to 120 individuals, while captive bonobo groups are divided in much smaller groups. Due to this separation into smaller populations, relationships and interactions are less diverse. Therefore, we suggest to repeat this study on a larger bonobo group with a more natural group composition.

- The overall captive bonobo population contains relatively young bonobos and therefore only few relationships between old individuals are present in our sample. As relationships strengthen over time, older dyads may contain interesting information. Therefore, more older individuals should be included. An interesting possibility is to conduct this study in 30 years when all bonobos in the study group will have aged.

- Only eleven maternal related dyads were included in this study: one mother-daughter dyad, three maternal brother dyads and seven mother-son dyads. Therefore, our sample size of related individuals may be highly biased (see appendix E). Larger bonobo groups would also include more related dyads and hence more interesting data could be found.

- Ideally, this study should be conducted on wild bonobos to test whether our findings are also applicable on wild populations as several conditions may be different. However, only few well habituated wild groups exist (currently only two), and observational conditions are not optimal. Therefore, collecting data on social interactions in these bonobo groups would take a considerable amount of time and money.

- Combining both relationship Value and Compatibility in one component, similar to what Morton *et al.* (2015) did, might allow us to compare the overall relationship quality between the different types of dyads in bonobos.

- Finally, social relationships between Japanese macaques have been shown to be very asymmetrical (Majolo *et al.*, 2010). Therefore, in addition to our symmetrical measures of relationship quality, asymmetrical measures should be quantified and included in the analyses.

8. References

Altmann, J. 1974. Observational study of behavior- sampling methods.

Badrian, A., and N. Badrian. 1977. Pygmy Chimpanzees. Oryx 13:463–468.

Baker & Aureli, 1997. Behavioural indicators of anxiety in chimpanzees. Behaviour 134: 1035-1053.

Beaton, E. a, L. a Schmidt, J. Schulkin, M. M. Antony, R. P. Swinson, and G. B. Hall. 2008. Different neural responses to stranger and personally familiar faces in shy and bold adults. Behavioral neuroscience 122:704–709.

Bergmüller, R., R. Schürch, and I. M. Hamilton. 2010. Evolutionary causes and consequences of consistent individual variation in cooperative behaviour. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 365:2751–2764.

Biossy, A. 2013. Fear and Fearfulness in Animals 70:165–191.

Blount, B. G. 1990. Issues in Bonobo (Pan paniscus) Sexual Behavior. American Anthropologist 92:702–714.

Bock, W. J. 2003. Ecological aspects of the evolutionary processes. Zoological science 20:279–289.

Budaev, S. V. 2010. Using principal components and factor analysis in animal behaviour research: Caveats and guidelines. Ethology 116:472–480.

Carter, A. J., A. E. G. Lee, H. Marshall, Harry, M. T. Ticó, and G. Cowlishaw. 2015. Phenotypic assortment in wild primate networks : implications for the dissemination of information. The Royal Society.

Castles, D. L., A. Whiten, and F. Aureli. 1999. Social anxiety , relationships and self-directed behaviour among wild female olive baboons:1207–1215. 2:140444.

Chapais, B. 2001. Primatenepotism: what is the explanatory value of kin selection? International Journal of Primatology 22:203–229.

Clarke, a. S., and S. Boinski. 1995. Temperament in nonhuman primates. American Journal of Primatology 37:103–125.

Clutton-Brock, T., and E. Huchard. 2013. Social competition and its consequences in female mammals. Journal of Zoology 289:151–171.

Cole, E. F., and J. L. Quinn. 2014. Shy birds play it safe: personality in captivity predicts risk responsiveness during reproduction in the wild. Biology letters 10:20140178.

Coleman, K., and D. Wilson. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. Animal behaviour 56:927–936.

Connor, B. P. O. 2000. Parallel analysis 32:396–402.

Coolidge, H. J. 1933. Pan paniscus. Pigmy chimpanzee from south of the congo river. American Journal of Physical Anthropology 18:1–59.

Cooper, M. A., I. S. Bernstein, and C. K. Hemelrijk. 2005. Reconciliation and Relationship Quality in Assamese Macaques (Macaca assamensis) 282:269–282.

Cote, J., and J. Clobert. 2007. Social personalities influence natal dispersal in a lizard. Proceedings. Biological sciences / The Royal Society 274:383–390.

Cords, M. & Aureli, F. (2000). Reconciliation and relationship qualities. — In: Natural conflict resolution (Aureli, F. & de Waal, F.B.M., eds). University of California Press, Berkeley, CA, 177-198.

Crawford MP. 1938. A behavior rating scale for young chimpanzees. Journal of Comparative Psychology 26:79–91.

Dall, S. R. X., A. I. Houston, and J. M. McNamara. 2004. The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. Ecology Letters 7:734–739.

David, H. a. 1987. Ranking from unbalanced paired-comparison data. Biometrika 74:432–436.

Digman, J. M. 1990. Personality Structure: Emergence of the Five-factor Model. Annual Review of Psychology 41:417–440.

Dingemanse, N. J., C. Both, P. J. Drent, K. Van Oers, and a J. Van Noordwijk. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. Animal Behaviour 64:929–938.

Dingemanse, N., and D. Réale. 2005. Natural selection and animal personality. Behaviour 142:1159–1184.

Dirienzo, N., and A. V. Hedrick. 2014. Animal personalities and their implications for complex signaling. Current Zoology 60:381–386.

Van Dongen, S. 2011. Short R Tutorial , course notes and exercises for the Biostatistics course.

Edgar, H. J. H. 2007. Microevolution of African American dental morphology. American journal of physical anthropology 132:535–544.

Field, A. 2009. Discovering Statistics Using SPSS.

Fraser, O. N., and T. Bugnyar. 2010. The quality of social relationships in ravens. Animal Behaviour 79:927–933.

Fraser, O. N., G. Schino, and F. Aureli. 2008. Components of relationship quality in chimpanzees. Ethology 114:834–843.

Freeman, H. D., and S. D. Gosling. 2010. Personality in nonhuman primates: A review and evaluation of past research. American Journal of Primatology 72:653–671.

Freeman, H., S. D. Gosling, and S. J. Schapiro. 2011. Personality and Temperament in Nonhuman Primates. Pages 17–40 Developments in Primatology: Progress and Prospects. Department of Psychology.

Fruth, B., G. Hohmann, and W. C. McGrew. 1999. The Pan Species. The Nonhuman Primates:64–72.

Furuichi, T. 1989. Social interactions and the life history of female Pan paniscus in Wamba, Zaire. International Journal of Primatology 10:173–197.

Furuichi, T. 1997. Agonistic interactions and matrifocal dominance rank of wild Bonobos (Pan paniscus) at Wamba. International Journal of Primatology 18:855–875.

Furuichi, T. 2009. Factors underlying party size differences between chimpanzees and bonobos: A review and hypotheses for future study. Primates 50:197–209.

Furuichi, T., and H. Ihobe. 1994. Variation in Male Relationships in Bonobos and Chimpanzees. Behaviour 130:211–228.

Gammell, M., and H. De Vries. 2003. David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. Animal Behaviour 66:601–605.

Goldberg, L. R., D. Sweeney, P. F. Merenda, and J. E. Hughes. 1996. The Big-Five factor structure as an integrative framework: an analysis of Clarke's AVA model. Journal of Personality 66(3):441-471.

Gosling, S. D. 2001. Gosling, 2001, from mice to men what can we learn about personality from animal research.pdf. Psychological Bulletin 127:45–86.

Groothuis, T. G. G., and C. Carere. 2005. Avian personalities: Characterization and epigenesis. Neuroscience and Biobehavioral Reviews 29:137–150.

Groothuis, T. G. G., and F. Trillmich. 2011. Unfolding personalities: The importance of studying ontogeny. Developmental Psychobiology 53:641–655.

Hashimoto, C., O. Takenaka, and T. Furuichi. 1996. Matrilineal kin relationship and social behavior of wild bonobos (Pan paniscus): Sequencing the D-loop region of mitochondrial DNA. Primates 37:305–318.

Hinde, R. A. 1976. Interactions, Relationships and Social Structure. Man 11:1–17.

Hohmann, G., U. Gerloff, D. Tautz, and B. Fruth. 1999. Social Bonds and Genetic Ties : Kinship , Association and Affiliation in a Community of Bonobos (Pan Paniscus). Behaviour 136:1219–1235.

Jokela, M., M. Kivimäki, M. Elovainio, and L. Keltikangas-Järvinen. 2009. Personality and having children: a two-way relationship. Journal of personality and social psychology 96:218–230.

Kano, Y. 1992. The Last Ape. Stanford University Press.

King, J. E., and a J. Figueredo. 1997. The five-factor model plus dominance in chimpanzee personality. Journal of Research in Personality 31:257–271.

Koolhaas, J. M., S. M. Korte, S. F. De Boer, B. J. Van Der Vegt, C. G. Van Reenen, H. Hopster, I. C. De Jong, M. a W. Ruis, and H. J. Blokhuis. 1999. Coping styles in animals: Current status in behavior and stress-physiology. Neuroscience and Biobehavioral Reviews 23:925–935.

Koski, S. E. 2011. Social personality traits in chimpanzees: Temporal stability and structure of behaviourally assessed personality traits in three captive populations. Behavioral Ecology and Sociobiology 65:2161–2174.

Koski, S. E., K. Koops, and E. Sterck. 2007. Reconciliation, Relationship Quality, and Postconflict ANxiety: Testing the Integrated Hypothesis in Captive Chimpanzees. American Journal of Primatology 69:158–172.

Koski, S. E., H. De Vries, A. van de Kraats, and E. H. M. Sterck. 2012. Stability and change of social relationship quality in captive chimpanzees. International Journal of Biological Sciences 33:905–921.

Kuroda, S. 1979. Grouping of the pygmy chimpanzees. Primates 20:161–183.

Kutsukake, N. 2003: Assessing relationship quality and social anxiety among wild chimpanzees using self-directed behaviour. Behaviour 140:1153—1171.

Lacambra, C., J. Thompson, T. Furuichi, H. Vervaecke, and J. Stevens. 2005. Bonobo (Pan paniscus). World Atlas of Great Apes and Their Conservation. 30–44.

López, P., D. Hawlena, V. Polo, L. Amo, and J. Martín. 2005. Sources of individual shy-bold variations in antipredator behaviour of male Iberian rock lizards. Animal Behaviour 69:1–9.

Maestripieri, D., G. Schino, F. Aureli, and A. Troisi. 1992. A modest proposal: displacement activities as an indicator of emotions in primates. Animal Behaviour 44:967–979.

Majolo, B., R. Ventura, and N. Koyama. 2005. Japanese Macaques 26:321–336.

Majolo, B., R. Ventura, and G. Schino. 2010. Asymmetry and Dimensions of Relationship Quality in the Japanese Macaque (Macaca fuscata yakui). International Journal of Primatology 31:736–750.

Manson, J. H., and S. Perry. 1999. Correlates of Self-Directed Behaviour in Wild White-Faced Capuchins. Ethology 106:301-317.

Massen, J. J. M., A. Antonides, A. M. K. Arnold, T. Bionda, and S. E. Koski. 2013. A behavioral view on chimpanzee personality: Exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. American Journal of Primatology 75:947–958.

