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# How do chimpanzees choose their partner for a coordinated cooperation problem?

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# Abstract

One widely spread definition of cooperation is when two or more individuals work together to achieve a common goal. This behaviour can be observed throughout the animal kingdom and is especially complex in human beings. To understand the evolution of cooperation, it is useful to study one of our closest relatives: chimpanzees. Chimpanzees are known to cooperate in groups when hunting monkeys or patrolling their territories. They also cooperate in small coalitions for the obtention of social benefits. In this thesis, we want to understand how chimpanzees choose their partner for a coordinated cooperation problem. We want to know if they choose their partner based on social tolerance, rank difference, age difference, relationship quality, sex, maternal relatedness, or an interaction of these parameters.

At the Wolfgang Köhler Primate Research Centre (WKPRC), Leipzig, Germany, we tested a new experimental design: the “Cooperation Box”. It consists of a metal cage with a tray and an automated peanut dispenser. The peanuts can only be accessed when the tray is lifted to the top of the cage. To lift the tray, two chimpanzees must, at the same time, lift two handles, which are too far apart to be held by just one. The chimpanzees were free to access the box whenever and with whom they wanted to. The experiment was not successful. We hypothesize that because the chimpanzees received food every 2 hours, they might not have been motivated enough to try to solve the task.

Next, we tried to answer our research questions using part of the data collected by Nolte, Sterck and van Leeuwen (under review). They reproduced the experiment by Hare *et al.* (2007) where social tolerance of chimpanzees and bonobos was compared, using the loose-string paradigm by Hirata and Fuwa (2007). We confirm the conclusion of Hare *et al.* (2007) that chimpanzees only cooperate when food is not monopolizable. Furthermore, we observed that chimpanzees chose to cooperate with partners with whom they shared high social tolerance, but only when rank difference between the two was above the group average. Relationship quality seemed to follow the same trend, but the interaction was strongly influenced by one outlier. We could not conclude on sex and maternal relatedness because of a small number of male and related dyads, albeit both seemed to cooperate more often than female and non-related dyads. Age difference did not influence cooperation.

We conclude that studying chimpanzees in a dyadic experimental setting can give us some insight into how chimpanzees cooperate, but it is indispensable to do experiments in social settings to fully understand how chimpanzees choose their partner for a coordinated cooperation problem.

# Résumé

La coopération est souvent décrite comme deux individus ou plus travaillant ensemble pour atteindre un but commun. Ce comportement peut être observé à travers le règne animal et il est particulièrement complexe chez l'homme. Pour comprendre l'évolution de la coopération, nous étudions l'un de nos plus proches parents : le chimpanzé. Il est connu que les chimpanzés coopèrent au sein de groupes pour chasser et patrouiller leur territoire. De plus, ils forment des coalitions afin d'atteindre un rang social plus élevé et récolter ainsi les privilèges sociaux qui y sont liés. Dans ce mémoire, nous voulons comprendre comment les chimpanzés choisissent leur partenaire pour résoudre une tâche coopérative et coordonnée. Nous voulons savoir si ce choix est basé sur la tolérance sociale, la différence de rang, la différence d'âge, la qualité de la relation, le sexe, l'apparentement ou l'interaction de ces paramètres.

Au « Wolfgang Köhler Primate Research Centre » à Leipzig, Allemagne, nous avons testé un nouveau design expérimental : la « Cooperation Box ». Il s'agit d'une cage avec un plateau et un distributeur de cacahuètes. Pour atteindre les cacahuètes, deux chimpanzés doivent soulever le plateau en même temps. Les chimpanzés était libre d'accéder la Cooperation Box quand et avec qui ils le souhaitaient. L'expérience n'a pas donné de résultat. Nous supposons que comme les chimpanzés recevaient de la nourriture toutes les deux heures, ils préféraient attendre d'être nourris au lieu de résoudre la tâche.

