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Evolution and Behaviour

Social tolerance in bonobos (*Pan paniscus*): What underlies individual and group variation?

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For the student of social organization
it is crucial to determine in which relationships
competition is avoided or mitigated,
because it is these relationships that hold the social fabric together.

- Frans de Waal,
Dominance style and primate social organization

We can never know, by studying ourselves alone,
whether important aspects of our mental capacities
reflect an ancestral evolutionary heritage
or new features evolved or socially acquired by our lineage.

- Stephen Jay Gould,
Introduction to 'In the Shadow of Man'

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Abstract 1

Living in group entails competition with group mates. According to the Relational Model, animals can react to competition in three ways; with aggression, avoidance and tolerance. Since both aggression and avoidance could be damaging to a group in the long run, the ability to be tolerant is an essential characteristic to social species.

High levels of tolerance have been linked to the evolution of typically human features such as cooperation, prosociality, social learning and an idea of fairness. In this context, studying social tolerance in the genus *Pan* could provide insight in the evolution of human behaviour and cognition.

Social tolerance in bonobos has mostly been studied in comparisons with chimpanzees. From wild observations, bonobos are typically described as the more tolerant species, but experiments have produced conflicting results. A possible explanation is that the variation in social tolerance within the *Pan* species is larger than the difference between them.

This study attempted to identify for nine captive bonobo groups which factors underlie variation in social tolerance between groups and individuals. Two group experiments were done, yielding both group and dyadic measures for social tolerance. The first test consisted of repeating a previous experiment. This allowed testing for repeatability and making a comparison with chimpanzee groups that were tested in the same paradigm. The second test was done with different bonobo groups, and allowed to test for factors underlying variation in group tolerance. The dyadic measures from both tests could be used to test for factors underlying variation in social tolerance between individuals.

Group social tolerance was found to be repeatable, but variation with the previous experiment was found as well. Underlying factors were not found for group tolerance. For dyadic tolerance, mean age, difference in dominance status, relationship value and gender combination were found to have a significant influence.

Abstract 2

Animals that live in group need to be able to stay together without wasting their energy and time in frequent fights. The evolutionary answer to this problem is social tolerance. Social tolerance is the phenomenon of two animals being in close proximity around a resource, without fighting. Studies have shown a link between high social tolerance and the origin of typically human features like cooperation, social learning and an idea of fairness. This raises the question: how did social tolerance influence the human evolution? To bring us closer to an answer, it's necessary to explore social tolerance in our closest relatives: bonobos and chimpanzees. Studies in the wild typically show that bonobos are the most tolerant of the two, but experimental results are in conflict. One explanation for these conflicting results is

that differences within the same species are larger than the differences between the two species.

In my study, I tried to test why there are differences in social tolerance between different groups and individuals. Two group tests for social tolerance were done; the peanut plot experiment with one bonobo group and the puzzle feeder experiments with eight groups. The peanut plot experiment was done before on the same group, and the aim was to test whether the same results would be found and to compare the results with chimpanzee groups that had undergone the same test. Social tolerance was indeed found to be similar to the first result, but there also seemed to be some variation. The puzzle feeder experiments were used to test if there were underlying factors that caused differences in tolerance between the groups. An effect of these factors was not found. From both tests, I could also calculate the tolerance between pairs of bonobos. I found that differences in age, dominance, relationship and gender could cause differences in the tolerance between two bonobos.

Samenvatting

Leven in groep brengt per definitie competitie met zich mee. Volgens het Relationeel Model kunnen dieren op drie manieren reageren op competitie: met agressie, vermijdingsgedrag of tolerantie. Aangezien zowel agressie als vermijdingsgedrag het groepsleven op lange termijn kunnen schaden, is het vermogen tot tolerantie een noodzakelijke eigenschap voor sociale soorten.

Hoge levels van tolerantie blijken een rol te spelen in de evolutie van typisch menselijke eigenschappen zoals samenwerking, altruïsme, sociaal leren en een rechtvaardigheidsgevoel. In deze context kan het bestuderen van sociale tolerantie in het genus *Pan* inzicht brengen in de evolutie van menselijk gedrag en cognitie.

Sociale tolerantie bij bonobo's werd voornamelijk bestudeerd in vergelijkingen met chimpansees. Observaties in het wild beschrijven de bonobo als de tolerantste van de twee, maar experimentele resultaten spreken elkaar vaak tegen. Een mogelijke verklaring hiervoor is dat de variatie in sociale tolerantie binnen elke *Pan* soort groter is dan de verschillen tussen de soorten.

Deze studie probeerde voor negen bonobogroepen in gevangenschap onderliggende factoren te vinden die variatie in sociale tolerantie veroorzaken tussen de groepen en tussen individuen. Hiertoe werden twee groepsexperimenten uitgevoerd, die zowel een groepsmaat als een dyadische maat voor tolerantie voortbrachten. De eerste test bestond uit het herhalen van een reeds uitgevoerd groepsexperiment. Hierdoor kon getest worden of het experiment herhaalbaar was en kon een vergelijking gemaakt worden met chimpanseegroepen die hetzelfde experiment ondergingen. De tweede test werd uitgevoerd

met verschillende bonobogroepen, en maakte het mogelijk te testen welke onderliggende factoren groepstolerantie beïnvloedden. De dyadische maten uit beide experimenten werden gebruikt om te testen welke factoren zorgden voor variatie in tolerantie tussen individuen. Groepstolerantie bleek herhaalbaar te zijn, al werd er een licht verschil gevonden met het vorige experiment. Onderliggende factoren werden niet gevonden voor groepstolerantie, maar wel voor dyadische tolerantie; gemiddelde leeftijd, verschil in dominantiestatus, waarde van de relatie en de geslachtscombinatie bleken een significante invloed te hebben.

1. Introduction

1.1 Social tolerance as a foundation for group living

Group living evolves when the net benefits of close association with conspecifics exceed the costs (Silk, 2007). General benefits of group living are protection against predators, group foraging and access to mates, while an important cost is the increased competition with group members for resources (Clark & Mangel, 1986; Sterck et al., 1997; Silk, 2007).

According to the Relational Model, animals can react to competition in three ways: with conflict avoidance, aggression or tolerance (de Waal, 1996). Conflict avoidance is not always possible due to limitations in space and the disadvantages of dispersion, and high rates of aggression can be costly and will eventually lead to avoidance or dispersal as well (e.g. Healey, 1967). Therefore, mechanisms that attenuate aggression and consequently allow close proximity between conspecifics are advantageous, if group living is (De Waal, 1989; Lührs & Kappeler, 2013).

Social tolerance can be defined in a broad sense as ‘withholding aggression’ and in a more narrow sense as ‘the propensity to be in proximity to conspecifics around valuable resources with little or no aggression’ (Cronin & Sánchez, 2012; Smith, 2014). If indeed an adaptation to group living, levels of tolerance can be expected to correlate with parameters like group size, group cohesion and sociality; the degree to which an individual tends to associate with conspecifics.

These correlations have been found indeed in different taxa. Tolerance measures appear to be related with different degrees of sociality in African mole-rat species (*Georychus capensis*, *Cryptomys hottentotus pretoriae*, *Cryptomys darlingi*, *Cryptomys damarensis*); solitary mole-rats express a lower level of tolerance towards an unknown conspecific than social species do (Ganem & Bennett, 2004). In meadow voles (*Microtus pennsylvanicus*), levels of tolerance fluctuate according to seasonal variations in levels of sociality. Increased tolerance allows this species to perform energetically beneficial ‘huddling behaviour’ in winter (Madison & McShea, 1987; McShea, 1990).

The correlation between group size and tolerance has been studied mainly in chickens (*Gallus gallus domesticus*). A larger group size forces the dominance hierarchy to break down, followed by an increased level of tolerance in most individuals, in order to avoid costly aggressive encounters (Pagel & Dawkins, 1997; D’Eath & Keeling, 2003; Estevez et al., 2003).

The cohesion of social bonds within groups is maintained and improved by social tolerance, resulting in both increased tolerance and social cohesion as a response to between group competition (De Waal, 1989; Wittemyer & Getz, 2007). Similarly, social tolerance allows for physical proximity, as mentioned in the example of the meadow vole huddling behaviour (Madison & McShea, 1987; McShea, 1990).

1.2 Social tolerance can allow for social and cognitive evolution

High levels of social tolerance may provide an opportunity for the evolution of cooperation (for example: Seed et al., 2008), prosociality (van Schaik & Burkart, 2013; Cronin, 2012), social learning (van Schaik & Burkart, 2011; Miller et al., 2014) and fairness (Brosnan, 2006; Amici et al., 2012)(glossary of terminology: Appendix 1).

In rooks (*Corvus frugilegus*) and chimpanzees (*Pan troglodytes*), more tolerant dyads perform better on a cooperation test (Seed et al., 2008; Melis et al., 2006). Moreover, chimpanzees that cooperated efficiently with a partner they were highly tolerant with, don't perform as well when paired with a less tolerant partner (Melis et al., 2006).

Prosociality, each behaviour that provides a benefit for others, is suggested to be influenced by tolerance on both the species and the inter-individual level (Yamamoto et al., 2009; Cronin, 2012). Since prosociality usually requires close proximity, high tolerance could be a logical precondition. However, unambiguous empirical support has not yet been found (Burkart & van Schaik, 2013).

Social learning improves the ability for, but is also more efficient than individual learning (van Schaik & Burkart, 2011). To allow for social learning, physical proximity is essential. In a study on rats, social learning only took place when naive animals were allowed to approach more experienced conspecifics. Moreover, individual learning didn't take place at all (Coussi-Korbel & Fragaszy, 1995). Van Schaik & Burkart (2011) found preliminary support for the relationship between opportunities for social learning and cognitive abilities across taxa. Their result suggests a possible role for tolerance in the evolution of intelligence.

It has been shown that a number of species can be aware of inequality, which is mostly suffered by subordinate individuals. However, only in relatively tolerant species, subordinates can be expected to protest against unfairness, because retributions are less severe in these species (de Waal, 1991; Brosnan, 2006). The study by Amici et al. (2012) on seven primate species supported this hypothesis.

Since fairness, cooperation, social learning and prosociality are typical aspects of the human social life, these findings are especially interesting in the light of human evolution (for example Burkart et al., 2009). In this context, research on primates and particularly on apes is very relevant.

1.3 Measuring social tolerance

Social tolerance can be measured in several ways. The method that needs the least interference is behavioural observation under (semi-)natural circumstances. For example Hurst & Barnard (1995) and Estevez et al. (2003) observed the rate of aggressive interactions in chickens and house mice (*Mus domesticus*), without experimental manipulation. In addition to this method, aggression can be estimated indirectly, as did Scott et al. (2005) by looking at tooth-rake marks in bottlenose dolphins (*Tursiops sp.*).

A method that is used more often is to bring conspecifics deliberately in contact and subsequently observe agonistic behaviour (*Microtus pennsylvanicus*: McShea, 1990; Hurst & Barnard, 1995), proximity (*Lacerta monticola*: Aragón et al., 2007) and/or physiological stress responses (*Georychus capensis*, *Cryptomys hottentotus pretoriae*, *Cryptomys darlingi*, *Cryptomys damarensis*: Ganem & Bennett, 2004).

Other experiments measure social tolerance in proximity of a desired resource. These tests are either in a dyadic or a group setting. Dyadic test mostly consist of offering the dyad different types of food, that are monopoliseable to different degrees. Aggression, cofeeding (eating simultaneously) and sharing are observed for each food type (*Pan troglodytes*: Melis et al., 2006; *Pan troglodytes*, *Pan paniscus*: Hare et al., 2007; Wobber et al., 2010; *Corvus frugilegus*: Seed et al., 2008; *Canis lupus*, *Canis lupus familiaris*: Range et al., 2015). A different dyadic test by Amici et al., (2012) was made of 2 drinkers, placed close to each other. The proportion of the time the dyad spent drinking simultaneously was used as a measure for tolerance. The test was done with chimpanzees, bonobos, gorillas (*Gorilla gorilla*), orangutans (*Pongo pygmaeus*), brown capuchinmonkeys (*Cebus apella*), spidermonkeys (*Ateles geoffroyi*) and longtailed macaques (*Macaca fascicularis*). Similar to the dyadic tests is the experiment by Hare & Kwetuenda (2010) and Tan & Hare (2013), where individual bonobos in a room provided with food had the choice to open a door to a conspecific and allow acces to the food. Bullinger et al., (2012) did the same test with bonobos, chimpanzees and marmosets (*Callithrix jacchus*).

Group tests mostly consist of the provision of food to the group, and subsequently observing some or all of the following behaviours: aggression, monopolisation of food, forced food claims, relaxed food claims and cofeeding. This was done with monopoliseable (*Pan paniscus*, *Pan troglodytes*: Parish, 1994; Jaeggi et al., 2010) and non-monopoliseable food sources (*Pan paniscus*, *Pan troglodytes*: de Waal, 1992; *Pan paniscus*: Cronin et al., 2015). In the experiments on bonobos and chimpanzees by Cronin et al. (2014, 2015) a limited resource zone was defined, and provided with non-monopoliseable food items. The percentage of the group present in the resource zone was taken as a measure for social tolerance. Cronin et al. (2014) and Burkart & van Schaik (2013) did a different group test, using monopoliseable food items. The items were provided to the group one by one, and the equality in the distribution of the food was used as a measure for social tolerance (*Macaca fuscata*, *Cebus apella*, *Callithrix jacchus*: Burkart & van Schaik (2013), *Pan troglodytes*: Cronin et al. (2014)).

Another group test by de Waal (1986) and de Waal & Luttrell (1989) on rhesus macaques (*Macaca mulatta*) and stump-tailed macaques (*Macaca arctoides*) consisted of depriving the group from water for 3 hours, and then providing water in a drinking basin. Although this test was in a group setting, dyadic measures for tolerance were calculated based on the total time an individual spent drinking, the time two individuals sat at the basin together and the total duration of the experiment.

My study attempted to measure social tolerance and investigate related factors in bonobos. Group setting experiments were used, that yielded both group and dyadic measures for tolerance.

1.4 The bonobo

Bonobos (*Pan paniscus*) were only described as a distinct subspecies for the first time in 1929, and as a species in 1933 (Schwarz, 1929; Coolidge, 1933). They live in the Democratic Republic of Congo and occupy a habitat range that includes different vegetation types: lowland rainforest, swamp forest, dry forest and grasslands (Kano, 1992; Stumpf, 2011). The Congo River and the Albertine Rift isolate bonobos from all other apes (Lacambra et al., 2005). Their diet mainly consist of plant foods like fruit, seeds, leafs, bark and pith, with the occasional addition of mushrooms, meat, insects, eggs, and other animal products (Kano, 1992).

Bonobos live in a fission fusion system, similar to chimpanzees. The largest unit within one territory is the community or unit-group (Kano, 1982). This unit-group splits up into foraging groups, that can encounter each other and merge or split up during the day. The unit-group is usually never together in one place (White, 1992). Females change unit-group permanently when they are about 7 to 14 years old. This results in groups where adult females are unrelated to each other, and adult males are kin (Kano, 1982; Furuichi, 1989, 2011).

In chimpanzees, the strongest bonds exist between adult males (Goodall, 1986). These coalitions are very important to rise in and maintain rank. In contrast, the bonobo society in the wild is founded on female bonds and maternal support (Furuichi, 2011; Surbeck et al., 2011a). In order to integrate in their new unit-group, immigrant female bonobos attempt to establish bonds with older resident females (Idani, 1991). The formation of alliances allows female bonobos to be higher ranking compared to chimpanzee females (Furuichi, 1989). The importance of female coalitions in wild bonobo is confirmed by the fact that in dyadic agonistic interactions, males seem to be often dominant, while a group of females can easily undermine his dominance. As a consequence, females get priority during feeding and are able to control resources (White & Wood, 2007). In captive populations, female alliances against males are less important. Groups are often small and a mother will rarely form an alliance against her son (Stevens et al., 2006, 2007).