Massen, J. J. M., and S. E. Koski. 2014. Chimps of a feather sit together: Chimpanzee friendships are based on homophily in personality. Evolution and Human Behavior 35:1–8.

McCrae, R. R., and O. P. John. 1992. An introduction to the five-factor model and its applications. Journal of personality 60:175–215.

McFarland, R., and B. Majolo. 2011. Exploring the components, asymmetry and distribution of relationship quality in wild barbary macaques (Macaca sylvanus). PLoS ONE 6:1-7.

Mcpherson, M., L. Smith-lovin, and J. M. Cook. 2001. B IRDS OF A F EATHER : Homophily in Social Networks. Annual Review of Sociology 27:415–444.

Morton, F. B., A. Weiss, H. M. Buchanan-Smith, and P. C. Lee. 2015. Capuchin monkeys with similar personalities have higher-quality relationships independent of age, sex, kinship and rank. Animal Behaviour 105:163–171.

Nelson, P. a., A. Thorne, and L. a. Shapiro. 2011. I'm outgoing and she's reserved: The reciprocal dynamics of personality in close friendships in young adulthood. Journal of Personality 79:1113–1148.

Nettle, D. 2005. An evolutionary approach to the extraversion continuum. Evolution and Human Behavior 26:363–373.

Van Elsacker, L., H. Vervaecke, and R. F. Verheyen. 1995. A review of terminology on aggregation patterns in bonobos (Pan paniscus). International Journal of Primatology 16:37–52.

Van Oers, K., M. Klunder, and P. J. Drent. 2005. Context dependence of personalities: Risk-taking behavior in a social and a nonsocial situation. Behavioral Ecology 16:716–723.

Palagi, E., and T. Paoli. 2008. Social Play in Bonobos: Not Only an Immature Matter. The Bonobos: Behaviors, Ecology, and Conservation:55–74.

Palagi, E., T. Paoli, and S. B. Tarli. 2006. Short-term benefits of play behavior and conflict prevention in Pan paniscus. International Journal of Primatology 27:1257–1270.

Parish, A. R. 1994. Sex and food control in the "uncommon chimpanzee": How Bonobo females overcome a phylogenetic legacy of male dominance. Ethology and Sociobiology 15:157–179.

Parish, A. R. 1996. Female Relationships in Bonobos (Pan paniscus): Evidence for Bonding, Cooperation, and Female Dominance in a Male-Philopatric Species. Human Nature 7:61–96.

Pritchard, A. J., L. K. Sheeran, K. I. Gabriel, J. H. Li, and R. S. Wagner. 2014. Behaviors that predict personality components in adult free-ranging Tibetan macaques Macaca thibetana. Current Zoology 60:362–372.

Prüfer, K., K. Munch, I. Hellmann, K. Akagi, J. R. Miller, B. Walenz, S. Koren, G. Sutton, C. Kodira, R. Winer, J. R. Knight, J. C. Mullikin, S. J. Meader, C. P. Ponting, G. Lunter, S. Higashino, A. Hobolth, J. Dutheil, E. Karakoç, C. Alkan, S. Sajjadian, C. R. Catacchio, M. Ventura, T. Marques-Bonet, E. E. Eichler, C. André, R. Atencia, L. Mugisha, J. Junhold, N. Patterson, M. Siebauer, J. M. Good, A. Fischer, S. E. Ptak, M. Lachmann, D. E. Symer, T. Mailund, M. H. Schierup, A. M. Andrés, J. Kelso, and S. Pääbo. 2012. The bonobo genome compared with the chimpanzee and human genomes. Nature 2012:1-5.

Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews 82:291–318.

Rebecchini, L., C. M. Schaffner, and F. Aureli. 2011. Risk is a Component of Social Relationships in Spider Monkeys. Ethology 117:691–699.

Rivas, J. 2008. Friendship Selection. EUI Working Papers 15:1–63.

Roelofs, S. 2014. Behavioral Assessment of Bonobo (Pan paniscus) Personality Traits.

Sakamaki, T. 2013. Social grooming among wild bonobos (Pan paniscus) at Wamba in the Luo Scientific Reserve, DR Congo, with special reference to the formation of grooming gatherings. Primates 54:349–359.

Sapolsky, R. M., S. C. Alberts, and J. Altmann. 1997. Hypercortisolism associated with social subordinance.pdf. Archives of General Psychiatry 54:1137–1143.

Schino, G., G. Perretta, a M. Taglioni, V. Monaco, and a Troisi. 1996. Primate displacement activities as an ethopharmacological model of anxiety. Anxiety 2:186–191.

Schuett, W., S. R. X. Dall, and N. J. Royle. 2011. Pairs of zebra finches with similar "personalities" make better parents. Animal Behaviour 81:609–618.

Schwartz, E. (1929). Das vorkommen des Schimpansen auf den linken Kongo-Ufer. Revue de Zoologie et de Botanique Africaines. 16:425-433.

Seeman, T. E., and B. S. McEwen. 1996. Impact of social environment characteristics on neuroendocrine regulation. Psychosomatic medicine 58:459–71.

Shea, B. T., and H. J. Coolidge. 1988. Craniometric differentiation and systematics in the genus Pan. Journal of Human Evolution 17:671–685.

Silk, J. B. 2002. Kin Seletion in Primate Groups. International Journal of Primatology 23:849–875.

Silk, J. B. 2007. The adaptive value of sociality in mammalian groups. Philosophical Transactions of the Royal Society B: Biological Science 362(1480):539–559.

Silk, J. B., S. C. Alberts, and J. Altmann. 2003. Social bonds of female baboons enhance infant survival. Science (New York, N.Y.) 302:1231–1234.

Silk, J. B., J. C. Beehner, T. J. Bergman, C. Crockford, A. L. Engh, L. R. Moscovice, R. M. Wittig, R. M. Seyfarth, and D. L. Cheney. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proceedings. Biological sciences / The Royal Society 276:3099–3104.

Sinn, D. L., S. D. Gosling, and N. a. Moltschaniwskyj. 2008. Development of shy/bold behaviour in squid: context-specific phenotypes associated with developmental plasticity. Animal Behaviour 75:433–442.

Stanford, C. B. 1998. The Social Behavior of Chimpanzees and Bonobos: Empirical Evidence and Shifting Assumptions. Current Anthropology 39:399–420.

Stevens, J. M. G., E. de Groot, and N. Staes. 2015. Relationship quality in captive bonobo groups. Behaviour 152:259–283.

Stevens, J. M. G., H. Vervaecke, H. De Vries, and L. Van Elsacker. 2005. Peering is not a formal indicator of subordination in bonobos (Pan paniscus). American Journal of Primatology 65:255–267.

Stevens, J. M. G., H. Vervaecke, H. de Vries, and L. van Elsacker. 2006. Social structures in Pan paniscus: Testing the female bonding hypothesis. Primates 47:210–217.

Stevens, J. M. G., H. Vervaecke, H. De Vries, and L. Van Elsacker. 2007. Sex differences in the steepness of dominance hierarchies in captive bonobo groups. International Journal of Primatology 28:1417–1430.

Stumpf, R. 2007. Chimpanzees and bonobos: diversity within and between species. *Primates in Perspective, 2nd Edition*. Ed. CJ Campbell, A Fuentes, KC MacKinnon, SK Bearder, and RM Stumpf. Oxford: Oxford University Press, 2011.

Surbeck, M., R. Mundry, and G. Hohmann. 2011. Mothers matter! Maternal support, dominance status and mating success in male bonobos (Pan paniscus). Proceedings. Biological sciences / The Royal Society 278:590–598.

Uher, J., and J. B. Asendorpf. 2008. Personality assessment in the Great Apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. Journal of Research in Personality 42:821–838.

Uher, J., J. B. Asendorpf, and J. Call. 2008. Personality in the behaviour of great apes: temporal stability, cross-situational consistency and coherence in response. Animal Behaviour 75:99–112.

Van Oers, K., P. J. Drent, P. de Goede, and A. J. van Noordwijk. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. Proceedings. Biological sciences / The Royal Society 271:65–73.

Vervaecke, H., H. De Vries, and L. van Elsacker. 1999. An Experimental Evaluation of the Consistency of Competitive Ability and Agonisitc Dominance in Different Contexts in Captive Bonobos. Behaviour 136:423–442.

Vervaecke, H., H. De Vries, and L. Van Elsacker. 2000. Dominance and its behavioral measures in a captive group of bonobos (Pan paniscus). International Journal of Primatology 21:47–68.

Vervaecke, H., L. Van Elsacker, and H. De Vries. 2000b. the Pivotal Role of Rank in Grooming and Support Behavior in a Captive Group of Bonobos (Pan Paniscus). Behaviour 137:1463–1485.

De Vos, H., E. Sterck, and J. Massen. 2010. Close social associations in animals and humans: functions and mechanisms of friendship. Behaviour 147:1379–1412.

De Waal, F. B. 1995. Bonobo sex and society. Scientific American 272:82–88.

De Waal, F. B. M., and L. M. Luttrell. 1986. The Similarity Principle Underlying Social Bonding among Female Rhesus Monkeys. Folia primatologica 46:215–234.

Ward, a. J. W., P. Thomas, P. J. B. Hart, and J. Krause. 2004. Correlates of boldness in three-spined sticklebacks (Gasterosteus aculeatus). Behavioral Ecology and Sociobiology 55:561–568.

Watters, J. V, and D. M. Powell. 2012. Measuring animal personality for use in population management in zoos: suggested methods and rationale. Zoo biology 31:1–12.

Weaver, A., and F. B. M. de Waal. 2002. An index of relationship quality based on attachment theory. Journal of comparative psychology 116:93–106.

Weiss, A., M. Inoue-Murayama, J. E. King, M. J. Adams, and T. Matsuzawa. 2012. All too human? Chimpanzee and orang-utan personalities are not anthropomorphic projections. Animal Behaviour 83:1355–1365.

Wildenburg, M. C. E. 2014. Pan Personality Differences.

Wildman, D. E., M. Uddin, G. Liu, L. I. Grossman, and M. Goodman. 2003. Implications of natural selection in shaping 99.4% nonsynonymous DNA identity between humans and chimpanzees: enlarging genus Homo. Proceedings of the National Academy of Sciences of the United States of America 100:7181–7188.

Wilson, D. S. 1998. Adaptive individual differences within single populations. Philosophical Transactions of the Royal Society B: Biological Sciences 353:199–205.

Wilson, D. S., A. B. Clark, A. Clark, K. Coleman, and T. Dearstyne. 1994. Adaptive individual differences within single populations. Philosophical Transactions of the Royal Society B. 353:199-205.

Wolf, M., G. S. van Doorn, O. Leimar, and F. J. Weissing. 2007. Life-history trade-offs favour the evolution of animal personalities. Nature 447:581–584.

Won, Y. J., and J. Hey. 2005. Divergence population genetics of chimpanzees. Molecular Biology and Evolution 22:297–307.

Wynne, C. D. L. 2004. Consciousness should be ascribed to animals only with extreme caution . Nature 428:2004.

Yamakoshi, G. 2004. Food seasonality and socioecology in Pan: Are west African chimpanzees another bonobo? African Study Monographs 25:45–60.

Yerkes RM. 1939. The life history and personality of the chimpanzee. The American Naturalist 73:97–112.