Pour répondre à nos questions de recherche, nous avons utilisé une partie des données récoltées par Nolte, Sterck et van Leeuwen (en cours de révision). Ils ont reproduit l'expérience de Hare *et al.* (2007) où la tolérance sociale des chimpanzés et des bonobos est comparée en utilisant le « loose-string paradigm » de Hirata et Fuwa (2007). Nous confirmons la conclusion de Hare *et al.* (2007) qui observent que les chimpanzés coopèrent uniquement lorsque la nourriture n'est pas monopolisable. En outre, nous observons que les chimpanzés coopèrent plus s'ils partagent une tolérance sociale élevée avec leur partenaire, mais uniquement lorsque leur différence de rang dépasse la différence de rang moyenne du groupe. La qualité de relation semble suivre une tendance similaire. Cependant, cette interaction est largement influencée par une valeur extrême. Nous ne pouvons pas conclure sur les effets ni de l'apparentement ni du sexe, en raison du faible nombre de répétitions. Nous avons néanmoins observé une tendance à une coopération plus fréquente des couples apparentés et des couples mâles. La différence d'âge n'a pas eu d'effet sur la coopération.

Nous concluons qu'étudier des couples de chimpanzés nous permet d'avoir un aperçu de comment les chimpanzés coopèrent. Néanmoins, il est indispensable d'étudier les chimpanzés dans un cadre social pour comprendre la façon dont les chimpanzés choisissent leur partenaire pour résoudre une tâche coopérative et coordonnée.

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# 1 Introduction

## 1.1 Cooperation in the living world

Cooperation, in the sense of two or more individuals working together to achieve a common goal, exists throughout the animal kingdom (Cronin and Sánchez, 2012). For instance, lions (*Panthera leo*) hunt in groups to tackle large prey like buffalo or prey that could outrun one single lion. Meerkats (*Suricata suricatta*) breed cooperatively with subordinates helping care for the young (Davies *et al.*, 2012). In eusocial societies different individuals take up different roles for the functioning of the group, and some even lose their capacity of reproducing (Bourke, 2011). Individual acts and sacrifices all eventually help the survival and reproduction of the colony (Bourke, 2011). In human beings, cooperation lies at the basis of the very complex societies that we live in (Bourke, 2011). In fact, cooperation is advanced as the behavioural mechanism that enabled the transition from hunter-gatherer societies to nation-states and is still today the decisive organizing principle of human society (Cronin and Sánchez, 2012; Melis *et al.*, 2006a). Furthermore, cooperation is crucial for exploiting natural resources and the formation of complex social interactions in humans (Bragard and Montedoro, 2019), and is probably unique in humans with respect to its complexity and frequency (Melis *et al.,* 2006a). Humans are also capable of collaboration, which is a form of cooperation in which individuals fulfil complementary actions to reach a common goal, also involving the coordination of movements (Boesch and Boesch, 1989). Humans are capable of maintaining long-term collaborative partnerships with non-kin through the active monitoring of the partner's role during collective efforts, and even base future collaborations on the contribution of each individual in the past (Melis *et al.*, 2006a).

Cooperation evolved through individuals obtaining more benefits by working together than working alone, and thus increasing individual fitness. It could only become an evolutionarily stable strategy (ESS) if the amount of individuals who take advantage of cooperating individuals without cooperating themselves (henceforth "cheating") stays at a low ratio (Bourke, 2011). In fact, an ESS is a strategy which, "when it is adopted by most members of a population, it cannot be invaded by the spread of any rare alternative strategy" (Davies *et al.,* 2012). The alternative strategy in this case would be selfishness and cheating. To ensue and sustain cooperation, these "cheaters" need to be excluded. This can be achieved through different mechanisms such as punishment and policing (Bourke, 2011; Cronin and Sánchez, 2012; Davies *et al.*, 2012). Punishment means that cheaters will directly be punished if they do not cooperate. In cooperatively breeding meerkats for example, subordinates who are pregnant at the same time as the dominant female, are temporarily evicted from the group, which leads to high stress levels and in most cases, abortion (Young *et al.,* 2006). Policing is common in social insects, where workers kill eggs of other workers to assure that only the queen reproduces. Only then can relatedness remain high inside the colony and the development of females into distinct castes can be regulated, hence ensuring cooperation (Ratnieks and Wenseleers, 2005). Another mechanism to make cooperation become an ESS is kin selection. Cooperating with kin brings indirect fitness benefits, which means that the alleles shared with your relatives will be passed on to the next generation if you help them survive and ultimately reproduce (Bourke, 2011; Cronin and Sánchez, 2012; Davies *et al.*, 2012).