The question whether females are more dominant than males doesn't have a simple answer. Some observations indicate a rather equal agonistic dominance, some show higher agonistic dominance in one of the sexes (Stevens et al., 2007; Furuichi, 2011). Nevertheless, females in the wild appear to be always dominant in a feeding context. An important finding for research on captive populations is that in captivity, female agonistic dominance seems to be higher (Vervaecke et al., 2000b; Stevens et al., 2007).

Regardless of the ambiguous outcome of tests for agonistic dominance, females do seem to have an important influence on male ranking. The mother's presence positively influences a male's rank, and adult sons are often supported by their mother in agonistic interactions (Surbeck et al., 2011a).

Thus, the strongest social bonds in bonobos exist between females and their adult sons, and among females. In chimpanzees, on the contrary, the most important bonds exist between adult males.

Proximate factors resulting in behavioural differences between chimpanzees and bonobos are found to be neural and hormonal (Wobber et al., 2010a; Rilling et al., 2012). Underlying genetic differences are as yet only discovered in the vasopressin receptor gene (Staes et al.,

2014). These differences are probably evolutionarily shaped by dissimilarities in ecology. Fruit availability appears to be the most significant ecological factor to differentiate bonobos from chimpanzees, with bonobos living in a habitat with less fluctuation in fruit availability (Doran et al., 2002).

1.5 Social tolerance in bonobos and chimpanzees

Comparative studies on our closest relatives, bonobos and chimpanzees, can answer questions concerning the evolution of human behaviours like cooperation, prosociality, social learning and tool use, and about the origin of a moral concept such as fairness (Huffman & Hirata, 2004; Brosnan, 2006; Hare et al., 2007; Hare & Kwetuenda, 2010; van Schaik & Burkart, 2013; Amici et al., 2012; Boose et al., 2013).

Bonobos are typically described as the peaceful ape, while chimpanzees are seen as more aggressive (for example Stanford, 1998; Furuichi, 2011). However, studies that experimentally measure tolerance produce contradictory results. The following section is an overview of observations of (non)tolerant behaviour in the wild, and tolerance measuring experiments.

When border patrolling chimpanzees encounter an individual from a neighbouring group, the outcome is often fatal. Direct physical aggression between males of different groups has been observed, together with heavily injured carcasses (Watts et al., 2006; Boesch et al., 2007; Wilson et al., 2014). Bonobos, on the other hand, infrequently direct physical aggression towards neighbouring groups, and mostly leave after aggressive but non-physical displays (Hohmann & Fruth, 2002). Occasions have been observed when bonobos mix with another group, interact peacefully and split up in the original groups afterwards. Sociosexual behaviour and grooming between individuals of the different groups can take place and is mostly initiated by females. At such events, more incidents of within-group than between-group aggression occur (Idani, 1990; Doran et al., 2002; Furuichi, 2011).

Agonistic within-group interactions in chimpanzees are most frequently initiated by males and can be very intense (Goodall, 1986). In bonobos too, males more often start the aggression than females, but overall it's less severe than in chimpanzees (Furuichi, 1997, 2011; Doran et al., 2002; Hare et al., 2012).

Occasions of within-group infanticide and cannibalism have been observed in chimpanzees but up to now never in bonobos (Hamai et al., 1992; Furuichi, 2011, but see Hohmann &

Fruth, 2002). In summary, observations in the wild seem to indicate that both between- and within-group tolerance is higher among bonobos than chimpanzees.

Both species occasionally share food under natural circumstances. There are differences, however, as to who shares with who. Chimpanzees share plant food most often between mother and offspring and meat between males or from male to female, while bonobo females share with each other or infants (White, 1994; Hohmann & Fruth, 1996; Mitani & Watts, 2001). From these observations, tolerance in a feeding context seems to be high in a different type of dyad in the two species. Having the Relational Model in mind, this might reflect a difference in the importance of certain relationships, because tolerance might be chosen over avoidance or aggression in order not to damage these particular relationships (De Waal, 1989).

Dyadic experiments to test for the difference in social tolerance between chimpanzees and bonobos have been carried out in four studies, three of which concluded that bonobos were more tolerant in this context (Hare et al., 2007; Wobber et al., 2010b; Amici et al., 2012). Hare et al. (2007) found that bonobos cofed more often than chimpanzees, with the most striking difference when food was monopolisable. In the study by Amici et al. (2012), bonobos spent slightly (<5%) more time drinking together. Wobber et al. (2010) concluded that young chimpanzees shared or cofed as often as bonobos of all age categories, but that sharing and cofeeding rates in chimpanzees declined with age. When given the choice to cofeed or not by opening a door to a conspecific, neither bonobos nor chimpanzees preferred cofeeding to eating alone (Bullinger et al., 2012). However, the result for bonobos was contrasting with the finding by Tan & Hare (2013).

Compared to experiments in dyads, the group experiments had a more variable outcome. The experiment by Parish (1994) revolved around an easily monopolisable 'fishing' site (an artificial termite mound) containing attractive food. She found that in the bonobo group, there was more cofeeding but less equality in fishing success, and that the fishing bout length, the number of displacements and the overall success corresponded with the dominance hierarchy. De Waal (1992) and Jaeggi et al. (2010) used a monopolisable food source that could be shared; a bundle of leafed branches and a bag with vegetables respectively. Both studies found more tolerant food transfers among chimpanzees. According to Jaeggi et al. (2010), the direction and character of food transfers in bonobos were heavily influenced by dominance relationships. Only the experiments by Cronin et al. (2014, 2015) used a food source that was rather hard to monopolize: peanuts distributed over a restricted area. They concluded that the portion of the group that was simultaneously present in the resource zone

was smaller for bonobos than for chimpanzees, which means that chimpanzees better tolerated the proximity of group members during feeding. Furthermore, the chimpanzees remained in the resource zone to eat their share, while bonobos collected the nuts and ate elsewhere.

To conclude: group experiments more often find chimpanzees to be more tolerant in a feeding context, while experiments with dyads more often show the opposite.

1.6 Variation between groups and individuals

Another possible reason behind the contradictory experimental results is that there is a great deal of variation between the tolerance levels in groups of the same species. For example, Hohmann & Fruth (2002) mention behavioural differences between the wild bonobo populations of Lomako and Wamba in agonistic and affiliative relations, and in food sharing. These differences would be due to differences in feeding competition. Similarly, substantial variation in aggression rates has been found in chimpanzees across study sites (Wilson et al., 2014).

Variation between groups of mammals are typically assigned to differences in population-level genetics, social learning and environmental factors (Langergraber et al., 2011). Cronin et al. (2014), however, found significant variation between 4 chimpanzee groups for which these variables were constant. In their study, differences in social tolerance and the ability to monopolise resources reflected individual variation in the behaviour of high ranking individuals of these groups. They also found that groups that behaved more tolerantly during the experiment showed more spatial cohesion under natural circumstances and that in tolerant groups, dyads showed more equality in who approached who.

These results are an empirical example of the conceptual framework proposed by Hinde (1976); individual variation in underlying factors can cause variation in tolerance between individuals and ultimately between groups (Cronin et al., 2014).

Possible factors underlying individual variation in tolerance, suggested by previous studies, are dominance, relationship quality (Box 1), kinship, age, the rate of tolerance stimulating behaviour and rearing history (Jaeggi et al., 2010; Hare et al., 2012; Tan & Hare, 2013; Cronin et al., 2014, 2015; Smith, 2014).

In general, a high difference in dominance position within a dyad leads to low tolerance towards the lower-ranking individual, while individuals that are more equal in rank express higher tolerance (de Waal, 1986a). Empirical data for the influence of dominance steepness

Box 1. Quantifying relationship quality

A relationship is described by Hinde (1976) as a series of interactions in time between two individuals known to each other, in which the nature and course of each interaction is influenced by the history of past interactions between the individuals concerned, and perhaps by their expectation for interactions in the future. Kummer (1978) added that a relationship can be seen as an investment which in some way, sooner or later, benefits the interactor. Starting from these definitions, Cords & Aureli (2000) proposed to describe relationship quality based on three components: value, compatibility and security. Relationship value represents the benefits an individual receives from the social partner, relationship compatibility is the general tenor of social interactions in a dyad, which is influenced negatively by aggressive interactions, and relationship security is the predictability and consistency of the relationship over time.

These components could be quantified for relationships in bonobos by and Stevens et al. (2015), following the method of Fraser et al. (2008). They choose a set of 9 (Fraser et al.) and 8 (Stevens et al.) behavioural variables, on which principal component analysis was done. From the analysis, respectively 3 and 2 components were extracted that strongly resembled the theoretical components from Cords & Aureli (2000).

on tolerance in the genus *Pan* comes from Jaeggi et al. (2010), who found lower tolerance in food sharing in a bonobo group, compared to chimpanzees. This was thought to be due to the more despotic dominance style in the bonobo group, while the chimpanzees were more egalitarian. Differences in dominance style could cause differences in tolerance in the same way between groups of the same species, as was shown for chimpanzees by Cronin et al. (2014). For bonobos, this could be an important factor when comparing wild groups with captive ones, since the artificial group composition of captive populations possibly causes steeper dominance hierarchies (Stevens et al., 2008).

The role of relationship quality could be ambiguous. On one hand, aggression can best be attenuated if it could possibly damage strong relationships (De Waal, 1989). On the other hand, strong relationships might overcome the negative effects of aggression better than weak ones, and combining aggression and reassurance can be a technique to strengthen bonds (de Waal, 1986b, 2000). The study by Jaeggi et al. (2010) suggested a positive relation between tolerance and affiliative relationship (similar to relationship value, see Box 1) in bonobos, but this didn't explain a significant amount of the variance. The opposite was observed by Tan & Hare (2013); in their study, (young) bonobos showed a preference to share with strangers rather than group mates.

Although kin selection theory predicts enhanced social tolerance towards kin, mammals and primates in general don't preferentially tolerate groupmates on basis of kinship (Smith, 2014). The study by Cronin et al. (2015) however, shows that the offspring of the alpha female was

better tolerated in the resource zone compared to the other bonobos. Jaeggi et al. (2010) found this effect in chimpanzees, but not in bonobos.

Tolerance has been shown to weaken with age in chimpanzees, but this effect was not present for bonobos (Wobber et al., 2010b). However, a study where bonobos voluntarily opened a door to a stranger could not be replicated with older individuals (Hare & Kwetuenda, 2010; Bullinger et al., 2012). In addition, urinary thyroid hormone concentrations suggest a delayed adulthood in bonobos compared to chimpanzees (Behringer et al., 2014). This would mean that if tolerance weakens with age, it will happen at a higher age than in chimpanzees. Possibly Wobber et al. (2010b) did not come to this conclusion because the bonobos were too young to notice an age effect on tolerance.

The function of sociosexual behaviour in bonobos is not yet entirely understood, but Hohmann & Fruth (2000) suggest two possible functions that could enhance tolerance: tension regulation and expression of status. Status communication has been observed to enhance tolerance in chimpanzees; by acknowledging dominance ranks prior to competition, the group is able to enter a relatively non-competitive mode with a more shallow hierarchy (de Waal, 1992). Consequently, it might be expected that groups or individuals that express these types of behaviour to a lesser extent are less tolerant. Cronin et al. (2015) mention that the lower tolerance they found in bonobos compared to chimpanzees, could be due to the lack of an opportunity for the bonobos to engage in anticipatory social interactions near the resource zone.

Rearing history may influence individual behaviour, considering the finding that mother-reared bonobos have a better ability to regulate their emotions and are more socially competent than orphans (Clay & de Waal, 2013). Cronin et al. (2015) suggested that this could possibly lead to differences in behaviour during food competition.

1.7 Which factors affect social tolerance between groups and individuals?

In this study, I tried to determine for which factors underlie variation in social tolerance between groups and individuals in bonobos. The study consisted of three parts.

In the first part, dyadic and group measures were calculated for dominance steepness and relationship quality, from behavioural data.

In the second part, I tested which factors may cause variation in social tolerance on the group level.

In the third part, I tested which factors may cause variation in social tolerance between dyads.

a. Calculating dominance steepness and relationship quality

Differences in dominance status were determined by calculating normalised David's scores, which are cardinal ranks of each individual of the group (method based on De Vries et al., 2006). These were subsequently used to calculate the dominance steepness (Appendix 1) per group.

For relationship quality, a principal component analysis (PCA) on eight behavioural variables yielded two components, similar to relationship value and relationship compatibility, as described by Cords & Aureli (2000) (methods based on Fraser et al. 2008; Stevens et al. 2015, see Box 1). Component scores were calculated for each dyad, and the mean of the dyadic scores was used in the comparison between groups.

b. Group-level social tolerance

This part again consists of 2 sub-parts.

Firstly, I repeated the peanut plot experiment from the study by Cronin et al. (2014, 2015), on the same bonobo group that was tested by Cronin et al. (2015) (their experiments took place in September and October 2012). This resulted in a group measure and dyadic measures for social tolerance. The group measure was compared with the results from Cronin et al. (2014, 2015), which allowed to test for repeatability in the bonobo group and to see if there was still a difference between this group and the chimpanzee groups. The dyadic measures were used in part two of the study.

Cronin et al. (2015) remarked that it would have been a good idea to quantify the sociosexual behaviour that took place before the experiment. This type of behaviour was observed during this study in order to make future comparisons with similar behaviour in bonobos or chimpanzees under the same study paradigm possible.

Secondly, I used video recordings from the puzzle feeder experiments done by Nicky Staes in eight bonobo groups. After coding these videos for proximity, it was possible to calculate group and dyadic measures for social tolerance.

The group measures were tested for correlation with mean age, the proportion of maternal kin dyads (Appendix 1) in the group, dominance steepness, group size, proportion of females

in the group and mean relationship quality. Group size was tested for because the experiments were not adapted to different group sizes.

c. Dyadic

The dyadic measures from the peanut plot experiment and the puzzle feeder experiments were analysed together, using generalised linear mixed models (GLMM). The data were tested for a relation between social tolerance and difference in dominance status, maternal kinship, gender combination, the dyad's mean age, difference in age, relationship quality, mean tenure (Appendix 1) and rearing-history. The effects of dominance status, maternal kinship, age, relationship quality and rearing history were expected based on the findings of previous experiments (section 1.6). Tenure might affect the relationship of two individuals, because individuals that have been together for a longer time can have built up a stronger relationship, as was supported by Stevens et al. (2015), and thus be more tolerant towards each other. The same way, bonobos of a more similar age could be possibly more tolerant towards each other because of a stronger bond, if similarity in age would mean that they grew up together. When two bonobo groups meet each other in the wild, females have been observed to display more tolerance towards the individuals from the other group than males did (Idani, 1990). This suggests gender effects on tolerance.

2. Methods

2.1 Data collection

2.1.1 Study sites and subjects

This study investigated social tolerance in nine bonobo groups (47 individuals) from six different zoos. In all zoos, the bonobos' diet mainly consisted of vegetables. In addition, they were given seeds, branches with leaves and a small amount of fruit. Water was provided *ad libitum*.

Juveniles under seven years old were excluded from the study. This age was chosen based on sexual maturation; females have their first menstrual cycle when they're between seven and ten years old (Vervaecke et al., 1999).

a. Planckendael

Dierenpark Planckendael is located in Mechelen, Belgium. From this group, data are included from 2011 and 2014. This will be referred to as PL11 and PL14.