Yu, N., M. I. Jensen-Seaman, L. Chemnick, J. R. Kidd, A. S. Deinard, O. Ryder, K. K. Kidd, and W. H. Li. 2003. Low nucleotide diversity in chimpanzees and bonobos. Genetics 164:1511–1518.

Zwick, W. R., and W. F. Velicer. 1982. Factors Influencing Four Rules For Determining The Number Of Components To Retain. Multivariate Behavioral Research 17:253–269.

9. Appendixes

Appendix A: Bonobos included in this study

Table A1. Bonobos included in this study with corresponding sex, studbook number, date of birth, origin, parents and period of observation.

Zoo	Name	Sex	Born	Mo	Fa	Origin	Period: Observer
Apenheul	HORTENSE	F	1/01/1978	W	W	WILD	2012: Nicky 2013: Linda
	JILL	F	15/07/1985	40	64	PARENT	
	ZUANI	F	1/01/1990	W	W	WILD	
	BOLOMBO	M	7/11/1997	166	111	HAND	
	ZAMBA	M	16/04/1998	**Hortense**	113	PARENT	
	KUMBUKA	F	9/07/1999	1006	1004	PARENT	
	YAHIMBA	*F*	*7/08/2009*	***Kumbuka***	***Zamba***	*PARENT*	
	MAKASI 2	*M*	*11/08/2009*	***Zuani***	***Zamba***	*PARENT*	
	MONYAMA	*F*	*17/07/2010*	***Jill***	*MULT*	*PARENT*	
Frankfurt	MARGRIT	F	1/01/1951	W	W	WILD	2012: Nicky 2014: Martina
	NATALIE	F	1/01/1964	W	W	WILD	
	LUDWIG	M	26/08/1984	67	57	HAND	
	KAMITI	F	21/01/1987	Kombote	54	PARENT	
	ZOMI	F	28/01/1998	Hermien	113	PARENT	
	KUTU	F	29/05/1998	Kombote	54	PARENT	
	HERI	M	23/01/2001	**Natalie**	**Ludwig**	PARENT	
	MIXI	F	18/12/2001	Chipita	177	PARENT	
	BASHIRA	F	30/01/2006	**Natalie**	Bolombo	Parent	
	NYOTA II	M	24/02/2007	Maringa II	**Ludwig**	PARENT	
	BILI II	*M*	*8/10/2008*	***Kamiti***	*Keke*	*HAND*	
	OMANGA	*F*	*18/12/2008*	*Kutu*	***Ludwig***	*PARENT*	
	PANGI	*F*	*16/07/2009*	***Zomi***	***Ludwig***	*PARENT*	
	PANISCO	*M*	*15/12/2009*	***Zomi***	***Ludwig***	*PARENT*	
	SAMBO	*M*	*8/01/2012*	***Zomi***	*?*	*HAND*	
	TIKALA	*F*	*20/04/2013*	***Mixi***	***Ludwig***	*PARENT*	
Planckendael	LINA	F	28/07/1985	59	58	PARENT	2012: Annemieke & Wiebe
	VIFIJO	M	23/07/1994	Hortense	113	PARENT	
	DJANOA	F	27/03/1995	96	99	PARENT	
	LOUISOKO	M	19/04/1998	**Lina**	54	PARENT	
	LUCUMA	M	29/10/2002	**Lina**	177	PARENT	
	BUSIRA	F	16/02/2004	Eja	Mato	PARENT	
	HABARI	M	29/01/2006	203	113	PARENT	
	LINGOYE	*F*	*29/11/2007*	***Lina***	*177*	*PARENT*	
	NAYOKI	*F*	*24/03/2012*	***Djanoa***	***Louisoko***	*PARENT*	

Stuttgart	KOMBOTE	F	1/01/1966	W	W	WILD	2013: Nicky 2014: Jonas
	HERMIEN	F	1/01/1978	W	W	WILD	
	MOBIKISI	M	1/01/1980	W	W	WILD	
	ZORBA	M	1/01/1980	W	W	WILD	
	CHIPITA	F	1/01/1993	W	W	WILD	
	XIMBA	F	1/01/1995	W	W	WILD	
	LIBOSO	F	17/12/1997	1006	Zuani	PARENT	
	HAIBA	F	16/11/2001	132	Ludwig	PARENT	
	BANBO	F	3/09/2002	Banya	Keke	HAND	
	KASAI	M	27/12/2004	**Chipita**	215	PARENT	
	NAYEMBI	F	26/04/2006	**Liboso**	1003	PARENT	
	HUENDA	F	6/07/2006	**Hermien**	Zamba	PARENT	
	LUBAO	*M*	*30/03/2013*	***Liboso***	*Zorba*	*PARENT*	
	ALIMA	*F*	*24/05/2013*	***Banbo***	*Zorba*	*PARENT*	
	BOBALI	*M*	*5/07/2013*	***Hermien***	*?*	*PARENT*	
Twycross	DIATOU	F	21/10/1977	55	54	HAND	2012: Nicky 2013: Marloes
	KAKOWET II	M	7/06/1980	23	34	HAND	
	BANYA	F	1/02/1990	86	97	PARENT	
	KEKE	M	2/01/1994	**Diatou**	**Kakowet II**	PARENT	
	CHEKA	F	18/03/1996	52	102	PARENT	
	MARINGA II	F	5/05/1998	96	85	PARENT	
	LUO	M	1/12/2002	**Diatou**	159	PARENT	
	KIANGA	F	17/07/2005	Kombote	215	PARENT	
	WINTON II	*M*	*26/06/2010*	***Cheka***	*MULT*	*PARENT*	
	MALAIKA 2	*F*	*23/07/2010*	***Diatou***	*?*	*PARENT*	
	LOPORI	*F*	*6/01/2012*	***Maringa II***	*93*	*HAND*	
	MOKONZO	*M*	*12/04/2013*	***Banya***	*?*	*PARENT*	
Wuppertal	MATO	M	22/12/1963	Margrit	15	PARENT	2012: Nicky 2013: Wiebe
	LUSAMBO	M	21/07/1980	Kombote	54	HAND	
	BIROGU	M	11/08/1989	55	38	PARENT	
	EJA	F	14/07/1990	42	102	PARENT	
	MUHDEBLUE	F	15/04/2001	142	171	PARENT	
	AYUBU	*M*	*1/01/2011*	***Eja***	*?*	*PARENT*	
	AZIBO	*M*	*1/01/2011*	***Eja***	*?*	*PARENT*	

Appendix B: Factors influencing contact sitting

Table B1 Effects of the variables on contact sitting, assessed with a Linear Mixed Model (LMM). An asterisk indicates a significant effect: p-value <0.05.

Effect	Num df	Denom df	F Value	P-Value
Abs. difference in Sociability (Socia)	**1**	**81.5**	**4.26**	**0.042***
Abs. difference in Positive Affect (Posi)	1	77.3	1.04	0.310
Abs. difference in Anxiety (Anxi)	1	88.0	2.24	0.138
Sex combination (Class)	**2**	**82.1**	**10.24**	**0.002***
Rank difference (Rankdif)	**1**	**79.7**	**10.24**	**0.002***
Age difference (Agedif)	**1**	**89.0**	**9.44**	**0.003***
Maternal kinship (Matkin)	**1**	**89.0**	**12.67**	**0.001***
Tenure	**1**	**84.4**	**15.31**	**<0.001***
SociaxClass	2	55.9	0.09	0.911
SociaxRankdif	1	58.3	0.00	0.945
SociaxAgedif	1	85.8	5.44	0.022
SociaxMatkin	1	75.0	1.42	0.237
SociaxTenure	1	63.9	0.19	0.665
SociaxPosi	1	63.6	0.18	0.677
SociaxAnxi	1	66.0	0.31	0.580
PosixClass	2	76.0	2.04	0.137
PosixRankdif	1	66.6	0.79	0.377
PosixAgedif	1	83.4	1.98	0.163
PosixMatkin	1	83.1	1.92	0.169
PosixTenure	1	72.5	1.02	0.317
PosixAnxi	1	65.7	1.48	0.228
AnxixClass	2	61.7	0.17	0.843
AnxixRankdif	1	76.2	2.03	0.158
AnxixAgedif	1	77.4	1.75	0.190
Anxixmatkin	1	70.0	0.60	0.440
AnxixTenure	1	68.9	4.40	0.040
ClassxRankdif	2	80.3	1.78	0.176
ClassxAgedif	2	69.5	1.01	0.370
ClassxMatkin	**2**	**88.7**	**7.12**	**0.001***
ClassxTenure	2	81.8	1.57	0.215
RankdifxAgedif	1	75.1	1.52	0.222
RankdifxMatkin	1	66.1	1.20	0.277
RankdifxTenure	**1**	**83.2**	**7.38**	**0.008***
TenurexMatkin	1	64.9	0.53	0.471

Contact sitting was, beside the dispositional effects we already discussed in the results section, significantly influenced by the following factors: sex combination, rank difference, age difference, maternal kinship and tenure. We also found interaction effects between sex combination and maternal kinship and between rank difference and tenure (Table B1).

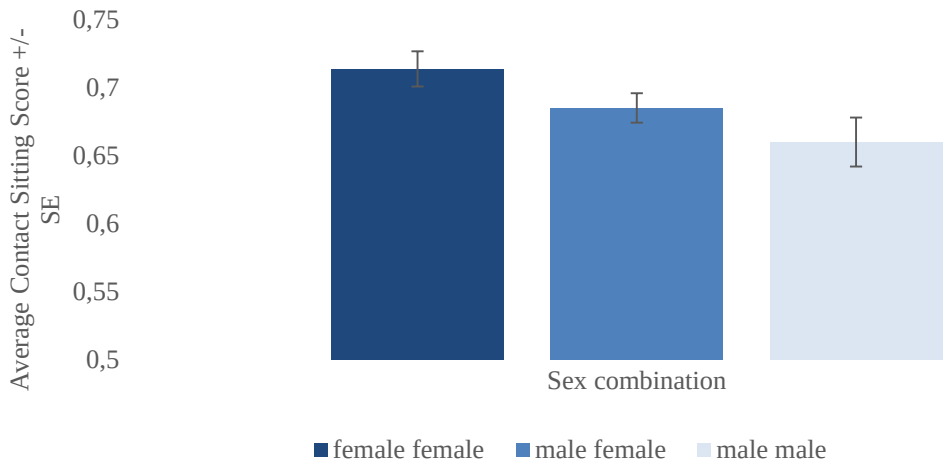

Figure B1. Average contact sitting scores for all sex combinations: female-female, male-female and male-male.

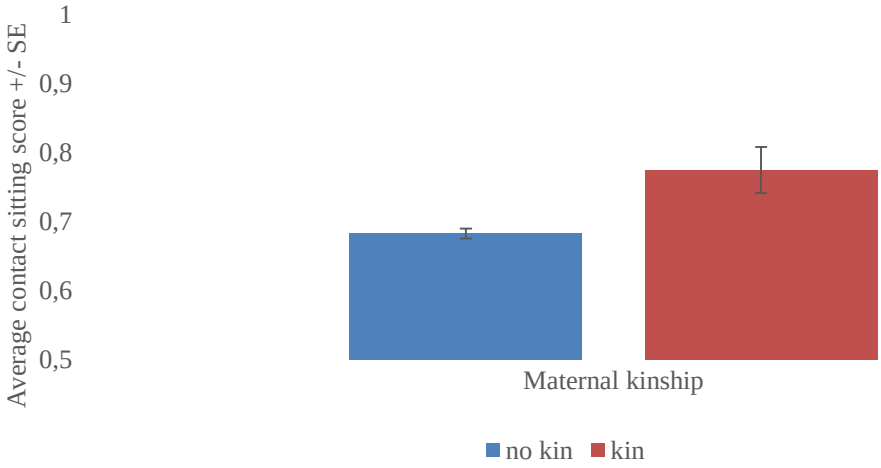

Figure B2. Average contact sitting scores for both maternal unrelated (no kin) and related (kin) dyads.