The mechanisms of gaining fitness benefits through cooperation and the exclusion of cheaters explain cooperation from a theoretical and evolutionary perspective. They are called “ultimate explanations" (Cronin and Sánchez, 2012; Suchak *et al*, 2014). Proximate explanations on the other hand are still missing. How do individuals achieve cooperation in a social environment (Cronin and Sánchez, 2012)? What are the social conditions that influence the emergence and stability of cooperation (Cronin and Sánchez, 2012)? Cooperation involves many complex decisions, such as the choice of when to cooperate and whom to cooperate with, when many potential partners are available (Suchak *et al*, 2014). In this study I will focus on the latter question and try to understand how partners are chosen for a cooperative purpose.

## 1.2 Cooperation in non-human primates

Cooperation has been much studied in non-human primates. There are two main reasons for this. The first is the evolutionary implication for human behaviour. Understanding how cooperation works in primates can help us understand the proximate mechanisms of the evolution of cooperation. The second reason is the ubiquity of cooperation among non-human primates. Many primate species cooperate in many ways, for instance they can form coalitions, share food, protect each other against predators through fighting or alarm calls, and some species even breed cooperatively (Duguid, 2016; Mitani, 2009; Silk, 2007).

Most studies have been done on chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) because they are our closest living relatives. Studying them allows us to better understand the evolution of unique human traits, like the high levels of cooperation (Melis *et al,* 2010; Mitani, 2009). In fact, differences between humans and the *Pan* genus are an indication for changes that occurred after the divergence from our last common ancestor approximately 7 million years ago (Yamamoto, 2020). Traits that are the same in all three species were, following the principle of parsimony, most probably already present in our last common ancestor. Because of the recurrent unstable political situations in the

Democratic Republic of Congo, the only country in the geographic range of bonobos, long term studies of their behaviour have been difficult to execute (Mitani, 2009). Field research on chimpanzees, however, is common (Mitani, 2009), which is why I am going to concentrate on chimpanzee cooperation. Nevertheless, it is important to keep in mind that to fully understand the evolution of cooperation in human beings, we must also consider cooperation in bonobos.

In the following sections, I will first talk about chimpanzees and how they cooperate in the wild. I will then do a summary of the laboratory experiments that have been done so far to explore how they choose their cooperation partner. The third point will focus on social tolerance, which is a very important factor influencing cooperation and partner choice. Finally, I will present my research questions and hypotheses, and how I will proceed to answer these questions.

## 1.3 Cooperation in chimpanzees

### 1.3.1 Observations from the wild

Chimpanzees live in permanent social groups with a mean of 35 individuals (IUCN). The largest known chimpanzee group comprises 150 chimpanzees and lives in Ngongo, in the Kibale national park in Uganda (Mitani, 2006). These groups consist of multiple females and males and work as fission-fusion societies. This means that the group splits into subgroups for an undefined duration and then merges again into one big group (Pusey and Schroepf-Worker, 2013). The different subgroups are mostly created during foraging and their sizes depend on the availability of resources. Less resources mean that there might be more intragroup competition, and the subgroups remain small. The subgroups merge again regularly, as being in a large group provides certain advantages like the protection from predators, easier access to mates, and territorial defence (Pusey and Schroepf-Worker, 2013). Chimpanzee societies are organized in linear dominance hierarchies. This means that there is little transitivity between ranks and that a high-ranking individual gains important fitness benefits. For instance, the alpha male sires up to 30 to 50% of all infants born during his time at the top of the group (Mitani, 2009).