The group consisted of nine individuals in 2014, and seven in 2011. For the PL11 group, the part of the group that was included in the study consists of two females and three males, with an average age of 16 years. In the PL14 group, the included individuals were four females and four males, with an average age of 15 years. The difference between PL11 and PL14 was the addition of a young female (Busira) and the birth of an infant (Nayoki) (Appendix 8). The bonobos were kept as a single group, in an enclosure that contains both an indoor building (600 m³) and an outdoor island (3000m²).

b. Apenheul

Apenheul is located in Apeldoorn, The Netherlands. Of the group of ten bonobos, four females and two males were included in the study (group AP). Their average age at the time of the experiments was 21 years (Appendix 8). The bonobos were always kept as one group. There were four connected indoor enclosures (in total $\pm 230 \text{ m}^2$) and an outdoor enclosure ($\pm 4000 \text{ m}^2$).

c. Stuttgart

Wilhelma is located in Stuttgart, Germany. The bonobos were divided in two groups under an artificial fission-fusion system. This means that there was exchange of individuals between the groups. However, the groups in Stuttgart remained stable for most of the time during the experiments and the observation period. The groups will be referred to as STA and STB. STA contained eight individuals, five females and two males of which were included in the study. Their average age was 31 years. STB contained five individuals, with three females that were included in the study. The average age was 14.8 years (Appendix 8). There were two indoor (in total $\pm 350 \text{ m}^2$) and two outdoor enclosures ((in total $\pm 1220 \text{ m}^2$).

d. Frankfurt

Zoo Frankfurt is located in Frankfurt, Germany. The group was kept under an artificial fission-fusion system, with frequent exchange of individuals. Together, the groups had 14 individuals, six females and three males of which were included in the study (group FR). These individuals were on average 26 years old (Appendix 8). There were two indoor (in total $\pm 254 \text{ m}^2$) and two outdoor enclosures (in total $\pm 1030 \text{ m}^2$).

e. Wuppertal

Zoo Wuppertal is located in Wuppertal, Germany. Of the group of nine, three females and three males were included in the study (group WU). Their average age was 28 years

(Appendix 8). The group was always kept together. Only an indoor enclosure was present ($\pm 88 \text{ m}^2$).

e. Twycross

Twycross Zoo is located in Warwickshire, United Kingdom. This zoo housed 2 groups of bonobos, that never mix. These were hereafter referred to as TWA and TWB. TWA consisted of five bonobos. Two females and two males, with an average age of 23 years, were included in the study. TWB consists of six bonobos, four females and one male of which were included in the study. Their average age is 17 years (Appendix 8). There were two indoor ($\pm 124 \text{ m}^2$) and two outdoor enclosures (in total $\pm 588 \text{ m}^2$).

2.1.2 Behavioural observations

For the group PL14, I did observations in Planckendael between 22/07/2014 and 11/09/2014. They were conducted under semi-natural, non-experimental circumstances. I followed the ethogram that is composed by Stevens & Staes (2014), and based on the ethograms by de Waal (1988, 1992) and (Vervaecke et al., 2000c) (Appendix 2). The used observational methods are a combination of 'all occurrences sampling', 'instantaneous scan sampling' and 'focal animal sampling' (Altmann, 1974). All behaviour was coded using the Noldus 'The Observer' software, version XT10.5.

All occurrences sampling was performed three times a day; during feeding at 9.00 AM, 2.00 PM and 5.30 PM. All incidents of socio-sexual behaviour, aggression, food claims and affiliative contact were observed. The sampling sessions lasted for 20 minutes, and made a total of 50 hours.

Focal sampling was performed twice a day for each individual. During ten minutes, I observed all occurrences of the behaviours that are described in the ethogram. If an individual was out of sight for longer than three minutes, the observation was aborted, deleted and restarted later. The observations were randomly distributed between 9.30 AM and 5 PM, the sequence in which individuals were observed was randomized. Each bonobo was observed as a focal 60 times, adding up to 80 hours in total.

Instantaneous scan sampling was done at the beginning of each focal sample. Each individual's behaviour and proximity to others was recorded. Three classes of proximity were distinguished: less than two meter, less than one meter or touching. One meter was chosen as a unit because it's about a bonobo's arm's length.

The same methods were used for observations in the other groups. These were performed by Nicky Staes and assisting students between November 2011 and September 2012,

roughly in the same period the experiments took place. The total duration of focal and all occurrences sampling is listed in Appendix 3. Behavioural observations did not take place for Stuttgart B.

Inter-observer reliability was high for all observers (N = 6, Spearman's rho >0.79).

2.1.3 Peanut plot experiment

The peanut plot experiment was done with the PL14 group on five days between 4/8/2014 and 11/8/2014, with one session a day. I followed the same protocol as Cronin et al., (2015), based on the one by Cronin et al. (2014).

Around 9 AM, an experimenter walked past the indoor enclosure with a bucket of peanuts. The experimenter shook the bucket audibly so the bonobos were aware of his presence. This way, the bonobos knew that they were about to be fed, and were able to prepare for competition and tension with sociosexual behaviour. The experimenter entered the outdoor area and distributed 96 peanuts over a fixed area of 1.6 x 1 meter (hereafter referred to as 'the peanut plot'). Peanuts were chosen because they were a desired food to all group members. The number of peanuts was determined by multiplying group size by 12, excluding infants. The surface area was calculated to create a density of 60 peanuts per square metre. After the distribution of the peanuts, the experimenter left the outdoor area and the bonobos were allowed to leave the building.

The bonobos were filmed by three camera's (one Sony HDR-CX280E and two Canon LEGRIA FS406), from the moment the experimenter passed with the bucket, until all peanuts were eaten. Each camera recorded for a minimum of ten minutes. One camera was held by an experimenter on the ground, and filmed all occurrences in the peanut plot. Two cameras were placed on an upper viewing deck. One camera was focused on the peanut plot, the other was held by an experimenter. The second camera filmed the bonobos before they were released and recorded the individuals that left or never entered the peanut plot.

2.1.4 Puzzle feeder experiments

The puzzle feeder experiments were done and video recorded by Nicky Staes and assisting students, with the following groups: AP, FR, PL11, STA, STB, TWA, TWB, WU. They took place between November 2011 and September 2012. There were three different puzzle feeder experiments, each on a different day. For the groups held under an artificial fission-fusion system, Appendix 8 shows of which group each bonobo was part during the experiments. Each puzzle feeder contained food that was preferred by the bonobos and was different from their daily diet.

The 'Mesh' experiment consists of a plastic crate, with a lid made of an iron mesh. The crate was filled with water and pieces of pear that sank to the bottom. In order to obtain the food, the bonobos had to put a stick through the mesh, since the openings were too narrow for their hands to fit through. To prevent the crate from falling over, it was attached by ropes to a fence or climbing structure.

'R&F' or 'Reel and Feed' was an experiment with a plastic crate that was attached to the outside of the enclosure fence. In the crate were food items. By pulling a rope that was attached both to the fence and to the far side of the crate, it was possible to tip the crate over towards the fence and take the food.

The 'Tubes' or 'Twisting tubes' consisted of an inner tube with holes in it and an outer tube in several sections, that could be twisted around and had a similar opening. To obtain food, the bonobos had to align the opening of a section of the outer tube with a hole in the inner tube. Inside were small items like corn, sunflower seeds and peanuts.

In the morning, the puzzle feeder was placed in the enclosure. After the bonobos were released, an experimenter video recorded interactions in the immediate vicinity of the puzzle feeder for 30 minutes.

2.1.5 Ethics statement

The research complied with the protocols approved by 'Dierenpark Planckendael', 'Apenheul', 'Wilhelma', 'Zoo Frankfurt', 'Zoo Wuppertal' and 'Twycross Zoo' and adhered to the legal requirements of the country in which the research was conducted (Belgium, The Netherlands, Germany and the UK).

2.2 Data analysis

The data were organised and analysed using the Noldus 'The Observer' software version XT 10.5, Microsoft Office Excel 2010 and statistical software R version 3.2.1 (R Core Team, 2015). Statistical analyses were performed using R and IBM SPSS Statistics version 22.0.

2.2.1 Observational data

The observational data were used to calculate dyadic and group measures for dominance steepness and relationship quality.

a. Dominance steepness

Dominance steepness calculations were done in R, using the package 'Steepness' (Leiva & De Vries, 2014). The methods and significance test were developed by De Vries et al. (2006).

For each group, a matrix was made with the number of times individual A won from B in a dyadic aggressive interaction. As a behavioural marker for dominance, 'fleeing upon aggression' was used; an individual won when the opponent fled (Vervaecke et al., 2000c). Based on this matrix, normalized David's scores were calculated per individual. These values are a cardinal rank measure for the dominance position of an individual in the group. Normalised David's scores range from 0 to N-1, with N representing the group size. By taking the difference between the normalised David's scores of two individuals, it was possible to determine the difference in dominance status within a dyad.

Linear regression was performed on the normalised David's scores of all group members, in order to get the dominance steepness of each group. This is the absolute value of the slope of the straight line fitted to the normalized David's scores, plotted against the subjects' ranks, and therefore lies between 0 and 1. David's scores and dominance steepness could not be calculated for Stuttgart B, since there were no observational data available for this group.

Statistical analyses were performed by comparing the win matrix with a generated win matrix, consisting of randomly drawn integers between 1 and the number of dyads. This procedure was repeated 9999 times. The p-value is the proportion of times that a randomly generated steepness is greater than or equal to the actually observed steepness.

b. Relationship quality

Dyadic measures for relationship quality were calculated following the method by Fraser et al. (2008) and Stevens et al. (2015). Based on the behavioural data, I calculated eight parameters for each dyad; grooming frequency, grooming symmetry, proximity, aggression frequency, aggression symmetry, support, contra-support and peering frequency. Similar to Stevens et al. (2015), this study didn't include 'consistency of affiliation', 'successful begging' and 'tolerance to approaches' from by Fraser et al. (2008) for practical reasons, but included 'aggression symmetry' and 'peering'.

Grooming frequency was the number of grooming bouts counted within a dyad, divided by the total time of focal sampling on both partners. Similarly, aggression frequency was the number of aggressive interactions within a dyad, divided by the total observation time. Occasions where one of the partners was giving support against the other (contra-support) weren't included. The time by which the number of respectively grooming bouts and

aggressive interactions has to be divided differs, since aggressive interactions were scored for all individuals at all times, while grooming or being groomed was only scored during the focal time of the individual involved.

Grooming symmetry was calculated for each partner of the dyad using the following formula for partner A: $\frac{A \text{ grooms } B}{A \text{ grooms } B + B \text{ grooms } A}$. Consequently, there were two values for each dyad. The lowest of the two was taken to represent the grooming symmetry. Thus, grooming symmetry ranged between 0 and 0.5, with higher values indicating higher symmetry. Aggression symmetry was calculated the same way, based on the number of aggressive interactions.

Support was defined as follows: A gives support to B when A is aggressive towards C within 30 seconds after an aggressive interaction between B and C. Events where more than three individuals interacted weren't included. Every aggressive interaction between B and any other group member except for A was seen as an opportunity for A to provide support to B, and the measure for support was corrected by the number of opportunities to provide support. In summary, support between A and B was calculated as follows:

$$\frac{(\text{support from A to B}) + (\text{support from B to A})}{\left(\frac{\text{aggressive interactions between A and anyone but B}}{\text{aggressive interactions between B and anyone but A}} \right) + \left(\frac{\text{aggressive interactions between B and anyone but A}}{\text{aggressive interactions between A and anyone but B}} \right)}$$

Contra-support between A and B was calculated in a similar way. It was defined as the number of times A provides support to C, within 30 seconds after an aggressive interaction between B and C. So the formula becomes:

$$\frac{(\text{contra-support from A to B}) + (\text{contra-support from B to A})}{\left(\frac{\text{aggressive interactions between A and anyone but B}}{\text{aggressive interactions between B and anyone but A}} \right) + \left(\frac{\text{aggressive interactions between B and anyone but A}}{\text{aggressive interactions between A and anyone but B}} \right)}$$

Proximity was the proportion of instantaneous scan samples the dyad was located within arm's reach of each other.

Peering occurs when A stares at B's face from a close distance. Peering frequency was calculated as follows: $\frac{(\text{occasions A peers to B}) + (\text{occasions B peers to A})}{(\text{focal time A}) + (\text{focal time B})}$. Similar to grooming

frequency, the focal time was used. This was because peering was only scored during focal sampling, and not during all occurrences sampling.

Stuttgart and Frankfurt exchanged bonobos between groups, although in Stuttgart the groups stayed roughly the same most of the time. To account for dyads that were split during some of the observations, I only counted behavioural interactions that occurred when dyads were in the same group. In the parameters that express a frequency, I divided by the focal or all

occurrences sampling time that dyads actually spent together. Dyads that were together for less than 70% of the observational time were excluded.

On these eight parameters, principal component analysis (PCA) was performed in SPSS. To improve normality, all frequency data (grooming, peering and aggression frequency, support, contra-support) were transformed by taking the square root. The number of components to extract from the PCA was first determined based on Kaiser's criterion that eigenvalues must be greater than 1. This method was applied in order to be able to compare components with other studies, since Kaiser's criterion is usually used in other relationship quality studies. However, Kaiser's criterion often leads to an overestimation of the number of components. Therefore, Parallel Analysis was also used as a more reliable method to determine the number of components.

An orthogonal varimax rotation was used, in order to make components better interpretable. Varimax rotation minimizes the number of variables that have high loadings on each component. To determine minimum factor loading, the classic cut off value of 0.4 was used, following Budaev (2010). This was appropriate since the sample size was large enough (>100).

Afterwards, a component score was calculated for every dyad. This score represents the dyad's 'performance' on each component.

To obtain group-level values for relationship quality, the mean component score was calculated per group.

2.2.2 Measures for social tolerance

Social tolerance was measured based on the video recordings from the peanut plot experiment and the puzzle feeder experiments.

a. Group level

A group level measure for tolerance was calculated by monitoring the fraction of the group that was present within an arm's length (± 1 m) of the puzzle feeder or the peanut plot. For the peanut plot, this was counted every 15 seconds from the start of the experiment. In the puzzle feeder experiments, an interval of 30 seconds was used. This difference was due to the length of the experiment: the peanut plot was mostly depleted after two minutes, while the puzzle feeders could contain food for longer than 30 minutes. The 'start' was defined as the moment the bonobos were allowed to enter the area with the peanut plot or the puzzle

feeder. For each group, the median fraction was calculated. The groups from Frankfurt were excluded from this part of the study, due to too much instability of the group composition.

b. Dyadic

For dyadic measures of tolerance, individuals that were sitting within an arm's length of the puzzle feeder or the peanut plot were monitored continuously. For the puzzle feeder experiments, this was already done partly by Nicky Staes and finished by myself. Based on the time two individuals spent in reach of the puzzle feeder or peanut plot, dyadic social tolerance was calculated based on the formula $\frac{2T_t}{T_{tot1} + T_{tot2}}$,

where T_t represents the time the dyad spent simultaneously within an arm's length of the feeder or peanut plot, T_{tot1} and T_{tot2} the total time individual 1 and 2 respectively spent within an arm's length of the feeder or peanut plot. This measure was never used before in tolerance studies. It was chosen rather than the mean of the dyadic values for $\frac{T_t}{T_{tot1}}$ because it accounts better for low tolerance between individuals when one spent only a short total time in the plot or by the feeder. For example, when A spends a long time in the plot, a short time of which B is present, and B spends a short time in the plot, but A is present the entire time, the measure will be influenced more heavily by the small $\frac{T_t}{T_{totA}}$ value than would be the mean value. In other words, it is more influenced by the lowest tolerance expressed within a dyad.

For the zoos where individuals were exchanged between groups, Stuttgart and Frankfurt, I determined the time individuals spent alone or together at the feeder per dyad, in order to count only the time when the dyad was actually together. Dyads that were together for less than 70% of the time were excluded.