Post-hoc comparisons showed that female-female dyads did not sit significantly more in contact than male-female dyads (P_{adj} = 0.3101) but sat significantly more in contact than male-male dyads (P_{adj} = 0.0005). Male-female dyads also sat significantly more in contact than male-male dyads (p_{adj} = 0.0003) (Figure B1). Kin sat more in contact than non kin (p_{adj} = 0.0005, Figure B2).

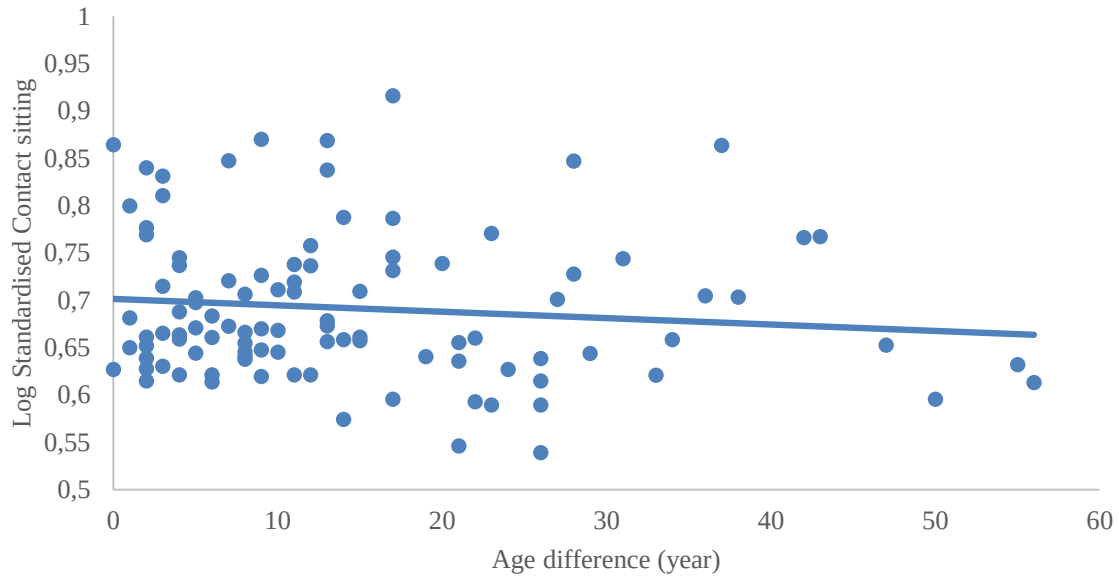

Figure B3. Relation between contact sitting (log of standardised values) and age difference.

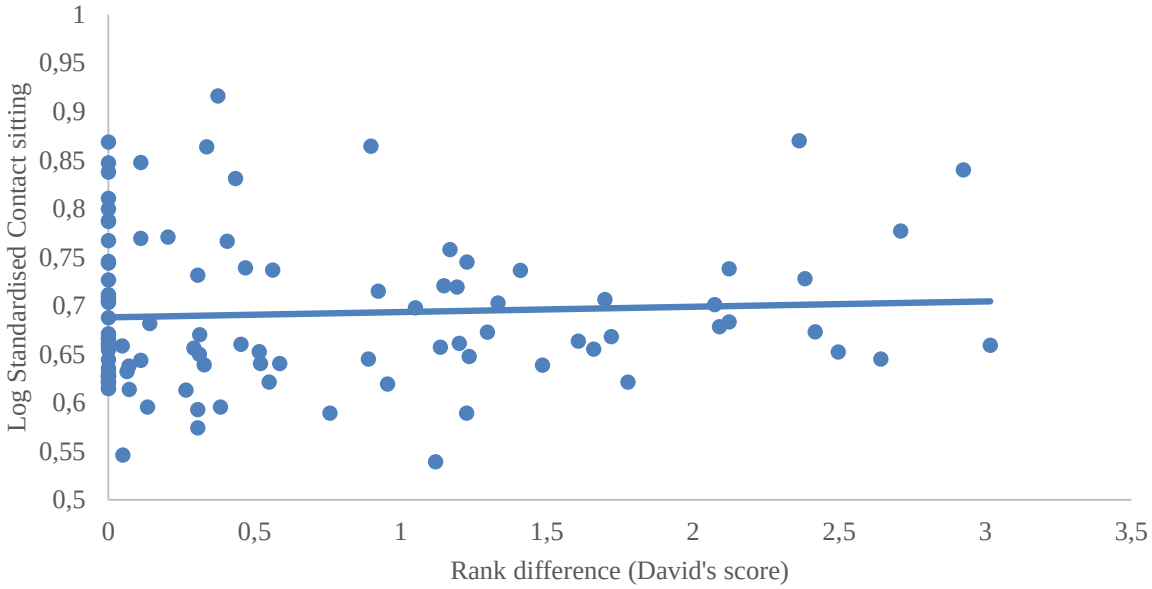

Figure B4. Relation between contact sitting (log of standardised values) and rank difference.

Dyads between individuals of greater age difference sat significantly less together (Figure B3). Individuals with great rank differences sat slightly, but significantly, more together (Figure B4). Animals which resided for more years, possessed significantly better friendships than animals which only lived together for a shorter period (Figure B5). All combinations between sex combination and maternal kinship are presented in table B2 and figure B6. For the interaction between rank difference and tenure, no unambiguous conclusion could be made (Figure B7).

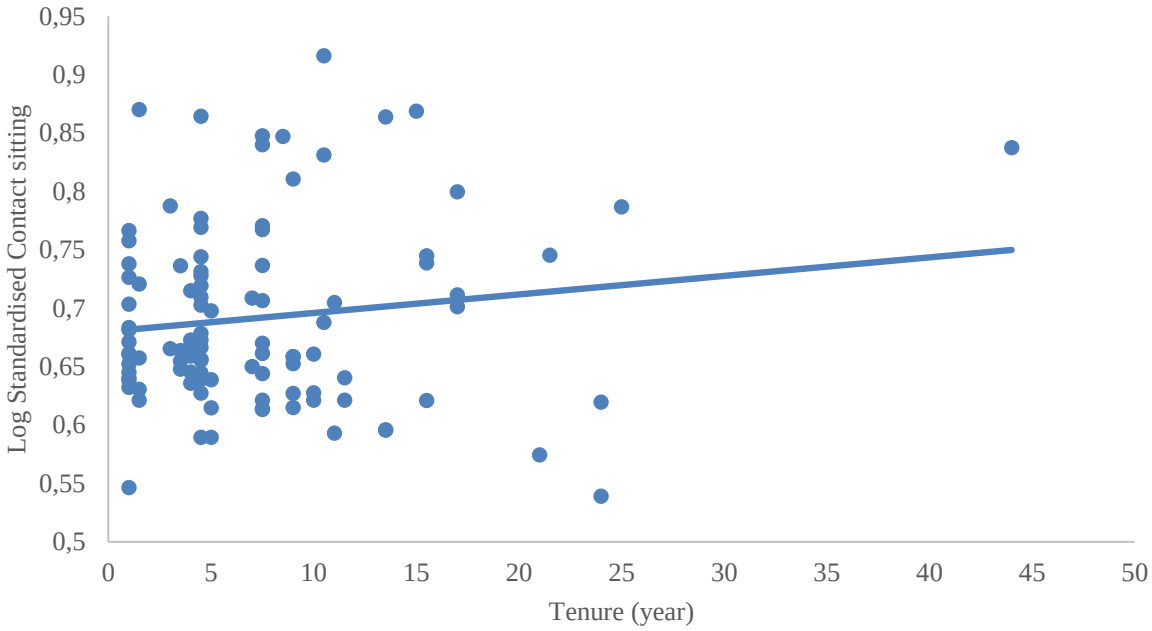

Figure B5. Relation between contact sitting (log of standardised values) and tenure.

Table B2. All combinations of the interaction between sex combination and maternal kinship, assessed with a Linear Mixed Model (LMM). An asterisk indicates a significant effect: p-value <0.05.

Effect	Sex Combination	Maternal kin	Sex combination	Maternal Kin	Adj P
Class*matkin	FF	0	FF	1	0.1028
Class*matkin	**FF**	**0**	**MF**	**0**	**0.0316***
Class*matkin	**FF**	**0**	**MF**	**1**	**0.0027***
Class*matkin	FF	0	MM	0	0.2033
Class*matkin	FF	0	MM	1	0.2735
Class*matkin	**FF**	**1**	**MF**	**0**	**0.0147***
Class*matkin	FF	1	MF	1	0.963
Class*matkin	**FF**	**1**	**MM**	**0**	**0.0153***
Class*matkin	**FF**	**1**	**MM**	**1**	**0.0121***
Class*matkin	**MF**	**1**	**MF**	**1**	**<0.0001***
Class*matkin	MF	0	MM	0	0.7511
Class*matkin	MF	0	MM	1	0.3411
Class*matkin	**MF**	**1**	**MM**	**0**	**<0.0001***
Class*matkin	**MF**	**1**	**MM**	**1**	**<0.0001***
Class*matkin	MM	0	MM	1	0.4869

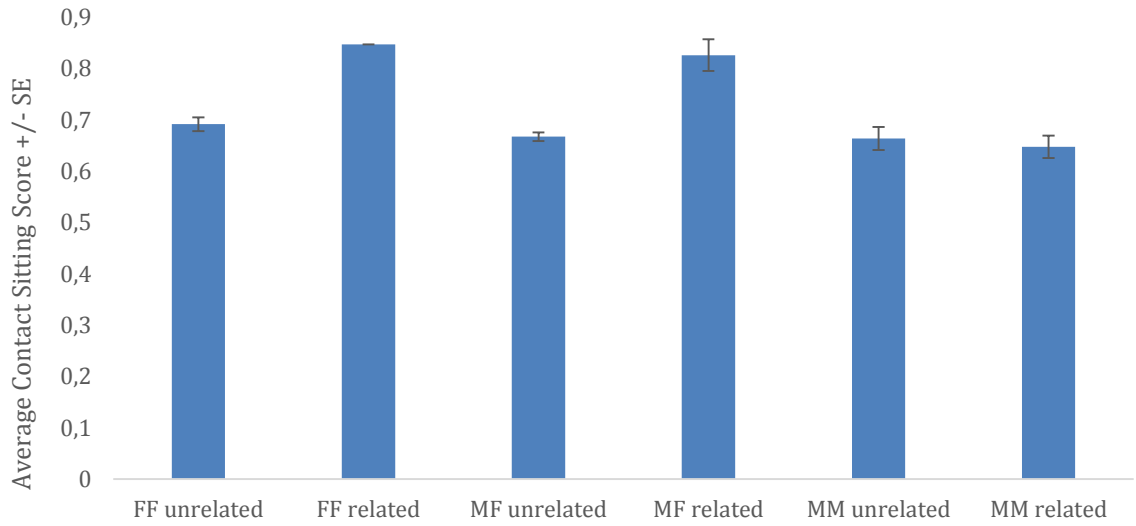

Figure B6. Mean contact sitting (log of standardised values) for the interaction between sex combination and maternal kinship