Male chimpanzees belonging to one chimpanzee group show high rates of group cooperation and coordination (Yamamoto, 2020). They work together to protect their territory from foreign chimpanzees by supporting each other in agonistic interactions with other groups, patrolling their borders together, and coordinating attacks on strangers (Melis *et al.*, 2010). They also cooperate when hunting monkeys in dense forest canopies. Here, monkeys have many escape routes and chimpanzees need to coordinate their positions and perform different complementary actions to be successful in their hunt (Boesch, 1994). Subsequently, the meat is shared between group members, albeit opinions differ on whether this is only done to avoid harassment from beggars, or if it is a sign of reciprocal relationship (Melis *et al.*, 2010; Yamamoto, 2020). Another sign of group cooperation and coordination is road crossing (Matsuzawa, 2018; Yamamoto, 2020). Before crossing a road, chimpanzees of the same group wait for all the group members to join. Then, male chimpanzees take on different roles. One male is at the lead and scans the road. He often stops in the middle of the road to look after the group members. A second male chimpanzee is at the rear, watching over the entire group (Matsuzawa, 2018; Yamamoto, 2020).

On top of this group cooperation, chimpanzees, and mostly males, cooperate in smaller groups of two or three to direct aggression towards conspecifics, for example, when competing over food (Mitani, 2006; Muller and Mitani, 2005). These small groups are called coalitions. Sometimes the same coalitions form repeatedly over months or years. In this case the coalitions are called alliances (Mitani, 2006; Muller and Mitani, 2005). Alliances are especially important in chimpanzee status competition (Melis *et al.*, 2010; Mitani, 2006; Muller and Mitani, 2005). In fact, reaching the alpha male position is often impossible without alliances (Mitani, 2009; Muller and Mitani, 2005). Males who form alliances help each other guard ovulating females, preventing them from copulating with any other males. Thus, they gain higher shares of copulation than if they would be guarding the females alone (Melis *et al.*, 2010). Male chimpanzees are known for maintaining their alliances by reciprocating social favours like grooming, meat sharing, and support in agonistic interactions with other group members (Melis *et al.,* 2006a; 2010; Mitani, 2009). They also trade different types of social favours like grooming for support, grooming for meat or meat for support (Muller and Mitani, 2005). Higher-ranking individuals can cede matings to lower-ranking individuals to assure that they will receive the lower-ranking's help to maintain their position in the dominance hierarchy (Mitani, 2009).

Regarding female chimpanzees, they were long considered asocial, making little social interactions and most studies have concentrated on female competition, rather than their cooperation (Mitani, 2009). Most females disperse from their natal group after reaching sexual maturity, while males stay in their natal group. Hence, the probability for females to have repeated interactions, to reciprocate social favours, and the possibility to make up for losses that happened in previous interactions are smaller than in males (Cronin and Sánchez, 2012). This makes the bonds they form with other chimpanzees generally less strong than the bonds formed between males, even though this can vary from population to population (Gilby and Wrangham, 2008; Lehmann and Boesch, 2008). Females can build strong coalitions in sites where they stay in their natal group. For example, at the Gombe National Park, Tanzania, mothers and daughters who do not disperse can have high association rates (Gilby and Wrangham, 2008). A long life in a stable community after dispersal, also favour female cooperation

(Lehmann and Boesch, 2008). Female cooperation is especially strong in places where the costs of sociality are reduced, and they can therefore spend more time together in larger groups. This is notably the case in captivity, where food is never limited (Gilby and Wrangham, 2008; Melis *et al.*, 2010). For females, forming coalitions can for example facilitate their access to food or ensure the survival of the offspring in case the mother dies (Lehmann and Boesch, 2008).