2.2.3 The influence of different factors on social tolerance

a. Group level

The results from the peanut plot experiment were compared with those from Cronin et al. (2014, 2015). From Cronin et al. (2015) only the 'grass' conditions were included. In the other conditions, the potential for social conflict was artificially increased.

The mean proportion of individuals present in the peanut plot was compared between all groups tested in this paradigm. The proportion present every 15 seconds was compared with the results from Cronin et al. (2015). A comparison was made based on the mean values and visually. Statistical testing for differences was impossible, due to my lack of access to the complete datasets.

In addition, sociosexual and aggressive interactions before and during the experiment were observed in order to create a more complete image of the circumstances of the experiment. This was done between the moment the experimenter with the bucket passed the bonobos and 10 minutes after the start of the experiment.

The results from the puzzle feeder experiments were used to test for correlation between group tolerance and mean age, the proportion of maternal kin dyads in the group, group size the proportion of females in the group and mean relationship quality. Whether group tolerance levels were significantly different from each other was tested with a Kruskal-Wallis test and post hoc with a pairwise Wilcoxon signed-rank test, with Bonferroni-corrected p-values (p must be smaller than 0.002).

To test if the group measures for social tolerance corresponded with the dyadic measures of the group members, I tested for correlation between the group measures and the mean dyadic measure for each group. Kendall's correlation test was used, which works better on a small data set (Field, 2009).

b. Dyadic

The different parameters of which the effect on social tolerance was determined were difference in dominance status, maternal kinship, gender combination, the dyad's mean age, difference in age, relationship quality, mean tenure and whether an individual was hand-reared. Maternal kinship for a dyad could be either 1 or 0, with a 1 for individuals that were directly related through their mother (offspring-mother or maternal siblings). 'Hand-reared' per dyad could be 2, 1 or 0, representing whether both, only one or none of the individuals were hand-reared. Gender combination data consisted of the categories male-male (MM), male-female (MF) and female-female (FF). Tenure was the duration for which each individual was a part of its current group. The difference in dominance was calculated by taking the absolute value of the difference of the two normalised David's scores.

In order to test whether and how dyadic tolerance is influenced by these parameters, I fitted several generalised linear mixed models (GLMM) on the dataset. This was appropriate since dyadic tolerance data were non-normally distributed and group and individual were random effects. In these models the dependent variable was social tolerance, and the independent variables were difference in dominance status, maternal kinship, gender combination, the dyad's mean age, relationship quality (value and compatibility), mean tenure and whether an individual was hand-reared. To standardise all variables, Z-scores were calculated.

GLMM's were fit and tested in R, using the package 'lmerTest' (Kuznetsova et al., 2015).

Dyadic tolerance measures were calculated twice for the Planckendael group: once using the puzzle feeder experiments carried out in 2011 (PL11) and once based on the peanut plot experiment from this study (PL14). To be able to include both groups in the analysis, I ran it once with all groups except for PL14 (GLMM1a, GLMM2a and GLMM3a, see Table 1) and once with all groups except for PL11 (GLMM1b, GLMM2b and GLMM3b, see Table 1).

For 28 dyads (all from STB and 18 from FR), relationship quality and/or difference in dominance status could not be determined, due to a lack of observational data for STB and too few observations when the dyad was in the same group in FR. For another 31 dyads, the normalised David's score wasn't significant (TWA, TWB, WU). These dyads were excluded from GLMM1a and GLMM1b, bringing the sample size back to 46 and 64 respectively.

Subsequently, I ran the model again in GLMM2a and GLMM2b, with all dyads for which relationship quality could be calculated. This increased the sample sizes to 77 and 95. Dominance was not tested for, since not all dyads had significant normalised David's scores.

In GLMM3a and GLMM3b, all dyads were included. This meant that a part of the dyads didn't have a (significant) normalised David's score and/or values for relationship quality. Accordingly, all variables except for dominance and relationship quality were tested for, on the largest possible sample size (105 and 123).

Categorical variables with a significant effect and more than three categories were further analysed post-hoc using a Wilcoxon signed-rank test with Bonferroni correction (p must be smaller than 0.02). In case the effect of the variable was tested again on a larger dataset, post-hoc analyses were only done for the largest datasets.

Based on the results from the post-hoc test, I decided to do an extra test for the influence of gender combination on difference in dominance and relationship value in these study groups. This was tested with TukeyHSD tests and Wilcoxon signed-rank tests with Bonferroni correction (p must be smaller than 0.02). To test this for difference in dominance, the datasets from GLMM1a and 1b were used, for relationship value those from GLMM2a and 2b.

Table 1. An overview of the different GLMM's and the size of the dataset they were run on

Included variables	With PL11	With PL14
All	GLMM1a 46	GLMM1b 64
All except for dominance	GLMM2a 77	GLMM2b 95
All except for dominance, relationship value, relationship compatibility	GLMM3a 105	GLMM3b 123

3. Results

3.1 Dominance

The individual normalised David's scores for each individual are listed in Appendix 8, together with the individual's rank within the group. For three out of the eight groups, steepness was non-significant (Table 2). Normalised David's scores of the individuals belonging to these groups are listed in Appendix 8 as well, but are marked as non-significant (NS).

Table 2. Slopes and significance for the dominance steepness of each group. Significant results are marked with an asterisk.

Group	Members older than 7 years	Steepness	p-value
Apenheul	6	0.33*	0.02
Frankfurt	9	0.18*	0.02
Planckendael '11	5	0.55*	0.002
Planckendael '14	8	0.44*	0.0001
Stuttgart A	6	0.34*	0.004
Twycross A	5	0.24	0.2
Twycross B	4	0.22	0.2
Wuppertal	6	0.24	0.3

3.2 Relationship quality

Principal component analysis (PCA) was performed on the relationship quality data, with a sample size of 106. The Kaiser–Meyer–Olkin measure of sampling adequacy was 0.69, which is mediocre to good (Hutcheson & Sofroniou, 1999).

Based on Kaiser's criterion, PCA1 resulted in three components. After an orthogonal varimax rotation, these components explained respectively 32.81%, 23.39% and 14.16% of the variance. The first component had high loadings for grooming frequency, grooming symmetry, proximity and peering frequency. For the second component there were high loadings for aggression frequency, aggression symmetry and counter-intervention. The third component only included support. The Parallel Analysis showed that only the first two components had eigenvalues greater than the simulated 95 percentile, in contrast to the third component. Consequently, a second PCA was run, retaining two components.

The components from PCA2 explained 32.56% and 23.82% of the variance, after varimax rotation. The high loading factors were similar to those from PCA1, with high loadings on the first component for grooming frequency, grooming symmetry, proximity and peering frequency, and high loadings on the second component for aggression frequency, aggression symmetry and counter-intervention (Table 3). Variables contributing to the first component are similar to those defining 'relationship value' according to Cords & Aureli, (2000), while the ones under the second component suggest incompatibility (Box 1). Thus, similar to the study by Stevens, de Groot & Staes (2015), I labelled the first component 'relationship value' and the opposite value of the second component 'relationship compatibility'. However, in contrast to the study by Stevens, de Groot & Staes (2015), the first component didn't have high loadings for support.

The dyadic component scores were calculated and used in both the dyadic and group analyses of tolerance. Table 4 shows the group means and SEM for Value and Compatibility, which correspond to weighted densities of the social networks based on these variables.

Table 3. The two components resulting from the second principal component analysis (PCA2) with their factor loadings, eigenvalues and explained % of the total variance. Bold values indicate high loadings (absolute value > 0.4).

Variable	Value	Compatibility
Proximity	0.89	0.11
Grooming frequency	0.88	0.05
Grooming symmetry	0.74	0.05
Support	0.06	0.20
Peering frequency	0.67	0.18
Aggression frequency	-0.15	-0.86
Aggression symmetry	0.08	-0.75
Counter-intervention	-0.12	-0.72
% of variance explained	32.56	23.82
Eigenvalue	2.84	1.67

Table 4. Group mean and SEM for Value and Compatibility

Group	Value mean (\pm SEM)	Compatibility mean (\pm SEM)
Apenheul	0.253 (\pm 0.2)	-0.396 (\pm 0.2)
Planckendael11	0.581 (\pm 0.2)	-0.126 (\pm 0.2)
Planckendael14	-0.123 (\pm 0.1)	0.104 (\pm 0.1)
Twycross A	0.564 (\pm 0.2)	0.043 (\pm 0.2)
Twycross B	-0.019 (\pm 0.2)	0.221 (\pm 0.3)
Wuppertal	-0.260 (\pm 0.2)	-0.047 (\pm 0.2)

3.3 Group tolerance

3.3.1 Peanut plot experiment

The number of individuals simultaneously present in the peanut zone over the five days didn't follow a normal distribution ($W = 0.89$, $p < 0.001$). However, I will use the mean and standard error on the mean (SEM) to make a better comparison with previous peanut plot experiments on bonobos and chimpanzees (Cronin et al., 2014, 2015). Statistical

comparison with the other studies was impossible due to the lack of access to the entire datasets.

A Kruskal-Wallis test showed no significant difference between days ($H = 1.645$, $df = 4$, $p = 0.801$). On average, a proportion of 0.28 of the group was present in the peanut zone simultaneously (\pm SEM 0.03, median = 0.25, SD = 0.17). A comparison with the same test on four chimpanzee groups and on the same bonobo group in 2012 is shown in Figure 1, the mean values for the previous studies are included in Appendix 4. The average proportion of bonobos simultaneously present in the peanut plot each 15 seconds of the first two minutes of the experiment is shown in Figure 2 for this study and for (Cronin et al., 2015).

Intolerant behaviour before the experiments was limited to two aggressive intentions and one parallel display. During the experiments there were eight incidents; two forced claims, five aggressive intentions and one long charge.

Sociosexual behaviour before the experiments was surprisingly absent. Only one non-copulative mount and two sex presents took place. Other types of affiliative behaviour occurred more often before the experiments; six affiliative touches, six lateral embraces, one mounted walk and one buddy walk were observed (ethogram: Appendix 2).

During the experiments, no sociosexual behaviour was observed in the plot or outside of it.

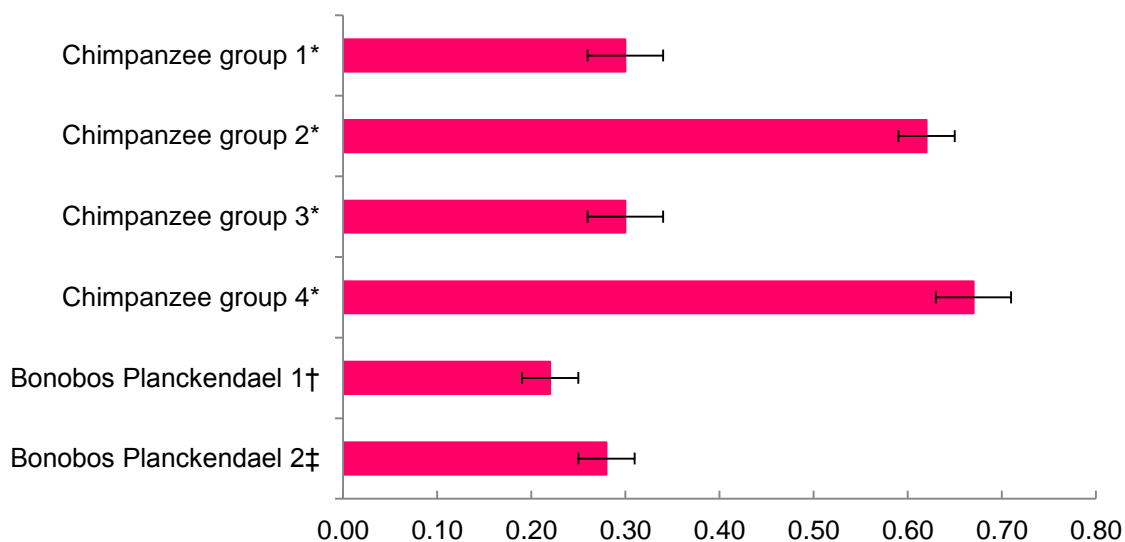


Figure 1. A comparison of the proportion of the group present in the peanut zone between this study and previous studies on the same bonobo group and on four chimpanzee groups. * Cronin et al. (2014) † Cronin et al. (2015) ‡ This study

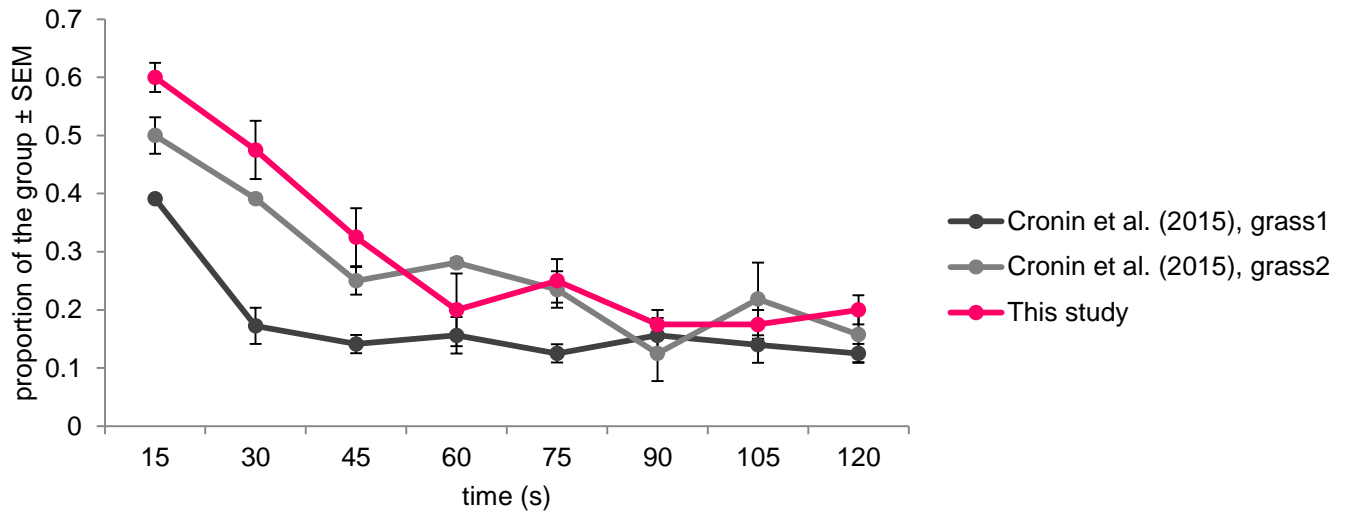


Figure 2. The average proportion of the group simultaneously present in the peanut zone each 15 seconds for two minutes after the start of the experiment, for the experiments by Cronin et al (2015) and this study.

3.3.2 Puzzle feeder experiments

As data were non-normally distributed for most groups (W-value for each group; AP: 0.80; PL11: 0.86; STA: 0.89; STB: 0.90; TWA: 0.86; TWB: 0.77; WU: 0.87; all p-values < 0.001), I used the median of each group and non-parametric tests. The Kruskal-Wallis test showed there were significant differences between groups ($H = 68.47$, $p < 0.001$). As a *post hoc* test, I performed a pairwise Wilcoxon, with Bonferroni-corrected p-values. 10 out of 23 pairs showed significant differences ($p < 0.002$). The social tolerance level of each group is visualised in Appendix 5.

However, these differences did not appear to reflect differences in the chosen parameters. Kendall's correlation test didn't show significant correlations between group tolerance and average age ($\tau = -0.45$, $p = 0.2$), proportion of kin dyads in the group ($\tau = 0.25$, $p = 0.4$), group size ($\tau = -0.56$, $p = 0.1$), proportion of females in the group ($\tau = -0.64$, $p = 0.08$) mean relationship value ($\tau = 0$, $p = 1$) and mean relationship compatibility ($\tau = 0$, $p = 1$). STB could only be included in the correlation tests for average age, proportion of female dyads and proportion of kin dyads, because there were no observational data on this group. To test for correlation with dominance steepness, only groups with a significant dominance steepness value were analysed; AP, PL11 and STA. The test was not significant ($\tau = 0.82$, $p = 0.2$).