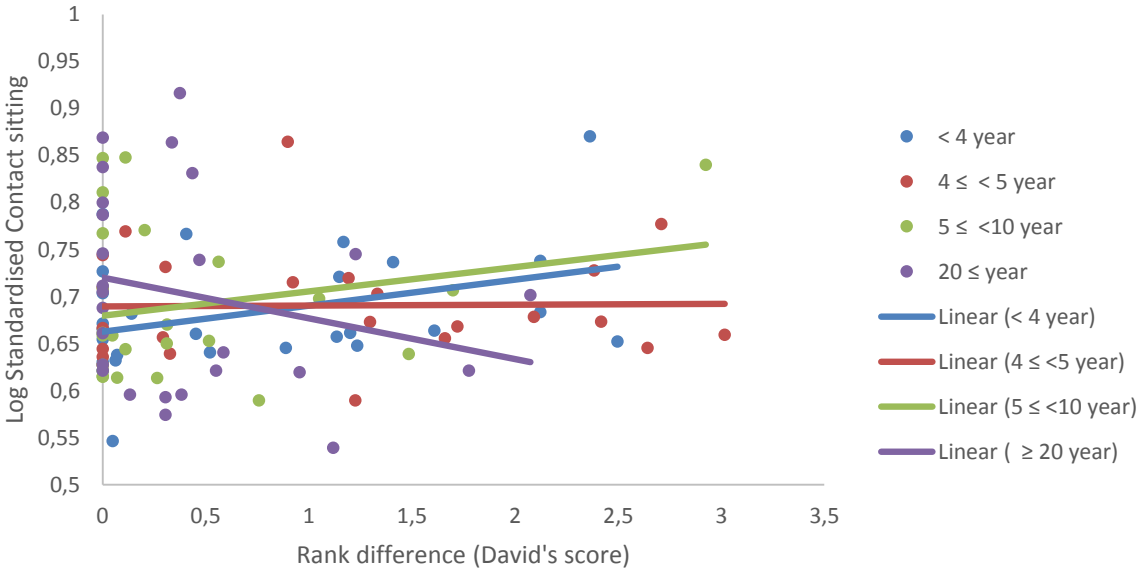

Figure B7. Contact sitting (log of standardised Values) for the interaction between rank difference and tenure.

Appendix C: Factors influencing relationship Value

Table C1 Effects of the variables on the component Value, assessed with a Linear Mixed Model (LMM). An asterisk indicates a significant effect: p-value <0.05.

Effect	Num df	Denom df	F Value	P-Value
Abs. difference in Sociability (Socia)	**1**	**70.9**	**11.01**	**0.001***
Abs. difference in Positive Affect (Posi)	1	73.2	3.25	0.076
Abs. difference in Anxiety (Anxi)	1	72.3	0.02	0.882
Sex combination (Class)	**2**	**75.3**	**8.54**	**0.001***
Rank difference (Rankdif)	1	68.3	3.5	0.066
Age difference (Agedif)	**1**	**62**	**19.23**	**<0.001***
Maternal kinship (Matkin)	**1**	**75.3**	**6**	**0.017***
Tenure	**1**	**75.3**	**4.63**	**0.012***
Socia*Class	2	58.9	0.44	0.645
Socia*Rankdif	1	53.3	0.06	0.808
Socia*Agedif	1	68.9	1.88	0.175
Socia*Matkin	**1**	**69.8**	**16.2**	**<0.001***
Socia*Tenure	1	59.8	0.14	0.715
Socia*Posi	1	59.8	0.18	0.673
Socia*Anxi	1	63.8	0.73	0.396
Posi*Class	2	62.4	1.47	0.238
Posi*Rankdif	1	71	1.72	0.194
Posi*Agedif	1	55.9	0.08	0.775
Posi*Matkin	**1**	**72**	**5.42**	**0.023***
Posi*Tenure	1	72.7	2.82	0.097
Posi*Anxi	1	49.5	0.04	0.833
Anxi*Class	2	60.7	0.63	0.535
Anxi*Rankdif	**1**	**63.3**	**4.07**	**0.048***
Anxi*Agedif	1	50.9	0.14	0.710
Anxi*matkin	**1**	**76**	**5.1**	**0.027***
Anxi*Tenure	**1**	**76.1**	**5.06**	**0.027***
Class*Rankdif	**2**	**71.8**	**4.65**	**0.013***
Class*Agedif	2	65.5	0.94	0.397
Class*Matkin	2	66.7	1.36	0.263
Class*Tenure	**2**	**77.3**	**6.44**	**0.003***
Rankdif*Agedif	1	57.4	0.14	0.708
Rankdif*Matkin	**1**	**69.3**	**5.3**	**0.024***
Rankdif*Tenure	1	75.6	1.64	0.204
Tenure*Matkin	1	74.7	5.72	0.019

Beside the dispositional effects which we already discussed in the results section, relationship Value was significantly influenced by sex combination, age difference, maternal kinship and tenure. The interaction effects between sex combination and rank difference, sex combination

and tenure, rank difference and maternal kinship and tenure and maternal kinship also significantly influenced relationship Value (Table C1).

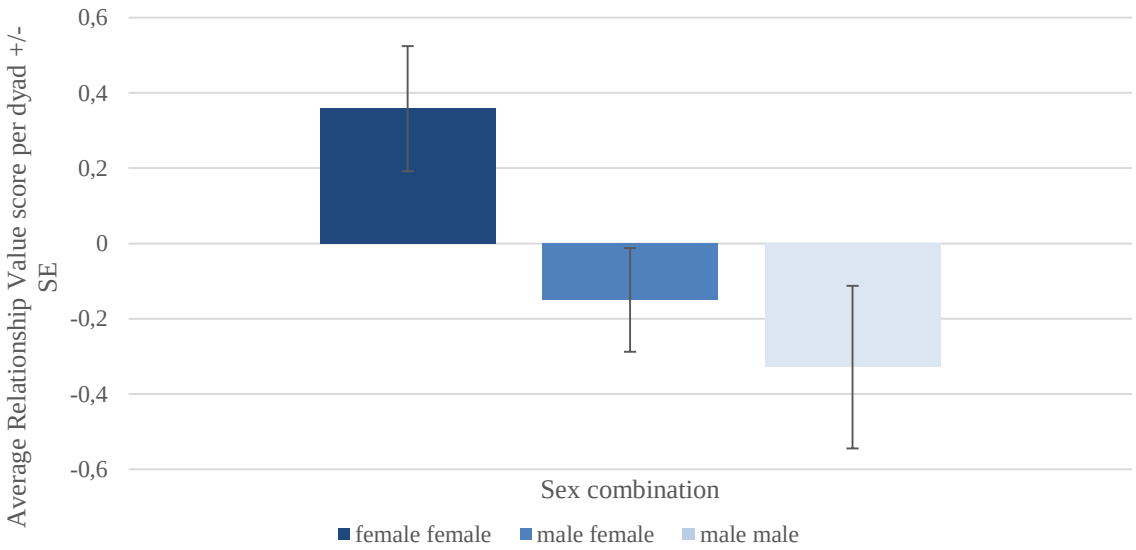

Figure C1. Average relationship Value for all sex combinations: female-female, male-female and male-male.

Post-hoc comparisons showed that female-female dyads had significantly higher relationship Values than male-female (p_{adj} = <0.0001) and male-male dyads. Male-female dyads did not have significantly higher relationship Values than male-male. (Figure C1).

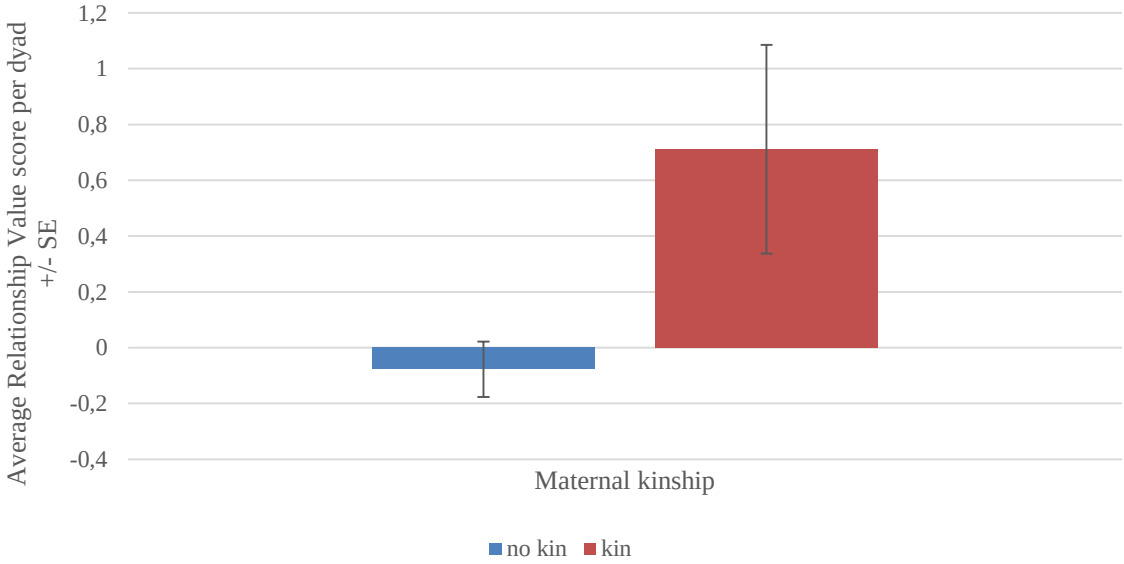

Figure C2. Average relationship Value for both maternal related and unrelated dyads.

Kin had significantly higher relationship Values than non-kin (p_{adj} = 0.0312, Figure C2). Dyads of individuals with great age difference had significantly lower relationship Values than dyads with small age differences (Figure C3). Longer relationship tenures also resulted in lower relationship Value (Figure C4).