Chimpanzees have been observed to cooperate more with related indivuduals than with non-related ones, albeit this effect might be limited (Langergraber *et al.,* 2007; Mitani *et al.*, 2000). It is probable that chimpanzees only cooperate preferentially with maternal siblings since these are easier to identify than paternal siblings (Langergraber *et al.*, 2007). Indeed, chimpanzee mothers create enduring social bonds with their offspring, making it more likely that maternal siblings recognize each other (Mitani *et al*, 2002). Furthermore, even though kinship, and thus, indirect fitness benefits probably do play a role in the choice of cooperation partners, direct fitness benefits might be even more important (Langergraber *et al.*, 2007; Mitani, 2009). In a field study on the large community of chimpanzees at Ngogo, Kibale National Park, Uganda, it was found that male chimpanzees formed coalitions, shared meat, and patrolled together with other males from the same age and a similar rank more often than expected by chance, and this, regardless of their kin (Mitani *et al.,* 2002). In fact, individuals of the same age and rank are likely to be familiar with each other, share similar social interests, have similar access to resources and the ability to exchange them (Mitani *et al*, 2002). Kin might be unavailable or unsuitable as allies, while unrelated individuals might do tactical decisions to cooperate with other chimpanzees, to form coalitions and increase their social rank (Mitani *et al,* 2002). Forming coalitions, and cooperating with unrelated individuals, but with the same age and rank, might thus increase the direct fitness and be much more rewarding than cooperating with kin. Hence, most of the time, male chimpanzees create strong affiliative and cooperative social bonds depending on the direct fitness benefits they will obtain, regardless of whether the partner is related or not (Langergraber, 2012).

To summarise, chimpanzees are capable of cooperating and coordinating their movements in large groups and in small coalitions. Chimpanzees are capable of cooperating when pursuing a common goal, like obtaining a higher social rank and the social benefits that come with it, for instance access to females and resources. They are also capable of coordination when hunting monkeys or crossing roads. Factors that influence partner choice for these cooperative activities are age and rank difference (Mitani *et al*, 2002), kinship, but to a probably limited extent (Langergraber *et al.*, 2007), and sex, with male chimpanzees cooperating more often and having stronger coalitions than females (Gilby and Wrangham, 2008).

Even though these field studies give us already some insight into how chimpanzees choose their partner, it is difficult to understand what social and individual factors this depends on more precisely, since we cannot control for the different factors (Melis *et al.*, 2006a). Therefore, many laboratory experiments have been conducted.

### 1.3.2 Laboratory studies

The first experiment on cooperation in chimpanzees was run by Crawford in 1937 and consisted of a heavy box containing fruits placed at a certain distance from the chimpanzees. Two chimpanzees were required to pull the box since it was too heavy for one individual to pull it alone. Only three of the seven tested pairs managed to solve the task after instructions were given by the experimenter. Two chimpanzees learned to recruit a partner, showing that they were able to communicate to solve a common task, that they understood the role of the partner, and that they understood when they needed to cooperate (Crawford (1937) cited in Duguid *et al.,* 2020, Schmelz and Call, 2016, and Silk, 2007). Nevertheless, this understanding was limited, as it occurred rarely and only after hundreds of trials (Crawford (1937) cited in Melis *et al.*, 2010).

Crawford's design (1937) was upgraded by Hirata and Fuwa (2007). The weights attached to the box were replaced by a system of sliding ropes and the food was placed on a tray. The rope was pulled through holes on both ends of the tray and both ends of the rope were placed at a distance which made it impossible for one chimpanzee to pull both ends simultaneously. If one end of the rope was pulled before the other, the rope would slide through the holes and the tray with the food attached to it would not move. This famous paradigm, sometimes called the "loose-string" paradigm (Massen *et al.,* 2020), has been used by numerous researchers afterwards and on various species (Massen *et al.*, 2020) and allowed a better understanding of what influences cooperation. For example, in one experiment using the loose-string paradigm, the rope was presented in two different ways. In the first way, one chimpanzee could pull at both ends of it and did not need a partner, while in the second, both ends were too far apart for one chimpanzee to pull them alone (Melis *et al.,* 2006a). The chimpanzees had the option to unlock a door to recruit a second chimpanzee. Interestingly, they only did so in the second option, when they could not pull at both ends of the rope alone, indicating that they understood when they needed a partner and when not (Melis *et al.,* 2006a). In addition, the same researchers developed a second task, where chimpanzees could choose between two partners. The results showed that they would always unlock the door of the chimpanzee with whom they had had positive previous experience solving this task. In other words, they chose the better co-operator when they had the choice between two potential partners (Melis *et al.,* 2006a).