No correlation was found between the group measures and the median of the dyadic measures per group ($\tau = 0.39$, $p = 0.2$). Results are summarised in Appendix 6.

3.4 Dyadic tolerance

Dyadic tolerance data were non-normally distributed ($W = 0.80$, $p < 0.001$). A complete overview of the outcome of the 6 GLMM's is given in Appendix 7. Table 5 contains a summary of the significance (p-value) of the influence of each variable on tolerance, the correlation coefficient for continuous variables and the difference in intercept for categorical variables (β). Analyses and figures were made based on the standardised values of each variable.

Table 5. An overview of the p-values of the variables in each GLMM. Significant p-values are printed bold. The correlation coefficient for continuous variables and the difference in intercept for categorical variables (β) is given in italics.

Variable	GLMM1a	GLMM1b	GLMM2a	GLMM2b	GLMM3a	GLMM3b
Relationship value	0.08	0.2	0.01 <i>0.27</i>	0.02 <i>0.24</i>	-	-
Relationship compatibility	0.9	0.6	0.9	0.4	-	-
Hand-reared	0.03 <i>1: +0.68</i>	0.4	0.1	0.5	0.7	0.7
Difference in dominance status	0.0009 <i>-0.35</i>	<0.0001 <i>-0.41</i>	-	-	-	-
Maternal kinship	0.07	0.2	0.2	0.1	0.09	0.03 <i>kin: +0.56</i>
Gender combination	0.001 <i>MF: -0.58</i> <i>MM: -1.05</i>	0.2	0.02 <i>MF: -0.54</i> <i>MM: -0.48</i>	0.02 <i>MF: -0.38</i> <i>MM: -0.35</i>	0.0001 <i>MF: -0.84</i> <i>MM: -1.18</i>	0.0007 <i>MF: -0.72</i> <i>MM: -0.89</i>
Tenure	0.6	0.5	0.4	0.5	0.3	0.9

Mean age	0.1	0.4	0.7	0.5	0.007	0.04
					-0.27	-0.21
Age difference	0.5	0.3	0.9	0.3	0.5	0.2

3.4.1 GLMM1a and GLMM1b

In these analyses, only dyads with a significant normalised David's score were included. Difference in dominance had a significant negative effect for both GLMM's (with PL11: $p = 0.0009$, $\beta = -0.35$; with PL14: $p < 0.0001$, $\beta = -0.41$). Figures 3 and 4 show the relationship between social tolerance and dominance difference in each dataset. For the dataset containing PL11, rearing history ($p = 0.03$, $\beta_1 = 0.68$) and gender combination ($p = 0.001$, $\beta_{MF} = -0.58$, $\beta_{MM} = -1.05$) also had a significant effect. This dataset only contained dyads where no one or only one individual was hand-reared. The dyads with one hand-reared individual had a higher social tolerance. The effect of different gender-combinations will be discussed later.

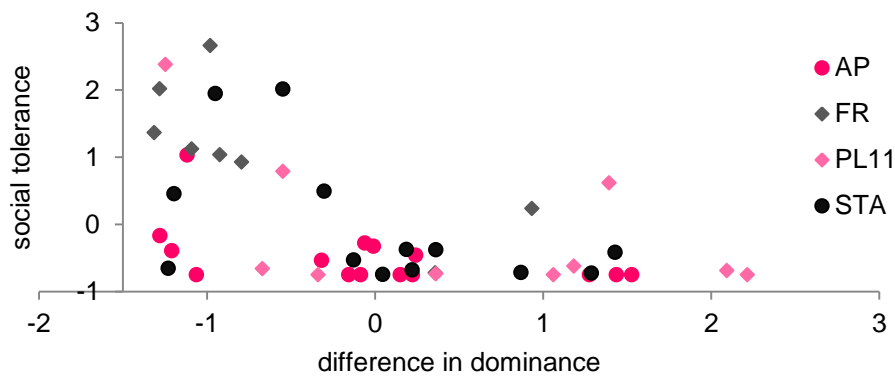


Figure 3. The relationship between social tolerance and difference in dominance, for the dataset containing PL11. Dyads from different groups are represented by a different symbol.

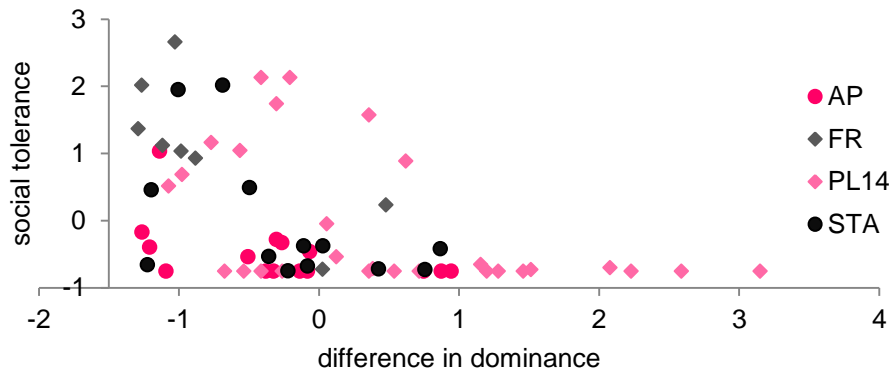


Figure 4. The relationship between social tolerance and difference in dominance, for the dataset containing PL14. Dyads from different groups are represented by a different symbol.

3.4.2 GLMM2a and GLMM2b

In these analyses, all dyads for which relationship value and compatibility could be calculated were included. Since not all dyads had a significant normalised David's score, dominance was not tested here. In contrast to GLMM1a and GLMM1b, relationship value had a significant positive effect for both analyses (with PL11: $p = 0.01$, $\beta = 0.27$; with PL14: $p = 0.02$, $\beta = 0.24$). Figures 5 and 6 show the relationship between social tolerance and relationship value in each dataset. Both analyses showed a significant effect of gender combination (with PL11: $p = 0.02$, $\beta_{MF} = -0.54$, $\beta_{MM} = -0.48$; with PL14: $p = 0.02$, $\beta_{MF} = -0.38$, $\beta_{MM} = -0.35$).

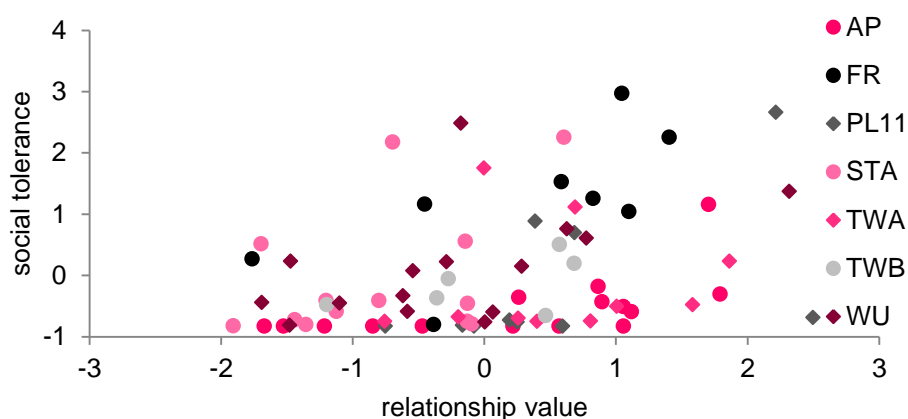


Figure 5. The relationship between social tolerance and relationship value, for the dataset containing PL11. Dyads from different groups are represented by a different symbol.

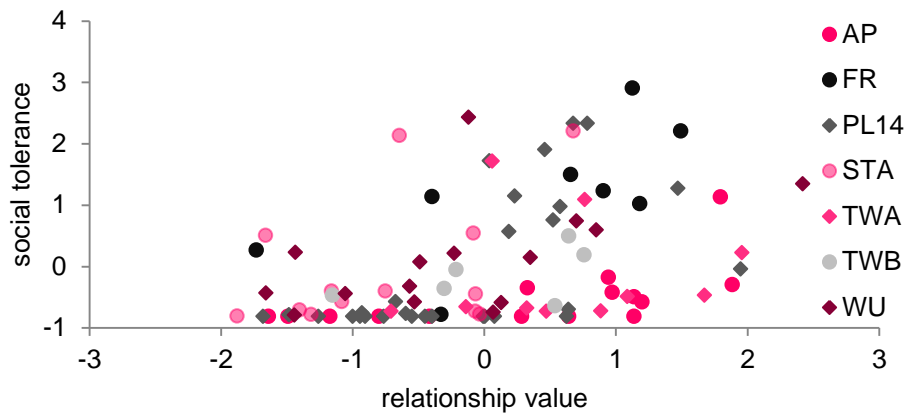


Figure 6. The relationship between social tolerance and relationship value, for the dataset containing PL14. Dyads from different groups are represented by a different symbol.

3.4.3 GLMM3a and GLMM3b

In these analysis, dominance, relationship value and relationship compatibility were excluded, because not all dyads had (significant) values for these variables. In both GLMM's, gender combination (with PL11: $p = 0.0001$, $\beta_{MF} = -0.84$, $\beta_{MM} = -1.18$; with PL14: $p = 0.0007$, $\beta_{MF} = -0.72$, $\beta_{MM} = -0.89$) and mean age (with PL11: $p = 0.007$, $\beta = -0.27$; with PL14: $p = 0.04$, $\beta = -0.14$) were significant factors. The effect of an increase in mean age on social tolerance was negative (Figures 7 and 8). For the dataset with PL14, maternal kinship was a significant factor, with higher social tolerance among related individuals ($p = 0.03$, $\beta_{related} = 0.56$).

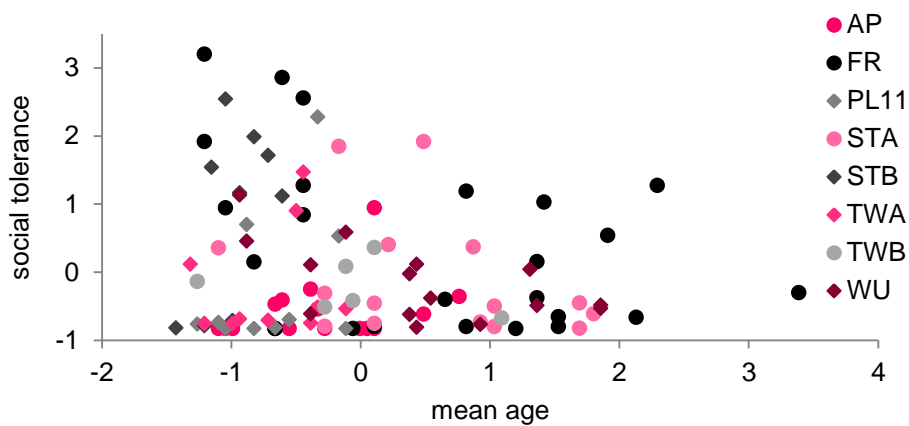


Figure 7. The relationship between social tolerance and the dyad's mean age, for the dataset containing PL11. Dyads from different groups are represented by a different symbol.

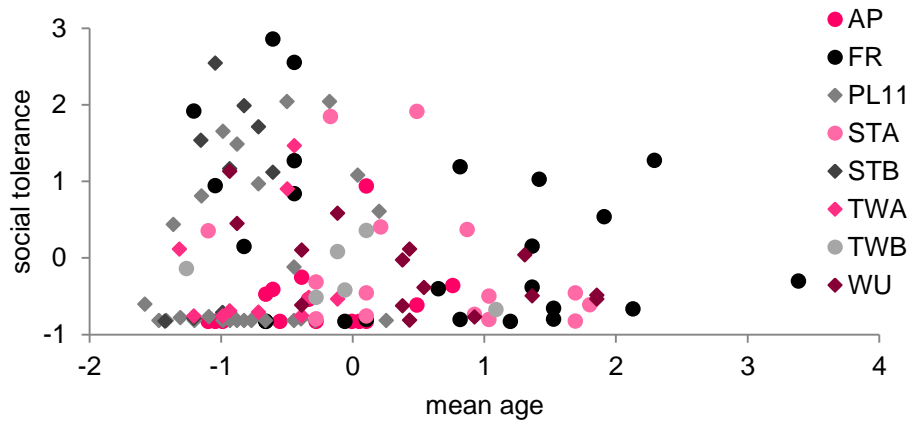


Figure 8. The relationship between social tolerance and the dyad's mean age, for the dataset containing PL14. Dyads from different groups are represented by a different symbol.

As a post hoc test for differences between the different classes of gender combination, a Wilcoxon signed-rank test was performed. This was done on the two complete datasets; one containing PL11 and one containing PL14 (sample sizes: 105 and 123). Since the comparison existed of three separate tests for each dataset, p must be smaller than 0.02 according to Bonferroni correction. For the dataset with PL11, there was a significant difference between female-female and male-female dyads ($W = 1660.5$, $p < 0.0001$) and between female-female and male-male dyads ($W = 104.5$, $p = 0.0009$). No significant difference was found between male-female and male-male dyads ($W = 244.5$, $p = 0.5$) (Figure 9). The same result was found for the dataset containing PL14; a significant difference between female-female and male-female dyads ($W = 2188$, $p < 0.0001$) and between female-female and male-male dyads ($W = 188$, $p = 0.002$) but not between male-female and male-male dyads ($W = 389$, $p = 0.7$) (Figure 10).

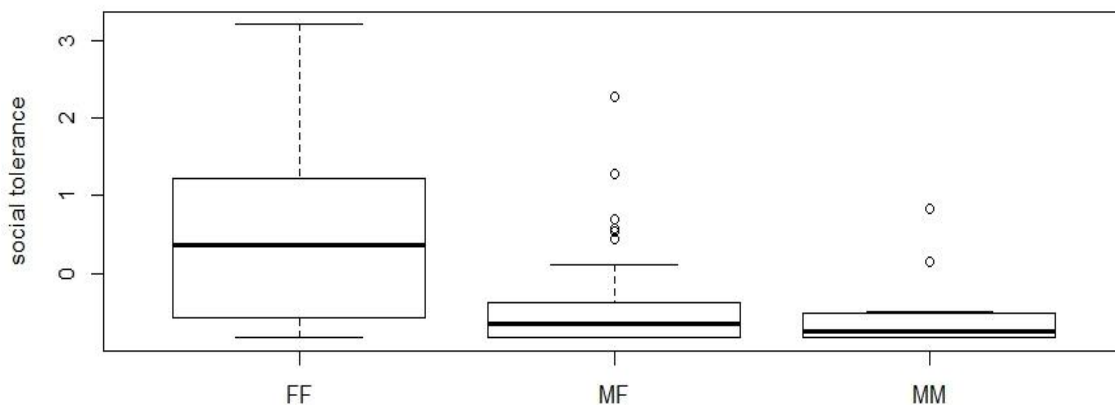


Figure 9. The difference in social tolerance between different gender combinations, for the dataset with PL11

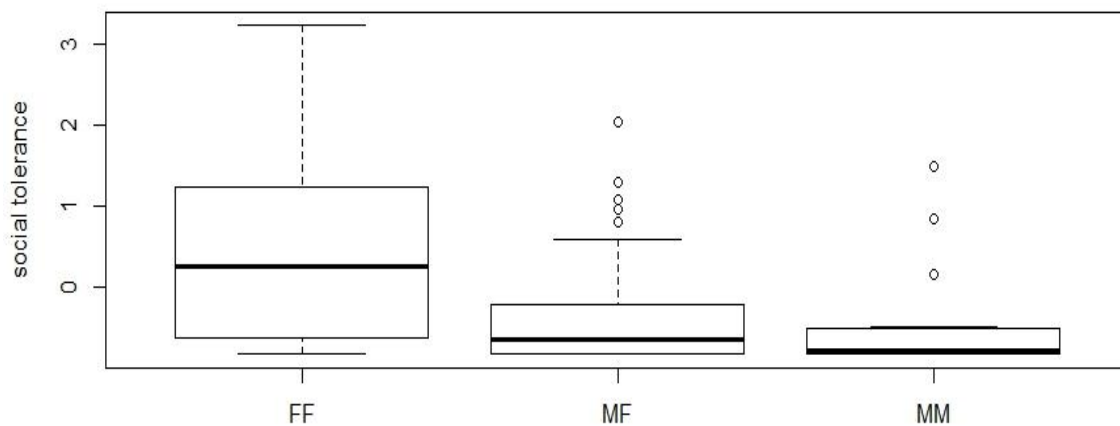


Figure 10. The difference in social tolerance between different gender combinations, for the dataset with PL14

3.4.4 The influence of gender combination on relationship value and difference in dominance

Based on these results, I decided to do additional tests for whether relationship value and difference in dominance differed between gender combinations in these study groups, as was reported for relationship quality by Stevens et al. (2015).