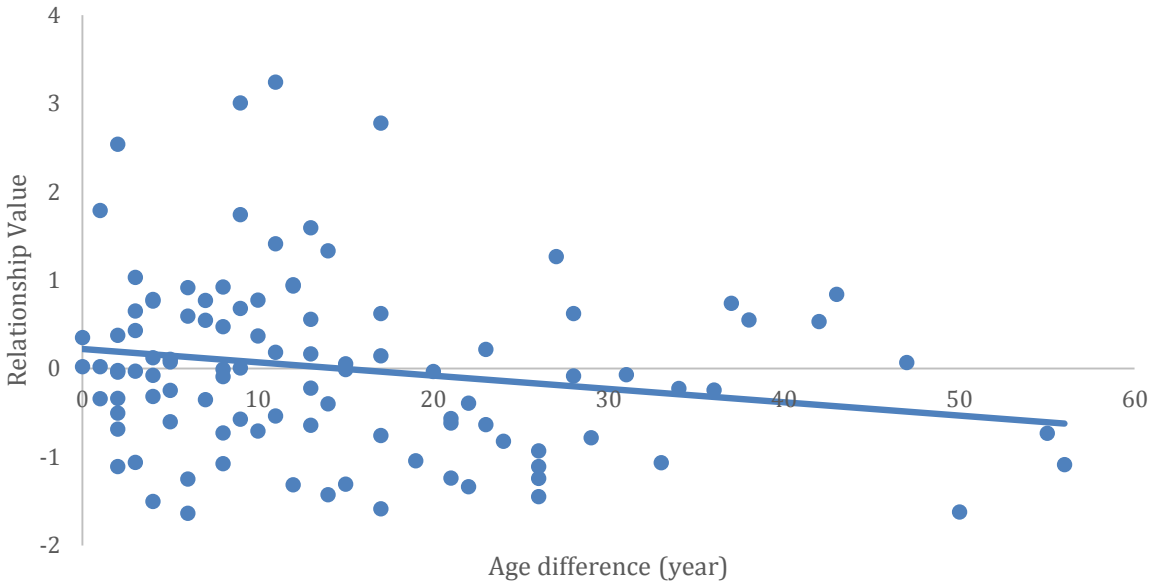

Figure C3. Relation between relationship Value and age difference.

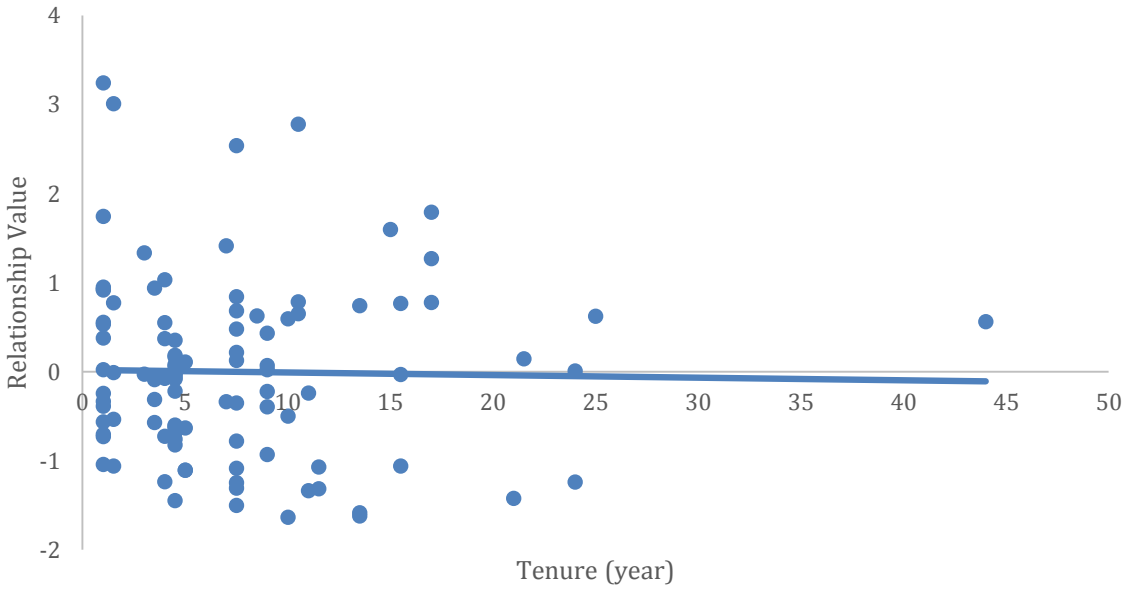

Figure C4. Relation between relationship Value and tenure.

The significant interaction effect of rank difference and sex combination shows that only in female-female dyads relationship Value will be higher between individuals of great rank differences (Figure C5). Male-female dyads obtain more valuable relationships with longer

tenure while female dyads will get less valuable relationships. For male-male dyads, relationships become slightly less valuable when residing for a longer period (Figure C6).

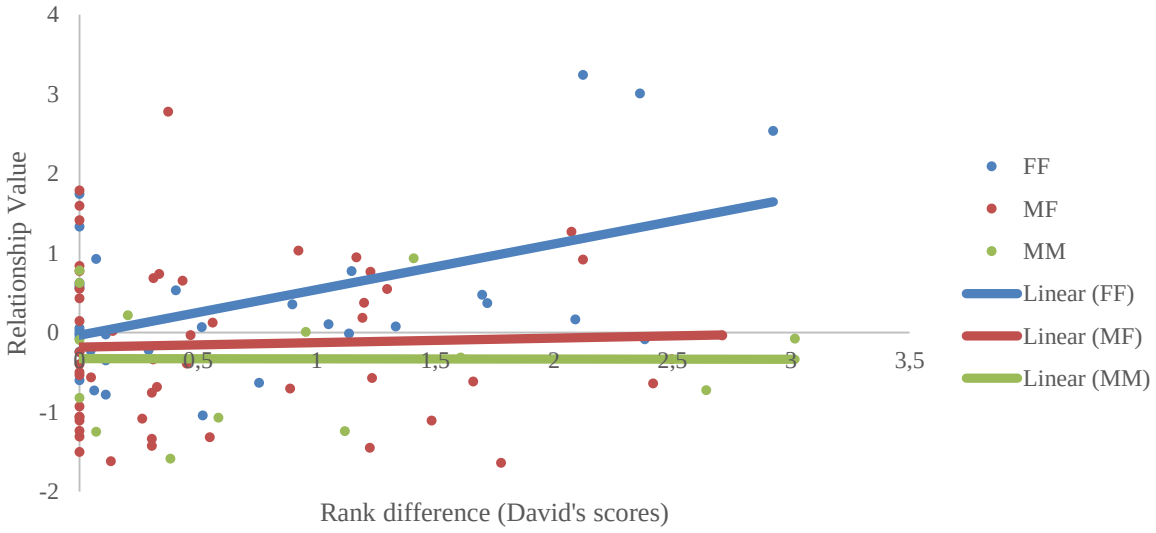

Figure C5. Relation between relationship Value and the interaction between sex combination and rank difference (FF: female-female; MF: male-female, MM: male-male).

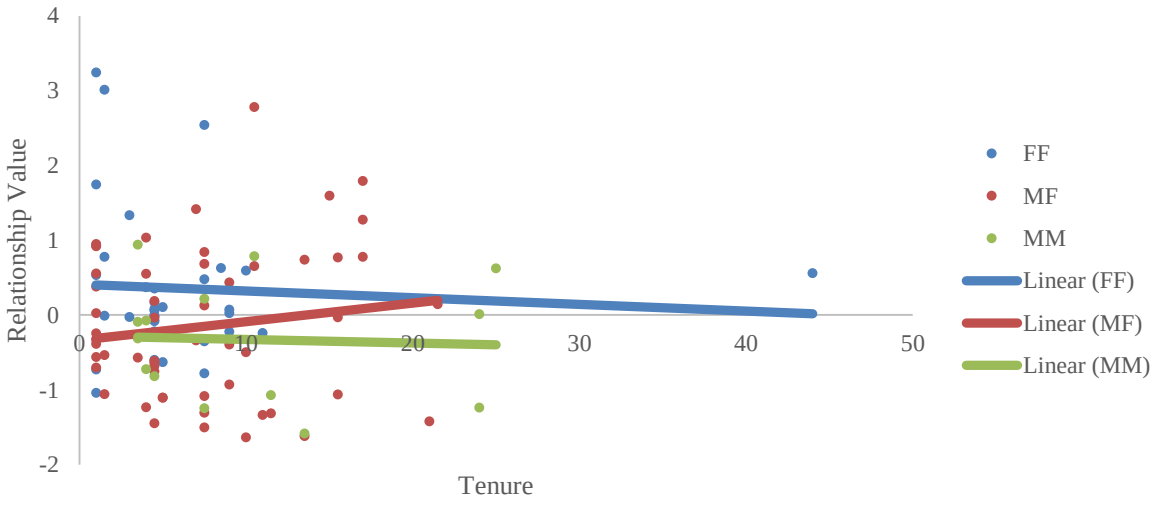

Figure C6. Relation between relationship Value and the interaction between sex combination and tenure (FF: female-female; MF: male-female, MM: male-male).

Related individuals with high rank differences have lower relationship Values than individuals with low rank differences. However, for unrelated individuals relationship Value is higher between dyads with high rank differences (Figure C7). However, related individuals obtain higher relationship Values with longer tenures, while unrelated individuals exhibit lower relationship Values when residing for longer periods (Figure C8).

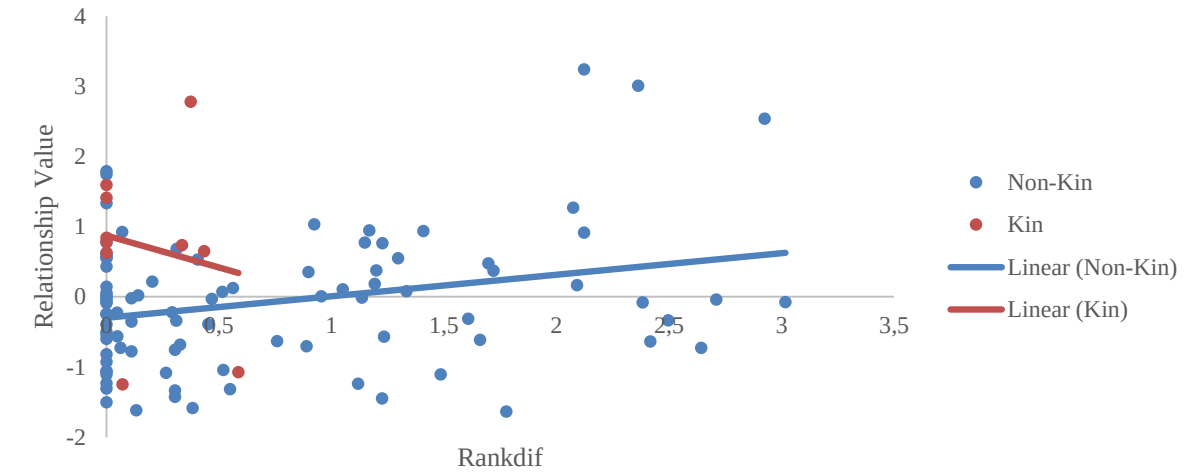

Figure C7. Relation between relationship Value and the interaction between maternal kinship and rank difference.

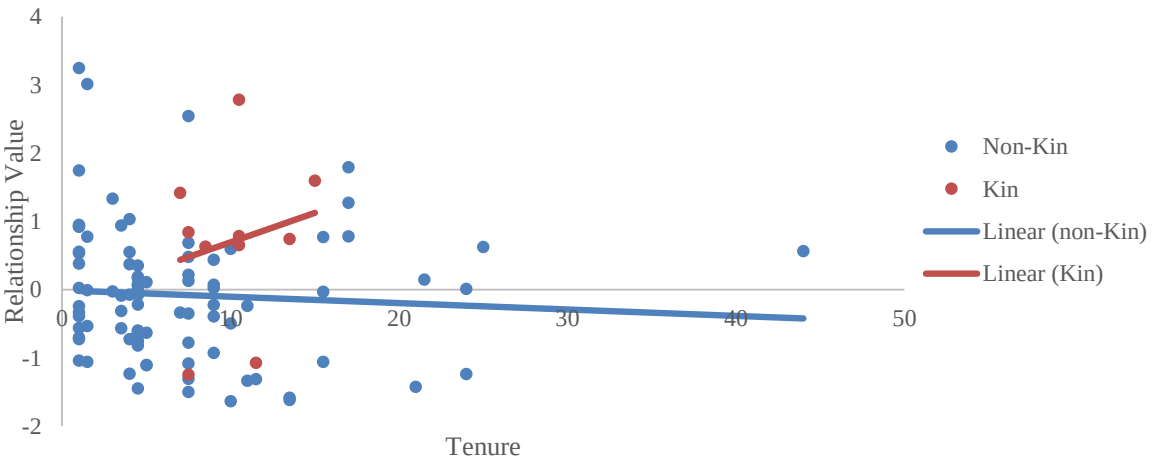

Figure C8. Relation between relationship Value and the interaction between maternal kinship and tenure.