The loose-string paradigm also played an important role in identifying the role of social tolerance in cooperation (Hare *et al.,* 2007; Melis *et al.,* 2006b). Social tolerance can be defined as the "probability that individuals will be in proximity to conspecifics around valuable resources with little or no aggression" (Cronin and Sánchez, 2012). In fact, chimpanzees who cooperated in the loose-string task shared food more often outside of the experimental setting (Melis *et al.,* 2006b). Furthermore, when individuals of a dyad who did not cooperate were paired with more socially tolerant individuals, they started cooperating. The opposite was also true. Individuals capable of solving the task in one dyad, would not cooperate when paired with a less socially tolerant individual (Melis *et al.,* 2006b). The role of social tolerance in cooperation, and how it evolved is discussed further in section *1.4 Social tolerance in great apes*. Furthermore, an effect of rank difference was detected. When individuals of a high rank were present, subordinates would mostly not approach the rope (Melis *et al.,* 2006b).

Finally, the loose-string paradigm showed that chimpanzees only cooperate when cooperation brings them an advantage, otherwise they prefer working alone (Bullinger *et al.,* 2011; Rekers *et al.,* 2011). In this experiment chimpanzees could choose between an individual task and a cooperative task. In the individual task, one chimpanzee could reach both ends of the rope, in the cooperative task, they could only reach one end. When the rewards they received in the individual and the cooperative task were the same, chimpanzees preferred to work alone. However, when the reward was higher for the cooperative task than the individual one, chimpanzees chose to cooperate (Bullinger *et al.,* 2011).

The before mentioned studies were all made in controlled conditions in laboratories and partner choice was made by the human experimenter, and not by the chimpanzee. Only in one experiment did the chimpanzees have a choice, but this choice was still very limited (Melis *et al.,* 2006a). Studying primates in a controlled setting has the advantage of excluding external factors and thus allowing the observation of one precisely chosen factor (Cronin *et al.*, 2017). However, it does not inform about the behaviours that chimpanzees would show in their natural environment, which are subject to natural selection (Cronin *et al.*, 2017). Cooperation is markedly influenced by the presence of conspecifics, their identity, and the relationship with the test subject, in many species of primates (Cronin *et al.*, 2017). Moreover, partner choice is an important social skill that can only be observed in a social setting (Molesti and Majolo, 2016). Choosing the right partner is crucial to reduce the risk of exploitation and increase the chance of cooperation (Molesti and Majolo, 2016). Also, in social species, separation from group mates may induce a negative physiological response in the test subject (Cronin *et al.*, 2017). Thus, maintaining individuals in their social environment increases the socio-ecological validity of the research (Cronin *et al.,* 2017). In the following section, we will have a look at studies done on chimpanzees in social settings.

### 1.3.3 Studying cooperation in a social setting

In the beginning, experiments done in a social environment did not always show the chimpanzee's ability to cooperate. For example, in one study where chimpanzees had to manipulate an apparatus cooperatively to obtain a food reward, the alpha male was always present at the apparatus (Chalmeau, 1994). Each time somebody cooperated with him to access the rewards, he would monopolize it. Hence, no one, except one infant, was willing to cooperate with him, and no other dyad could use the apparatus. The conclusion was that a lack of social tolerance and food rewards which could not be shared equally between individuals at the end of the task, represented obstacles for cooperation and these need to be taken into account in future research planning (Chalmeau, 1994).