The effect of gender combination on the dyadic difference in dominance was tested with TukeyHSD tests on the datasets from GLMM1a and 1b (groups with a significant dominance steepness). In both datasets, the difference in normalised David's scores was normally distributed (with PL11: $W = 0.94$, $p = 0.01$; with PL14: $W = 0.93$, $p = 0.0008$).

In the dataset with PL11, female-female dyads had significantly smaller differences in dominance than male-female ($p = 0.0008$) and male-male dyads (0.04). There was no significant difference between male-female and male-male dyads ($p = 0.8$) (Figure 11).

The test on the dataset with PL14 yielded the same results, female-female dyads had significantly smaller differences in dominance than male-female ($p = 0.0004$) and male-male dyads (0.002). There was no significant difference between male-female and male-male dyads ($p = 0.9$) (Figures 12 and 13).

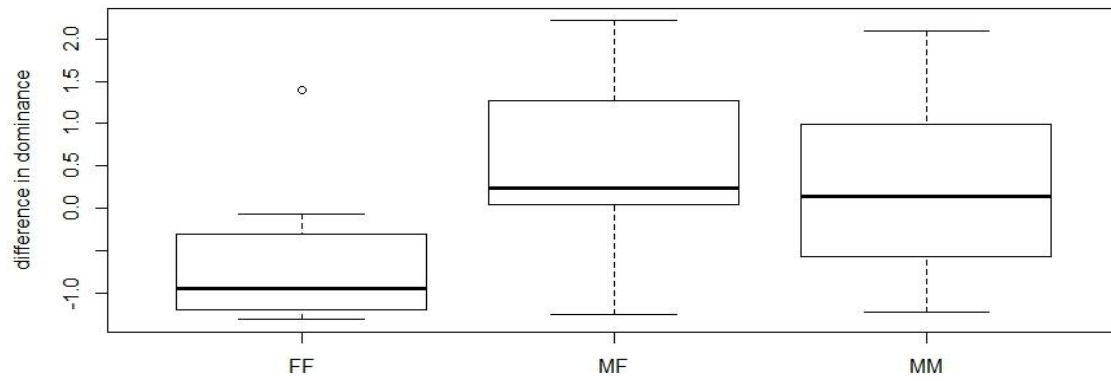


Figure 11. The difference in dominance for the three gender combinations, for the dataset with PL11

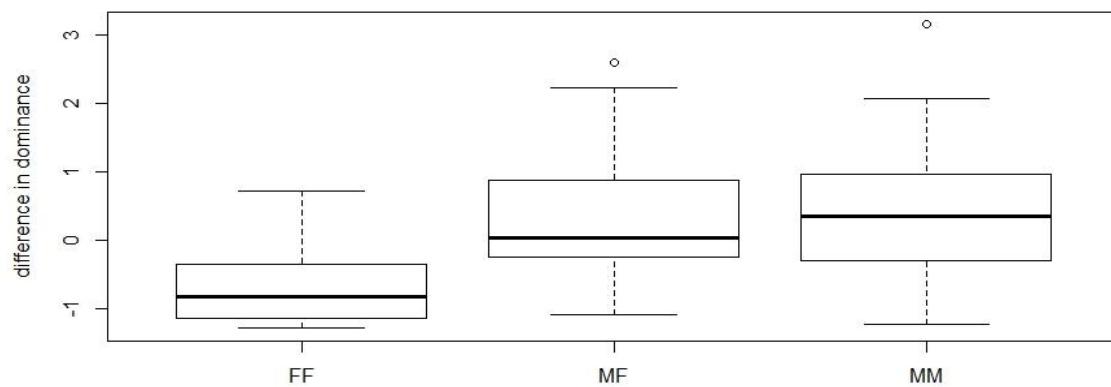


Figure 12. The difference in dominance for the three gender combinations, for the dataset with PL14

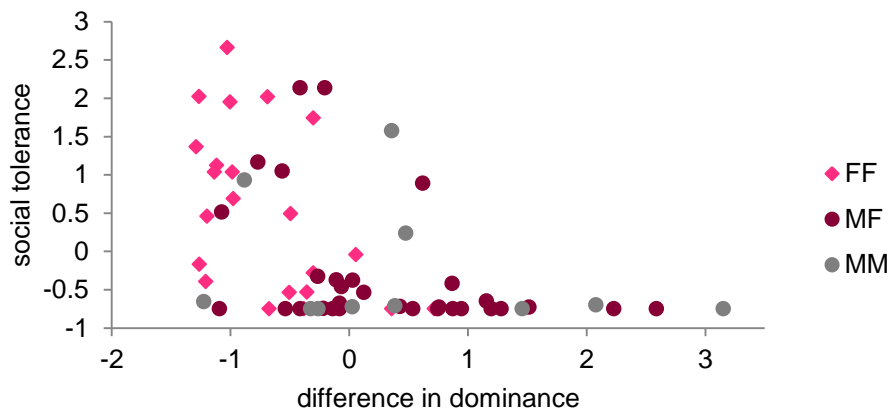


Figure 13. The relationship between social tolerance and difference in dominance, for the dataset containing PL14. Dyads from different gender combinations are represented by a different symbol.

In the dataset with PL11 (dataset from GLMM2a), the normality hypothesis could not be rejected for relationship value ($W = 0.98$, $p = 0.3$). The same was true for the data with PL14 (dataset from GLMM2b); relationship value wasn't significantly normally distributed ($W = 0.98$, $p = 0.2$). Consequently, a Wilcoxon signed-rank test was used.

For the dataset containing PL11, relationship value was significantly higher for female-female dyads compared to male-female ($W = 681$, $p = 0.03$) and male-male dyads ($W = 260$, $p = 0.002$). No significant difference was present between male-female and male-male dyads ($W = 144$, $p = 0.06$) (Figure 14). For the dataset with PL14, relationship value was significantly higher for female-female dyads compared to male-female ($W = 487$, $p = 0.005$) and male-male dyads ($W = 85$, $p = 0.0002$). Male-female dyads also scored significantly higher than male-male dyads ($W = 489$, $p = 0.04$) (Figures 15 and 16).

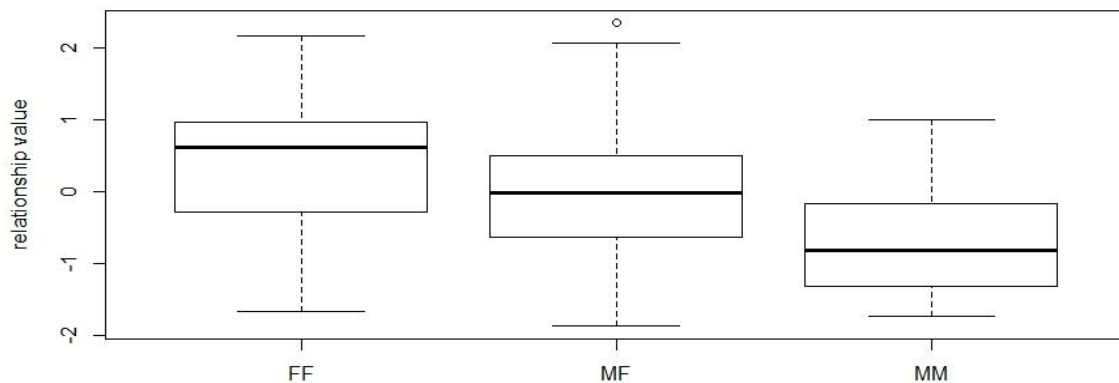


Figure 14. Difference in relationship value between different gender combinations, for the dataset with PL11

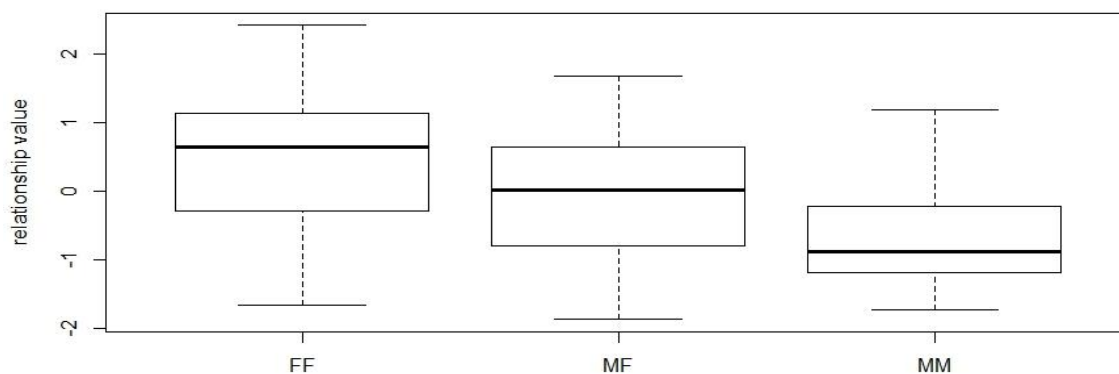


Figure 15. Difference in relationship value between different gender combinations, for the dataset with PL14

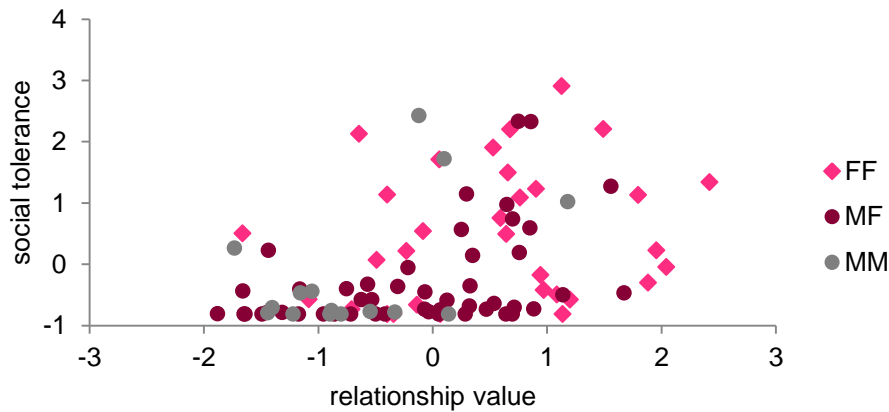


Figure 16. The relationship between social tolerance and relationship value, for the dataset containing PL14. Dyads from different gender combinations are represented by a different symbol.

4. Discussion

4.1 Dominance steepness

Using ‘fleeing upon aggression’ as a behavioural marker for dominance, normalised David’s scores and dominance steepness per group were calculated. A statistically significant dominance steepness could be determined for five of the eight groups, and was between 0.18 and 0.55 (Table 2). This was very low compared to the study by Stevens et al. (2007), who calculated dominance steepness for six bonobo groups using the same methods. Their results were all higher than 0.63, which is higher than the lowest value from this study. This is possibly due to a difference in sampling effort; compared to this study, Stevens et al. (2007) used observational data collected over a much greater total observation time. On average each group from Stevens et al. (2007) was observed for 1453 hours more. Although it is possible that groups in this study simply had a more shallow dominance hierarchy, it seems rather unlikely.

The results for TWA, TWB and WU were not significant, perhaps because these were the groups with the smallest total observation time. Another factor is group size; small group sizes have a negative effect on the calculation of the steepness measure, and these groups contained respectively four, five and six individuals (Balasubramaniam et al., 2012).

4.2 Relationship quality

Components of relationship quality were determined based on a PCA of eight behavioural variables; grooming frequency, grooming symmetry, proximity, aggression frequency, aggression symmetry, support, contra-support and peering frequency. Kaiser's criterion and the parallel analysis yielded a different number of components, showing the importance of using parallel analysis as a more reliable method to determine the number of components to extract. The two components were similar to two of the three relationship components defined by Cords & Aureli (2000): relationship value and relationship compatibility (Table 3). Stevens et al. (2015) obtained the same results in an analysis of six groups, except for the high loading of support on relationship value in their analysis that wasn't found in this study. Perhaps this was again due to a higher sampling effort by Stevens et al., 2015 and thus a higher number of observed occasions of support.

Fraser et al. (2008) found all three components (value, compatibility, security), but their method wasn't identical to the one used in this study and by Stevens et al. (2015). The variables 'consistency of affiliation', 'successful begging' and 'tolerance to approaches' were used by Fraser et al. (2008) but for practical reasons not by Stevens et al. (2015) and in this study, while the latter two used the variables 'peering' and 'aggression symmetry'. Additionally, Fraser et al. (2008) used Kaiser's criterion to determine the number of components. In Stevens et al. (2015) and in this study, using only Kaiser's criterion would also have resulted in three instead of two components. Stevens et al. (2015) found that this third component showed similarities to the component 'security' in Fraser et al. (2008), but this study didn't.

4.3 Group tolerance

4.3.1 Peanut plot experiment

The peanut plot experiment was carried out in order to test for repeatability of the experiment by Cronin et al. (2015) on the same group and to make a second comparison with the chimpanzee groups from Cronin et al. (2014).

The group tolerance, measured as the proportion of the group simultaneously present in the peanut plot, was consistent over the five days of the experiment. On average, this was 28% of the group. Results were similar to what was found by Cronin et al. (2015) for the same bonobo group in 2012 (Figure 2). Group tolerance was slightly higher in this study, especially

the first 50 seconds of the experiment and compared to grass 1 (but significance could not be determined).

Compared to the chimpanzee experiments, the tolerance in PL14 was lower (Figure 1, Appendix 4). This agreed with the findings of other studies in a group setting that found lower tolerance in bonobos than in chimpanzees (de Waal, 1992; Jaeggi et al., 2010). However, the difference in group tolerance between PL14 and chimpanzee groups 3 and 4 was smaller than the difference in group tolerance that was found for the bonobo group in this study and by Cronin et al. (2015). This suggests that inter-species differences aren't very large, but since no significance tests could be done yet, the results cannot be interpreted statistically.

To outline the circumstances of the experiment and to compare the rate of sociosexual behaviour in future experiments, I scored intolerant, sociosexual and affiliative behaviour starting from the moment the experimenter walked past the bonobos, shaking the bucket with peanuts, until ten minutes after the experiment. Intolerant behaviour before the experiments was limited to two aggressive intentions (by Louisoko) and one parallel display (by Louisoko and Djanoa). Eight incidents of intolerant behaviour were observed during the experiment (two forced claims, five aggressive intentions and one long charge), all by the same individual (Louisoko). Sociosexual behaviour before the experiment was rarer than expected: one non-copulative mount and two sex presents took place (all between Louisoko and Djanoa). Other types of affiliative behaviour occurred more often; six affiliative touches, six lateral embraces, one mounted walk and one buddy walk were observed (seven from Djanoa to Lina, four from Djanoa to Louisoko or Lucuma, three between Lina, Lingoye and Louisoko). Thus, all aggression went out from the individual with the highest agonistic dominance rank, and most affiliative behaviour from the second highest ranked female. To what degree tolerance was influenced by sociosexual and other affiliative behaviour in advance (or other tolerance stimulating behaviour in chimpanzees) could not be determined in this study, since this was the only tolerance study that quantified this behaviour so far.