Appendix D: Factors influencing relationship Compatibility

Table D1 Effects of the variables on relationship Compatibility, assessed with a Linear Mixed Model (LMM). An asterisk indicates a significant effect: p-value <0.05.

Effect	Num df	Denom df	F Value	P-Value
Abs. difference in Sociability (Socia)	1	75.7	1.51	0.223
Abs. difference in Positive Affect (Posi)	1	82.1	0.10	0.752
Abs. difference in Anxiety (Anxi)	1	86.9	3.49	0.065
Sex combination (Class)	**2**	**83.0**	**6.67**	**0.002***
Rank difference (Rankdif)	**1**	**86.4**	**4.86**	**0.030***
Age difference (Agedif)	**1**	**64.8**	**8.94**	**0.004***
Maternal kinship (Matkin)	**1**	**73.5**	**7.08**	**0.009***
Tenure	**1**	**74.5**	**9.99**	**0.002***
Socia*Class	2	66.9	0.51	0.603
Socia*Rankdif	1	68.7	0.21	0.651
Socia*Agedif	1	67.4	0.54	0.465
Socia*Matkin	1	60.4	2.20	0.143
Socia*Tenure	1	69.7	0.15	0.697
Socia*Posi	1	67.4	0.15	0.699
Socia*Anxi	1	58.7	0.03	0.856
Posi*Class	2	76.0	1.41	0.250
Posi*Rankdif	1	76.9	0.47	0.496
Posi*Agedif	**1**	**84.6**	**5.63**	**0.020***
Posi*Matkin	1	74.7	1.97	0.165
Posi*Tenure	1	77.0	2.85	0.095
Posi*Anxi	1	78.6	0.53	0.468
Anxi*Class	2	83.9	3.39	0.038
Anxi*Rankdif	**1**	**82.0**	**9.38**	**0.003***
Anxi*Agedif	1	62.2	0.73	0.396
Anxi*matkin	1	71.3	0.97	0.327
Anxi*Tenure	1	81.5	11.43	0.001
Class*Rankdif	2	76.1	2.35	0.102
Class*Agedif	2	52.9	0.10	0.905
Class*Matkin	2	43.1	0.21	0.812
Class*Tenure	2	58.8	0.17	0.844
Rankdif*Agedif	1	39.5	0.01	0.921
Rankdif*Matkin	1	45.9	0.05	0.825
Rankdif*Tenure	1	66.8	0.77	0.383
Tenure*Matkin	1	72.5	5.39	0.023

The non-dispositional main effects which influenced relationship Compatibility are: sex combination, rank difference, age difference, maternal kinship and tenure. Also one significant interaction was found between tenure and maternal kinship (Table D1). All dispositional effects are already discussed in the results section.

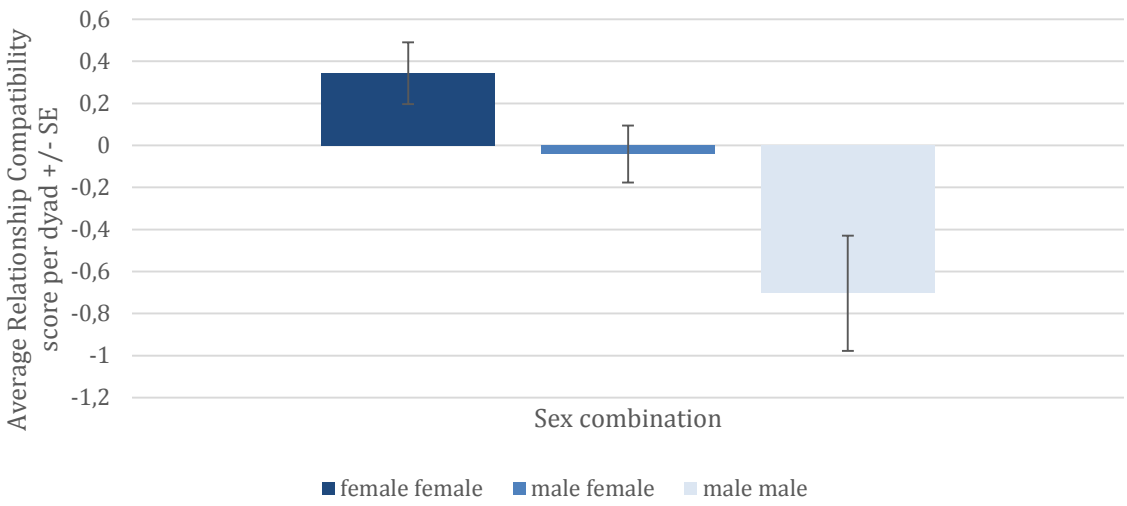

Figure D1. Average relationship Compatibility scores for all sex combinations.

Post-hoc comparisons showed that female-female dyads didn't have significantly higher relationship Compatibility than male-female (p_{adj} = 0.1142) dyads. However, female-female and male-female dyads did have significantly higher relationship Compatibility (respectively p_{adj} = 0.003 and p_{adj} = 0.0007) than male-male relationships (Figure D1). Maternal related individuals had also significantly higher relationship compatibilities than unrelated dyads (p_{adj} = 0.0064, Figure D2).

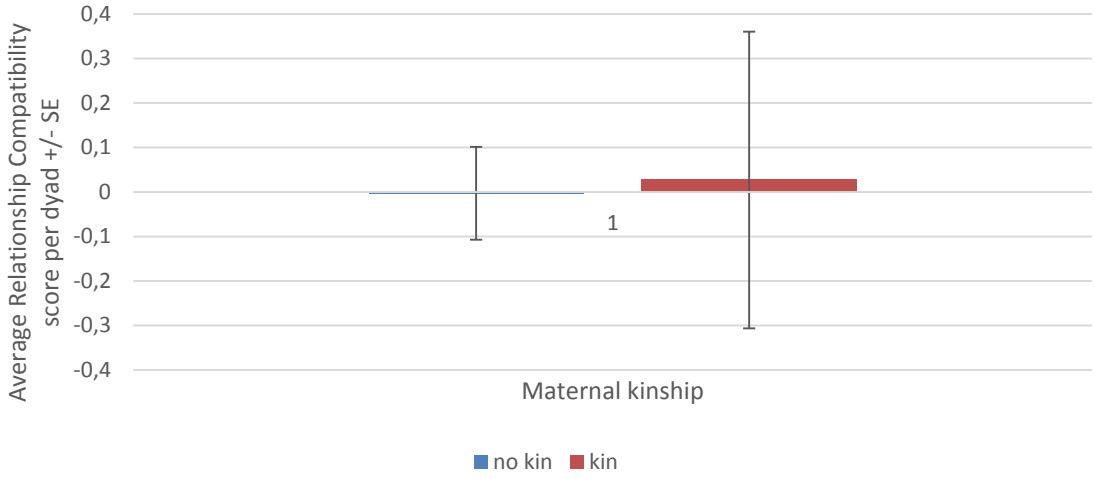

Figure D2. Average relationship Compatibility scores for both related and unrelated dyads.

Individuals with high rank differences have relationships of lower Compatibility (Figure D3) while in dyads where age difference is large, relationship Compatibility is higher than in dyads with smaller age differences (Figure D4).

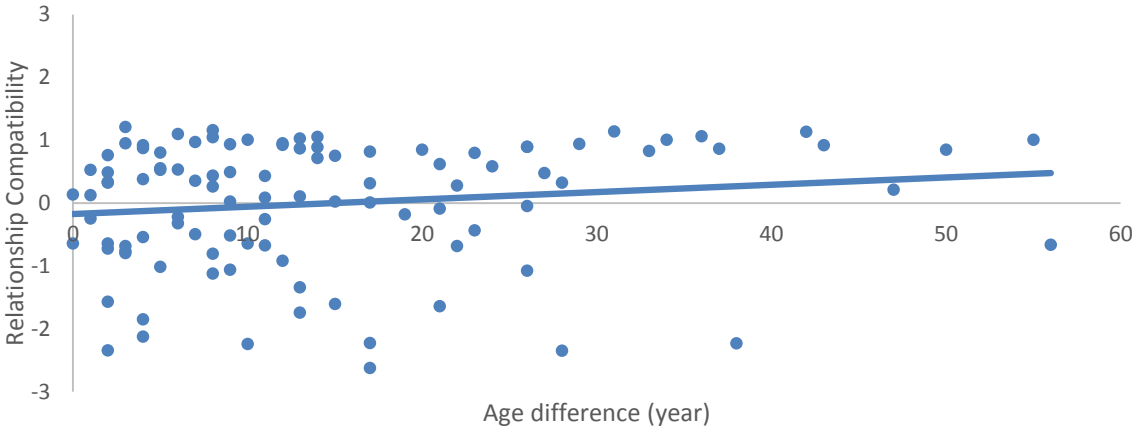

Figure D3. Relation between relationship Compatibility and age difference.

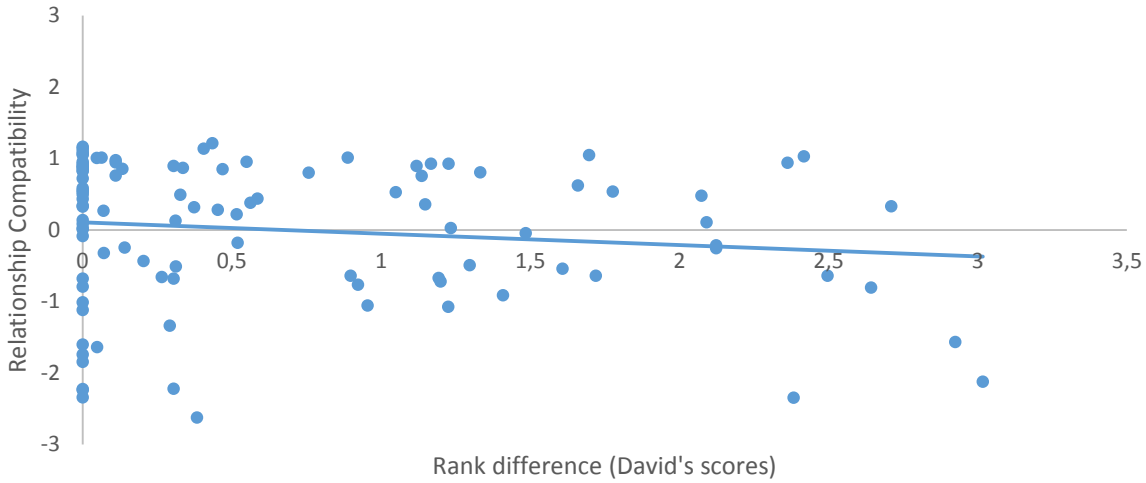

Figure D4. Relation between relationship Compatibility and rank difference.