It might also be necessary that the apes get the chance to perform this type of behaviour in proximity of the resource zone, as was possible for the chimpanzees from Cronin et al. (2014) but not for the bonobos in this study or from Cronin et al. (2015).

4.3.2 Puzzle feeder experiments

The aim of calculating group measures for social tolerance during the puzzle feeder experiments was to compare different bonobo groups. This way, I tried to find underlying variables that could influence social tolerance on the group level.

Although significant differences were present between 10 of the 23 group pairs (Appendix 5), none of the factors was found to be related to group level social tolerance (Appendix 6).

There was no significant correlation between group tolerance and average age, the proportion of kin dyads in the group, group size, the proportion of females in the group, mean relationship value and mean relationship compatibility. Mean relationship value and compatibility could not be calculated for STB, so only six groups were tested for these factors. Correlation with dominance steepness could only be tested for three groups, and was not significant. A remarkable result was that correlation between group tolerance and the proportion of females in the group was negative ($\tau = -0.64$) although non-significant ($p = 0.08$). From the dyad analysis (see further) appears that female dyads are more tolerant, so a lower tolerance in groups with more females would be contradictory. The lack of significant results is perhaps due to the small sample sizes of seven, six and three groups. Another remarkable result was the absence of a correlation between the group measures for social tolerance and the median of the dyadic measures for each group. This would mean that the group tolerance doesn't depend on the tolerance of all group members equally. Perhaps social tolerance in group is mainly determined by a limited number of key individuals with a high resource holding potential, as was proposed by (Cronin et al., 2014, 2015). This could be tested in the future by performing tolerance tests in different groups, accompanied by resource monopolisation tests.

4.4 Dyadic tolerance

Dyadic measures for social tolerance were calculated based on the peanut plot experiment for PL14 and based on the puzzle feeder experiments for the other groups. The aim was to test which factors could possibly affect social tolerance between two individuals. I tested for a relationship with difference in dominance status, maternal kinship, gender combination, the dyad's mean age, the difference in age, relationship value, relationship compatibility, mean tenure and rearing-history.

In order to get a better understanding of the results from the GLMM's, I tested whether relationship value and difference in dominance status were different for the three gender combinations.

4.4.1 Results from the GLMM's

No significant effects were found from tenure, age difference and relationship compatibility. The absence of a relation between social tolerance and relationship compatibility was surprising, since higher compatibility within a dyad would mean less aggressive interactions (Table 3) and social tolerance is often directly measured from aggressive interactions (for example Ganem & Bennett, 2004, see section 1.3). Following the Relational Model, there are

three outcomes to competition; aggression, avoidance and tolerance (de Waal, 1996). If tolerance is a mechanism to avoid aggression, a negative relationship would be expected. This result, however shows that dyads with a high tolerance not necessarily show less aggression. Perhaps in some dyads both individuals prefer aggression to avoidance. This might be true for individuals that are similar in dominance rank, when no one wants to 'give in' under competitive circumstances.

The absence of significant effects of tenure and age difference shows that individuals are not preferentially more tolerant towards conspecifics they knew for a longer time.

GLMM1a and GLMM1b were the only models in which difference in dominance was tested, and it had a significantly negative effect (Table 5, Appendix 7). A larger difference in dominance leads to lower social tolerance (Figures 3 and 4). The same effect was observed by de Waal (1986) for rhesus monkeys within the same tolerance class. An effect of dominance difference on tolerance was expected; dominant individuals have the most access to resources, and therefore the ability to prohibit or allow others to take their part. Thus, the 'choice' to be tolerant or not lays mainly with the dominant individuals. On the species level, this idea becomes clear in the 'tolerant dominance style', defined by de Waal (1996). He describes dominance styles as a continuum, from 'despotic' over 'tolerant' to 'egalitarian', that matches a continuum of dominance hierarchy steepness from more to less steep (de Vries et al., 2005). Jaeggi et al. (2010) reported the interaction between tolerance and dominance on the species level by showing both lower tolerance and steeper dominance in a bonobo group, compared to a chimpanzee group. The findings of my study show that in bonobos, dominance influences tolerance on the individual level as it does on the species level.

In GLMM1a, hand-reared individuals had a significantly higher social tolerance than mother-reared bonobos. This effect was not significant in the other analyses when the dataset became larger, or in the analyses with PL14. The effect was also inconsistent; when the dataset became larger, the difference in intercept decreased and eventually even became negative. Moreover, the results from GLMM2a, 2b and 3a show that dyads with one hand-reared partner expressed higher social tolerance, while dyads where both partners were hand-reared were less tolerant. These inconsistencies don't necessarily mean that there is no effect of rearing history on social tolerance. Hand-reared individuals were perhaps too poorly represented in this study to test for these effects (9 of the 128 individuals).

Although relationship value and compatibility didn't have a significant effect in GLMM1a and 1b, relationship value was significant in the larger datasets that GLMM2a and 2b were run

on. Dyads with a higher relationship value showed higher social tolerance towards each other (Figures 5 and 6). This effect might be expected if social tolerance is indeed a means to protect valuable relationships, as is proposed by the Relational Model (de Waal, 1996).

A positive correlation between relationship value and social tolerance is in agreement with Jaeggi et al. (2010), who found a positive but non-significant relation between 'affiliative relationship' and social tolerance. They also reported a significantly positive relation between relationship value and social tolerance in chimpanzees. The result is in contradiction with Tan & Hare (2013), who observed that bonobos preferred a stranger over a group mate to share with.

In both GLMM3a and b, an increase in mean age had a significantly negative effect on social tolerance (Figures 7 and 8). The effect was not significant in GLMM1a, 1b, 2a and 2b, but became significant after increasing the sample size. The effect of age on social tolerance has been demonstrated in chimpanzees (Wobber et al., 2010b) and suggested but not yet shown to be present for bonobos (Bullinger et al., 2012, Tan & Hare, 2013). Wobber et al., 2010 tested for and didn't find an age effect in bonobos, but individuals in their study were younger (4-23 years) than in this one (7-61 years).

Only in GLMM3b, a significantly positive effect of maternal kinship on social tolerance was found. This effect was shown to be present in chimpanzees (Jaeggi et al., 2010), but not yet in bonobos. Since only one GLMM suggests significantly higher tolerance among kin, these results should be interpreted with caution.

In five of the six GLMM's, gender combination had a significant influence. A post hoc Wilcoxon signed rank test on the largest two datasets showed that female-female dyads had a significantly higher tolerance than male-female and male-male dyads. No significant difference was found between male-female and male-male dyads. This agrees with observations of food sharing in the wild, where sharing occurred most often between female dyads or between females and their offspring and females are more tolerant towards groups of unknown conspecifics (Idani, 1990; Hohmann & Fruth, 1996). As mentioned before, this result is remarkable in combination with the group analysis that showed non-significant negative correlation between group tolerance and the proportion of females in the group. The effect of gender combination will be further looked at by testing for its effects on difference in dominance status and on relationship value.

Since all variables were standardised (Z-scores), it was possible to compare the different slopes. The results show that the effect of difference in dominance is the strongest ($\beta = -0.35$

and -0.41), compared to the effect of relationship value ($\beta = 0.27$ and 0.24) and mean age ($\beta = -0.27$ and -0.21). The effects of relationship value and mean age appear to be more equal in size. However, the effects are not entirely stable for the different datasets, as can be seen in the variation of the effect of gender combination between different GLMM's (Table 5, Appendix 7). Thus it might have been better to compare effect sizes from the outcome of the same analysis. Unfortunately, this was impossible for both relationship value and mean age only showed significant effects when tested on the largest possible datasets.

4.4.2 The influence of gender combination on difference in dominance status and relationship value

For both datasets, with PL11 and with PL14, female-female dyads had a significantly smaller difference in dominance than the other dyads. Between male-female and male-male dyads there was no significant difference (Figures 11 and 12). The relation between difference in dominance status, social tolerance and gender combination for the dataset with PL14 is illustrated in Figure 13 (Figure 4 redrawn with different symbols representing the gender combinations). A smaller difference in dominance status for females could be explained by what Vervaecke et al. (2000) call 'nonexclusive female dominance' in a study on captive groups: female dominance is prominent, but not all females are dominant over all males. The highest position is occupied by a female, while most males occupy low or middle ranks. Some males however, can occupy high ranks, often with support from their mother (Stevens et al., 2007; in the wild: Surbeck et al., 2011). This was true for my study groups: the lowest rank was always occupied by a male, and in all but one group (PL14), the highest ranking individual was a female. The one male that was highest ranking was the son of the alpha female. When most of the males in a group are low ranking, one or two are high ranking and females are middle or high ranking, this explains why differences between male-male and male-female dyads were larger on average than between female-female dyads.

High tolerance in this study means that that the dyad sits together for a large proportion of the total time each individual spent close to the puzzle feeder or in the peanut plot. Tolerance was often low because one of the two rarely visited the feeder or didn't spent time in the peanut plot. Those informal observations suggest that tolerance was mainly high in individuals that spent a large amount of time at the feeder or in the peanut plot. In combination with low dominance differences between females, the high social tolerance in female-female dyads could reflect high resource holding potential in dominant females, as was observed by Parish (1994).

Female-female dyads showed significantly higher tolerance levels than male-female and male-male dyads. If tolerance is preferred to the other two options of the Relational Model, aggression and avoidance, in order to maintain relationships, this suggests that relationships among females are particularly important, more so than relationships between males or between males and females. In case this is true, female relationship quality should be higher. Since only relationship value correlated significantly with social tolerance in this study, I will only discuss this component of relationship quality.

Stevens et al. (2015) tested for effects of gender combination on relationship quality. They found that female-female dyads had a significantly higher relationship value than male-female and male-male dyads, and male-female dyads scored significantly higher than male-male dyads. I tested the influence of gender combination on relationship value again for the groups in this study, and found similar results. For the dataset containing PL14, the results were identical to those from Stevens et al. (2015) (Figures 15 and 16). The dataset with PL11 showed a significantly higher relationship value for female-female dyads as compared to male-female and male-male dyads, but no significant difference between male-female and male-male dyads (Figure 14). These results suggest that social tolerance is the highest between female bonobos, because their relationships are more valuable.

Bonobo females are known to form close bonds in the wild, allowing them to obtain and maintain a high dominance status notwithstanding the male philopatry of the species (Furuichi, 2011). However, a study on six captive bonobo groups didn't find indications that bonds between females were stronger than between mother-son dyads or males and unrelated females (Stevens et al., 2006). There are earlier studies that reported the importance of female bonding in captivity (for example Vervaecke et al., 2000b), but these groups were relatively recently formed and bonds between females become less important when they have offspring (Furuichi, 1989). The high relationship value for female-female dyads found in this study and by Stevens et al. (2015) seems to contradict Stevens et al. (2006) again, and to support the idea that female bonding is important in captivity as well as in the wild. Male-male bonds have been observed to be weak both in captivity and in the wild (Kano, 1992; Stevens et al., 2006), which was supported in this study.

Another possible interpretation of the lower tolerance in male-female and male-male dyads could be that their relationships are not necessarily less important to conserve, but that the more frequent incidents of aggression in these dyads are resolved with reconciliatory behaviour (De Waal, 1989). This hypothesis, however, is contradicted by Palagi et al. (2004), who found lower rates of reconciliatory behaviour in male-female and male-male dyads, and higher rates in female-female dyads.

5. Conclusion

This thesis showed repeatability in the low tolerance levels of a bonobo group, as compared to four chimpanzee groups. However, the difference between the group level social tolerance found in this study and in the study by Cronin et al. (2015) appeared to be large compared to the difference in tolerance with the least tolerant chimpanzee groups, suggesting substantial within-species variability.

None of the studied factors was found to underlie variation in group tolerance in bonobos.

Dyadic social tolerance didn't show a significant relation with relationship compatibility, a component of relationship quality that is mainly determined by a dyad's agonistic relationship. Since tolerance is often measured based on aggressive behaviour, this finding was surprising. This is the first study to show a direct relation between dyadic social tolerance and age, difference in dominance status, relationship value and gender combination in captive bonobos. It supports the hypotheses that age has a negative influence on social tolerance, similar to what was found in chimpanzees, and that larger differences in dominance status lead to lower levels of social tolerance, as was observed in rhesus monkeys. A positive relation between social tolerance and relationship value supports the idea of social tolerance as a means to protect valuable relationships from the negative effects of aggression. Female-female dyads were found to be more tolerant than male-female and male-male dyads, which agrees with observations of wild bonobos.

The effects of gender combination, dominance difference and relationship value were not independent; female-female dyads have both higher relationship values and lower differences in dominance compared to male-female and male-male dyads. The high tolerance between females with a similar dominance status reflects perhaps the high resource holding potential of these individuals. Based on the behaviour of wild bonobos, female bonding was previously much emphasised in captive studies. This was brought into question when in older captive populations, relationships between females and their offspring seemed to gain in importance compared to the relationships between females. However, both Stevens et al. (2015) and this study found that relationship value was higher for female-female dyads. In addition to higher levels of social tolerance between females, these results again support the idea that female-female relationships are important in bonobos in captivity as well as in the wild.

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8. Appendix

Appendix 1. Glossary of terminology

agonistic dominance	dominance expressed by the outcome of agonistic encounters; the dominant individual is the one receiving submission or causing the opponent to retreat
cooperation	behaviour that increases the reproductive success or survival of individuals other than the actor
David's scores	cardinal rank measures for dominance position, calculated on the basis of a dyadic dominance index corrected for chance
dominance steepness	the absolute slope of the straight line fitted to the normalized David's scores (calculated on the basis of a dyadic dominance index corrected for chance) plotted against the subjects' ranks, gives an idea of how large dominance differences are within a group
fairness	in social psychology: people's subjective understanding of the equity of the situation. In nonhuman animals, this is measured as the aversion shown to inequity
group cohesion	the closeness of group members
maternal kin	in this study: mother-child dyads and siblings
prosociality	any activity that provides a benefit to others
rearing-history	whether or not an individual was reared by his mother
relationship	a series of interactions in time between two individuals known to each other, in which the nature and course of each interaction is influenced by the history of past interactions between the individuals concerned, and perhaps by their expectation for interactions in the future.
relationship compatibility	as an investment which in some way, sooner or later, benefits the interactor the general tenor of social interactions in a dyad, which is influenced negatively by aggressive interactions
relationship quality	the characteristics of a social relationship, can be described by the components value, compatibility and security
relationship security	the predictability and consistency of the relationship over time
relationship value	the benefits an individual receives from the social partner
social learning	(or: socially mediated learning) learning influenced by observation of, or

	interaction with, another animal
social tolerance	the propensity to be in proximity to conspecifics around valuable resources with little or no aggression
	sometimes broadly defined as withholding aggression
sociality	the degree to an individual tends to associate with conspecifics
sociosexual behaviour	genital contact between individuals of any gender or age, genital stimulation with hands or mouth
tenure	the total time an individual has been part of its current group

Definitions from Cronin & Sánchez (2012), Smith (2014), Burkart & van Schaik (2013), Cords & Aureli (2000), De Vries et al. (2006), Vervaecke et al. (2000), Hinde (1976), Kummer (1978), Brosnan (2006), Gardner et al. (2009), Wilson (1975)

Appendix 2. Ethogram, showing only behaviours occurring in this study and mentioned in the report

aggressive intention	sudden tense hand or body movements in the direction of another individual in a non-playful context, or hitting, kicking etc. without locomotion
cofeed	the subject joins the receiver to feed on the same food item or branch or bundle of branches. Both individuals may hold the food/branch/bundle of branches (also used for individuals feeding from the same plate, or in close proximity)
flee	the subject moves away from the receiver, after the receiver behaved aggressively towards the subject
forced claim	the subject takes food, an object or an infant away from the receiver in a forced, aggressive manner, with protest or resistance from the receiver
groom	the subject manipulates the receiver's body surface and hair with lips, fingers, ...
long charge	the subject shows tensed running at the receiver over more than a few meters (more than five steps)
non-copulative mount	mount without intromission of the penis in the vagina, or without thrusting of the pelvis, or any genital contact between individuals of the same sex, or sexual contact involving immature individuals
relaxed claim	the subject takes food, an object or an infant away from the receiver in a relaxed manner, without protest from the receiver
short charge	the subject shows tensed running at the receiver over a few meters (up to five steps)
steal	the subject takes away food, an object or an infant from the receiver and then runs away while carrying the food/object/infant
affiliative touch	the subject touches the body of the receiver with hand or fingers in a non-

	aggressive manner
mount walk	the subject rests its head, arms and chest on the back of the receiver from behind, while they both move forward
buddy walk	the subject walks next to the receiver and has put an arm on the shoulder of the receiver (there is interaction between subject and receiver)
lateral embrace	the subject gently places one arm around the receiver's shoulder, back or waist, or puts both arms around the receiver while pulling him closer
support	the subject intervenes in an agonistic behaviour (excluding pestering) between the receiver and a third party; within 30 sec upon the start of an agonistic interaction to aid in defence
sex present	the subject clearly shows its genital to the receiver, with the intention to copulate or perform a non-copulative mount

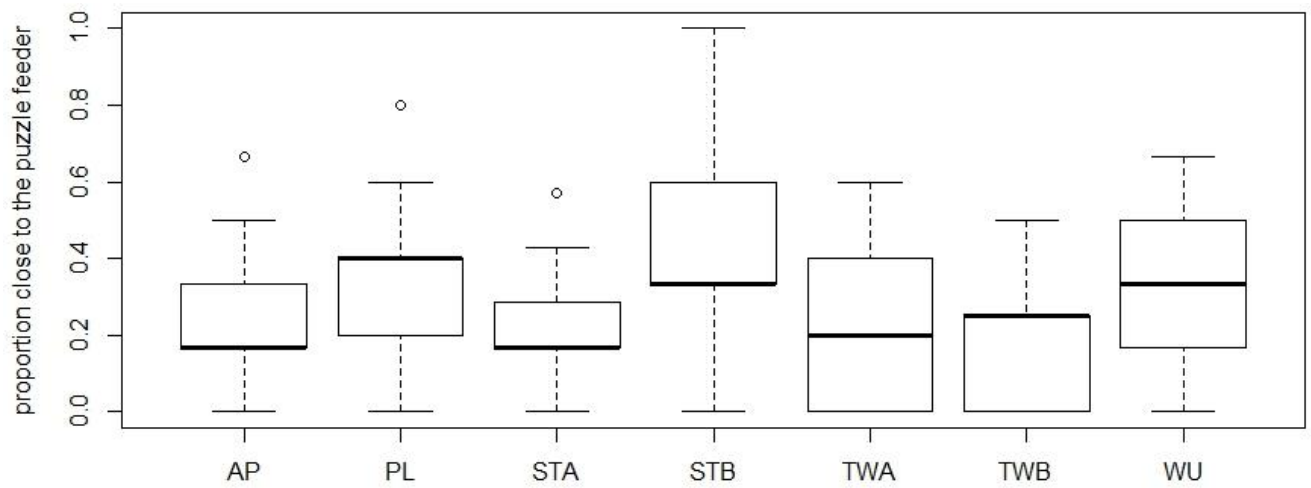
Appendix 3. The total duration of focal and all occurrences sampling in all groups other than PL14; observations by Nicky Staes & students

Group	Total duration focal sampling (hours)	Total duration all occurrences (hours)
AP	128.63	23.08
FR	116.85	5.51
PL11	108.68	79.72
STA	135.07	27.85
STB	-	-
TWA	67.58	12.5
TWB	54.99	13.5
WU	91.89	8.03

Appendix 4. A comparison of the proportion present in the peanut zone between this study and previous studies on the same bonobo group and on four chimpanzee groups

Group	Mean \pm SEM
Chimpanzee group 1 ¹	0.30 \pm 0.04
Chimpanzee group 2 ¹	0.62 \pm 0.03
Chimpanzee group 3 ¹	0.30 \pm 0.04
Chimpanzee group 4 ¹	0.67 \pm 0.04
Bonobos Planckendael 1 ²	0.22 \pm 0.03

Appendix 5. Group tolerance levels during the puzzle feeder experiments



Appendix 6. The results of the Kendall's rank correlation tests for correlation between group-level social tolerance and different variables

Variable	p-value	tau
Average age	0.2	-0.45
Proportion of kin dyads	0.4	0.25
Group size	0.1	-0.56
Mean relationship value	1	0
Mean relationship compatibility	1	0
Dominance steepness (only AP, PL11, STA)	0.2	0.82
Proportion of females	-0.64	0.08
Median of the dyadic measures per group	0.2	0.39

Appendix 7. The results of all GLMM's. For continuous variables the correlation coefficient is given, for categorical variables the difference in intercept.

GLMM1a

	p-value	β correlation coefficient or difference in intercept	F-value	DF numerator	DF denominator
relationship value	0.08	0.22	2.57	1	29.08
relationship compatibility	0.9	0.04	0.11	1	28.80
hand-reared	0.03	1: 0.68	7.95	1	38.08
difference in dominance status	0.0009	-0.35	11.77	1	31.88
maternal kinship	0.07	yes: 0.49	4.02	1	37.81
gender combination	0.001	MF: -0.58 MM: -1.05	9.22	2	37.53
tenure	0.6	-0.03	0.09	1	29.72
mean age	0.1	-0.19	1.12	1	25.06
age difference	0.5	-0.04	0.13	1	29.35

GLMM 1b

	p-value	β correlation coefficient or difference in intercept	F- value	DF numerator	DF denominator
relationship value	0.2	0.15	1.22	1	52.06
relationship compatibility	0.6	-0.02	0.05	1	49.52
hand-reared	0.4	1: 0.30	0.63	1	24.75
difference in dominance status	<0.0001	-0.41	15.39	1	49.88
maternal kinship	0.2	yes: 0.36	0.99	1	48.91
gender combination	0.2	MF: -0.37 MM: -0.57	1.00	2	43.63
tenure	0.5	0.06	0.24	1	50.81
mean age	0.4	-0.10	0.45	1	40.86
age difference	0.3	0.02	0.02	1	50.47

GLMM 2a

	p- value	β correlation coefficient or difference in intercept	F- value	DF numerator	DF denominator
	p- value	correlation coefficient	F- value	DF	DF denominator
relationship value	0.01	0.27	6.81	1	71.33
relationship compatibility	0.9	-0.09	0.64	1	60.71
hand-reared	0.1	1: 0.29 2: - 0.45	1.25	2	48.36
difference in dominance status	-	-	-	-	-
maternal kinship	0.2	yes: 0.29	1.35	1	60.96
gender combination	0.02	MF: -0.54 MM: -0.48	4.01	2	60.63
tenure	0.4	-0.08	0.26	1	58.83
mean age	0.7	-0.06	0.18	1	45.20
age difference	0.9	0.003	0.001	1	55.13

GLMM 2b

	p-value	β correlation coefficient or difference in intercept	F-value	DF numerator	DF denominator
relationship value	0.02	0.24	6.32	1	86.54
relationship compatibility	0.4	0.07	0.73	1	83.06
hand-reared	0.5	1: 0.10 2: -0.66	0.38	2	56.52
difference in dominance status	-	-	-	-	-
maternal kinship	0.1	yes: 0.28	2.35	1	79.86
gender combination	0.02	MF: -0.38 MM: -0.35	4.05	2	76.03
tenure	0.5	-0.007	0.61	1	86.61
mean age	0.5	-0.03	0.56	1	57.48
age difference	0.3	0.008	0.90	1	77.70

GLMM 3a

	p-value	β correlation coefficient or difference in intercept	F-value	DF numerator	DF denominator
relationship value	-	-	-	-	-
relationship compatibility	-	-	-	-	-
hand-reared	0.7	1: 0.02 2: -0.32	0.14	2	74.49
difference in dominance status	-				
maternal kinship	0.09	yes: 0.43	2.04	1	84.73
gender combination	0.0001	MF: -0.84 MM: -1.18	10.77	2	85.40
tenure	0.3	0.07	0.28	1	55.34
mean age	0.007	-0.27	7.25	1	62.17
age difference	0.5	-0.12	1.08	1	71.18

GLMM 3b

	p-value	β correlation coefficient or	F-value	DF numerator	DF denominator
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difference in intercept					
relationship value	-	-	-	-	-
relationship compatibility	-	-	-	-	-
hand-reared	0.7	1: -0.08 2: -0.40	0.18	2	97.71
difference in dominance status	-				
maternal kinship	0.03	yes: 0.56	4.99	1	111.13
gender combination	0.0007	MF: -0.72 MM: -0.89	7.75	2	103.87
tenure	0.9	0.02	0.02	1	86.63
mean age	0.04	-0.21	4.15	1	64.10
age difference	0.2	-0.14	1.64	1	102.66

Appendix 8.

Information on all individuals in the study groups, including infants. Normalised David's scores with (NS) are from groups with a non-significant dominance steepness. For the Planckendael groups, the year is mentioned. The name of the mother is only mentioned for individuals whose siblings or mother were present in the group. If the name was unknown, the studbook number is given.

Name	Sex	Birth year	Zoo	In the group since	Mother	Wild / Hand raised	Group during puzzle feeder experiments			Normalised David's score	Rank in the group
							Mesh	R&F	Tubes		
Margrit	F	1951	Frankfurt	1959		Wild	1	1	1	4.33	3
Mato	M	1963	Wuppertal	1988						2.62 (NS)	4
Natalie	F	1964	Frankfurt	1970		Wild	2	2	1	4.26	4
Kombote	F	1966	Stuttgart A	1973		Wild	1	1	1	2.57	4
Diatou	F	1977	Twycross B	1992		Hand	1	1	1	1.50 (NS)	3
Hermien	F	1978	Stuttgart A	2010		Wild	1	1	1	3.28	1

Hortense	F	1978	Apenheul	2008		Wild				2.34	4
Kakowet II	M	1980	Twycross B	1992		Hand	1	1	1	1.72 (NS)	1
Lisala I	F	1980	Wuppertal	1984	55	Hand				2.78 (NS)	3
Lusambo	M	1980	Wuppertal	1984		Hand				2.94 (NS)	1
Mobikisi	M	1980	Stuttgart A	2010		Wild	1	1	1	1.68	6
Zorba	M	1980	Stuttgart A	1994		Wild	1	1	1	1.76	5
Ludwig	M	1984	Frankfurt	1999		Hand	1	1	2	3.62	8
Jill	F	1985	Apenheul	1997						3.09	1
Lina	F	1985	Planckendael	2009						2.81 (2011)	1 (2011)
										4.51 (2014)	2 (2014)

Kamiti	F	1987	Frankfurt	2002	Kombote	2	2	1	4.42	2
Birogu	M	1989	Wuppertal	1989	55				2.30 (NS)	5
Kichele	F	1989	Twycross A	1992	Diatou	2	2	2	2.39 (NS)	1
Banya	F	1990	Twycross A	1998		2	2	2	2.26 (NS)	2
Eja	F	1990	Wuppertal	1996					2.79 (NS)	2
Zuani	F	1990	Apenheul	1998	Wild				2.94	3
Bondo	M	1991	Frankfurt	2011		1	2	2	2.63	9
Chipita	F	1993	Stuttgart B	1997	Wild	2	2	2		
Keke	M	1994	Twycross A	1994	Diatou	2	2	2	1.54 (NS)	5

Vifijo	M	1994	Planckendael	2009					0.76 (2011)	5 (2011)
									1.66 (2014)	8 (2014)
Djanao	F	1995	Planckendael	2002					2.34 (2011)	3 (2011)
									4.25 (2014)	3 (2014)
Ximba	F	1995	Stuttgart A	2008	Wild	1	1	1&2	2.67	3
Cheka	F	1996	Twycross A	2004		2	2	2	2.23 (NS)	3
Bolombo	M	1997	Apenheul	2011	Hand				1.43	6
Liboso	F	1997	Stuttgart B	2010		2	2	2		
Kutu	F	1998	Frankfurt	2005	Kombote	2	2	1	4.20	5
Louisoko	M	1998	Planckendael	2009	Lina				2.74 (2011)	2 (2011)
									4.92 (2014)	1 (2014)
Maringa II	F	1998	Twycross B	2006		1	1	1	1.70 (NS)	2

Zamba	M	1998	Apenheul	2008	Hortense				2.17	5
Zomi	F	1998	Frankfurt	2005		2	2	1	4.45	1
Kumbuka	F	1999	Apenheul	1999					3.04	2
Haiba	F	2001	Stuttgart B	2010		2	2	2		
Heri	M	2001	Frankfurt	2001	Natalie	1	1	2	3.94	7
Mixi	F	2001	Frankfurt	2011		2	2	1	4.15	6
Banbo	F	2002	Stuttgart A	2005	Hand	1	1	1	3.04	2
Lucuma	M	2002	Planckendael	2009	Lina				1.35 (2011)	4 (2011)
									3.69 (2014)	4 (2014)
Luo	M	2002	Twycross B	2002	Diatou	1	1	1	1.07 (NS)	4

Busira	F	2004	Wuppertal Planckendael	2004 2012	Eja				1.59 (2011, NS)	6 (2011)
									3.02 (2014)	6 (2014)
Kasai	M	2004	Stuttgart B	2004	Chipita	2	2	2		
Gemena	F	2005	Twycross A	2005	Cheka	2	2	2	1.59 (NS)	4
Kianga	F	2005	Stuttgart A	2005	Kombote	1	1	1		
Habari	M	2006	Planckendael	2006	Djanoa				2.44	7
Hongo	M	2006	Apenheul	2006	Hortense					
Huenda	F	2006	Stuttgart A	2010	Hermien	1	1	1		

Luebo	M	2006	Wuppertal	2006	Lisala I			
Nayembi	F	2006	Stuttgart B	2010	Liboso	2	2	2
Lingoye	F	2007	Planckendael	2009	Lina			3.50 5
Nyota II	M	2007	Frankfurt	2007	Natalie	2	2	1
Bili II	M	2008	Frankfurt	2008	Hand	2	2	1
Omanga	F	2008	Frankfurt	2008	Kamiti	2	2	1
Makasi II	M	2009	Apenheul	2009	Zuani			
Pangi	F	2009	Frankfurt	2009	Kutu	2	2	1
Panisco	M	2009	Frankfurt	2009	Zomi	2	2	1

Yahimba	F	2009	Apenheul	2009	Kumba			
Malaika II	F	2010	Twycross	2010	Diatou	1	1	1
Monyama	F	2010	Apenheul	2010	Jill			
Winton II	M	2010	Twycross	2010	Cheka	2	2	2
Ayubu	M	2011	Wuppertal	2011	Eja			
Azibo	M	2011	Wuppertal	2011	Eja			
Lopori	F	2012	Twycross	2012	Maringa II	Hand	3	3
Nayoki	F	2012	Planckendael	2012	Djanoa			