Relationship Compatibility also becomes higher when individuals lived together for a longer period (Figure D5). However for kin, relationship Compatibility is lower for individuals which resided for a longer time (Figure D6).

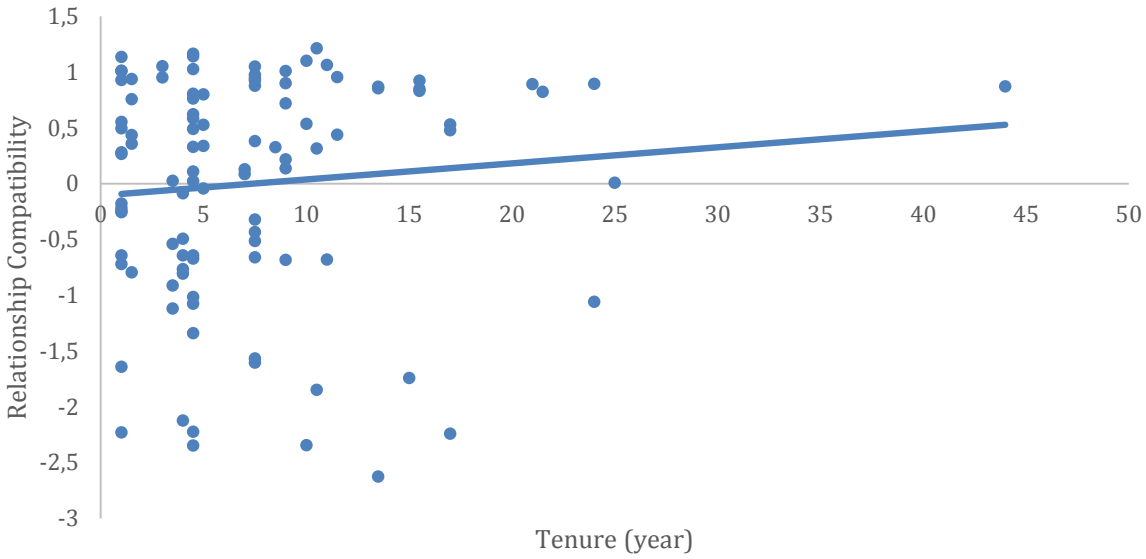

Figure D5. Relation between relationship Compatibility and tenure.

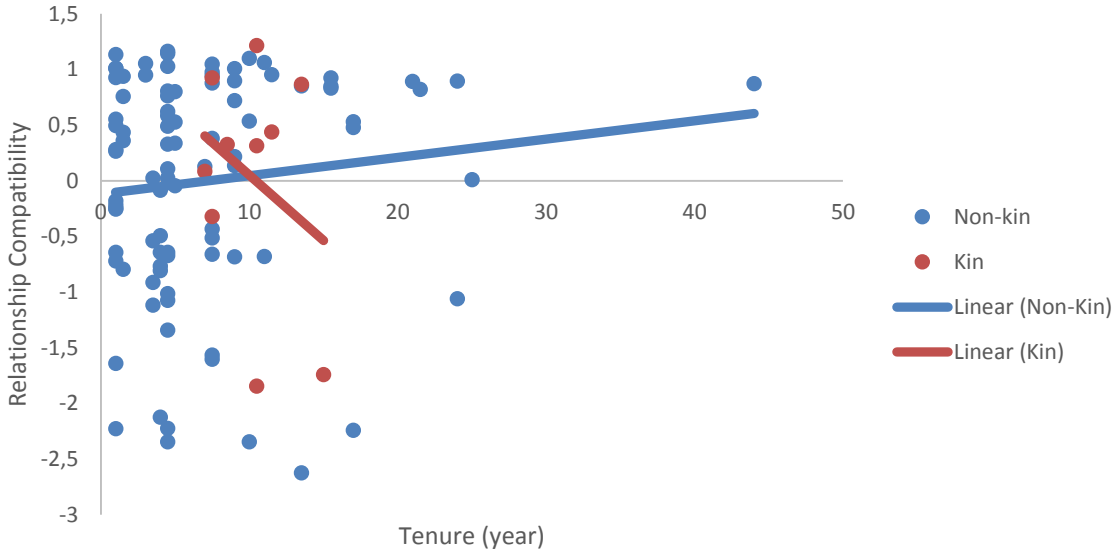

Figure D6. Relation between relationship Compatibility and the interaction between maternal kinship and tenure.

Appendix E: Maternal related dyads

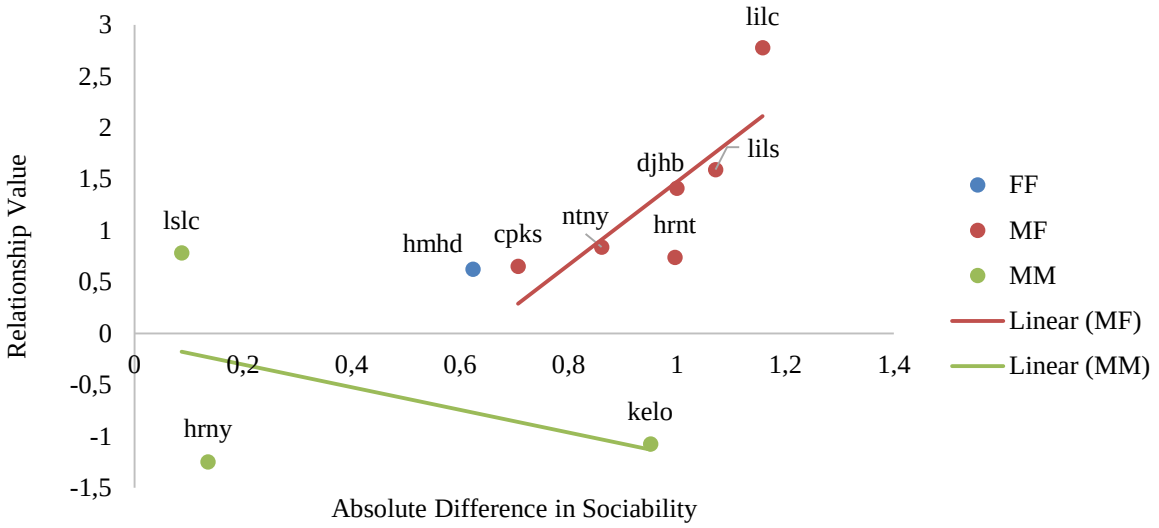

Figure E1. Influence of the absolute difference in Sociability on relationship Value in related dyads. (FF: female-female dyad; MF: male-female dyad; MM: male-male dyad).

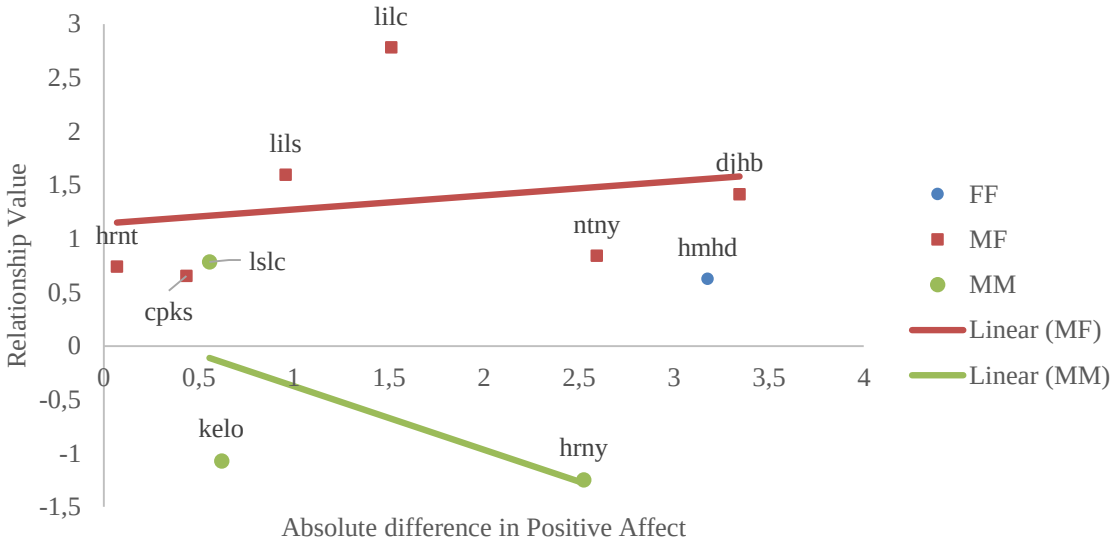

Figure E2. Influence of the absolute difference in Positive Affect on relationship Value in related dyads. (FF: female-female dyad; MF: male-female dyad; MM: male-male dyad).

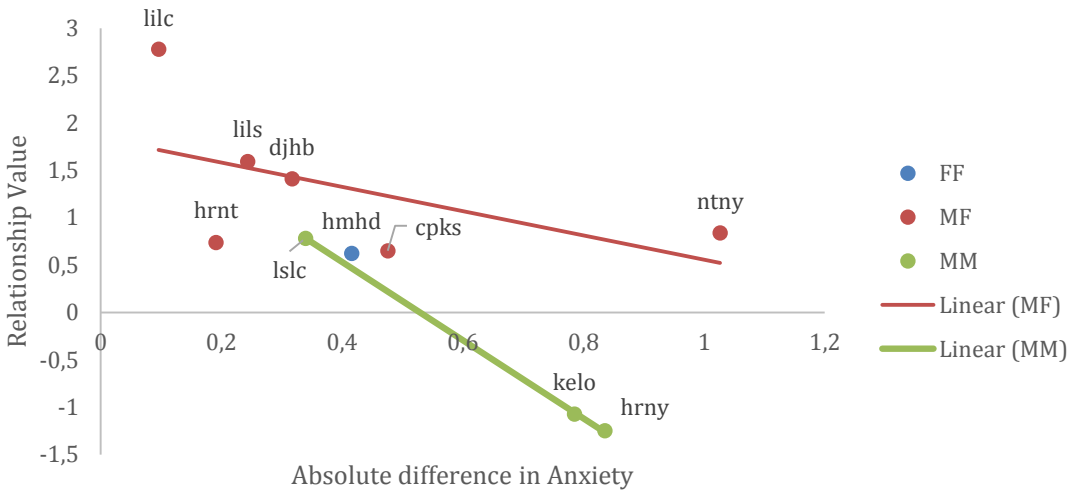

Figure E3. Influence of the absolute difference in Anxiety on relationship Value in related dyads. (FF: female-female dyad; MF: male-female dyad; MM: male-male dyad).

Related dyads:

Lilc: Dyad between Lina and Lucuma
Lils: Dyad between Lina and Louisoko
Djhb: Dyad between Djanoa and Habari
Hrnt: Dyad between Heri and Natalie
Ntny: Dyad between Natalie and Nyota
Cpks: Dyad between Cipita and Kasai
Hmhd: Dyad between Hermien and Huenda
Lslc: Dyad between Louisoko and Lucuma
Kelo: Dyad between Keke and Luo
Hrny: Dyad between Heri and Nyota