In a later experiment in 2014, chimpanzees were also free to choose their partner, but the food reward was not monopolizable (Suchak *et al.,* 2014). Here, 11 chimpanzees in an outdoor enclosure at the Field Station of the Yerkes National Primate Research Center, used an apparatus with two pull rods which required two chimpanzees to pull simultaneously to release food. The food was distributed in equal parts to each cooperating chimpanzee. Individuals were found to rather cooperate with kin and individuals of similar social rank. When an individual was from a different rank yet kin, they would also choose to cooperate. However, the fact that chimpanzees choose their partners based on kin has been questioned in field studies (Langergraber, 2012; Langergraber *et al.,* 2007; Mitani *et al.,* 2002; and see section 1.3.1). Interactions between individuals from the same social rank are characterized by a higher tolerance, than interactions between individuals with high differences in rank. If the difference is high, the higher-ranked individual can forcefully monopolize all the food (Suchak *et al.,* 2014). Furthermore, individuals with a greater dominance advantage over the second individual engaged more frequently in freeloading (the stealing of food without participating in solving the task) (Suchak *et al.*, 2016). In subsequent trials, the victims of the freeloaders would often withdraw from the apparatus or withhold pulling on the hand gear until the freeloader moved away (Suchak *et al.,* 2016). In addition, cooperation was shown to be reciprocal. If individual A approached individual B frequently when he was at the apparatus, individual B would also approach individual A more frequently. This kind of reciprocity has also been observed in other studies. For instance, chimpanzees who anticipated to aggress another individual the next day, groomed their supporters the day before the aggression, which improved the likelihood of support (Kayoma *et al.,* 2006).

Finally, we saw before, that chimpanzees recruit the best collaborator (Melis *et al.,* 2006a). Suchak and colleagues (2014) concluded that in a social environment, where chimpanzees are free to choose their partner, chimpanzees will take into account other social factors, allowing for the establishment of long-term relationships, which also allow other social interactions like grooming, sex, play or food sharing (Suchak *et al.*, 2014). Hence, the aptitude of the potential partner to solve a specific task is not always considered (Suchak *et al.,* 2014). Individuals who often share social benefits like grooming, sex or play, will henceforth be said to have a high relationship quality.

Even though the cited experiments give us a lot of insight into the social factors influencing cooperation in primates and that testing primates in their social environment can have many advantages, it also comes with limitations that need to be thought of when organizing the experiment. First, in a social group, whether it is in the wild or in captivity, it can be difficult to elicit participation from all the group members (Cronin et al, 2017). The lack of participation can be due to competition within the social group, interference from other group members, the ability to scrounge without participating, and the tendency of individuals to not participate if a higher-ranking individual is present (Cronin et al, 2017). In addition, there is reduced experimental control, since it is not always possible to control design aspects, such as the number of trials per individual or the order of participation (Cronin et al, 2017). It can also be difficult to identify individual responses, both in real-time and from video (Cronin et al, 2017). Finally, the sample size is reduced, because when testing an entire social group, the subjects of the group are not independent of one another (Cronin et al, 2017). These limitations come with statistical and logistical challenges that need to be taken care of to avoid drawing spurious conclusions.

To summarise, the loose-string paradigm and experiments in social settings, showed that chimpanzees are capable of cooperation and coordination (Melis *et al.,* 2006a; 2006b; Suchak *et al.,* 2014), but they only cooperate when it provides them an advantage (Bullinger *et al.,* 2011). Moreover, cooperation only happened with certain individuals, hence showing the importance of partner choice (Melis *et al.,* 2006b; Suchak *et al.,* 2014). Social tolerance is an important factor influencing partner choice, as well as the difference in social rank (Cronin and Sánchez, 2012; Cronin *et al.,* 2014; Hare *et al.,* 2007; Melis *et al.*, 2006b; Suchak *et al.*, 2014). The higher the social tolerance and the smaller the difference in rank, the more individuals cooperate. The role of kin remains unclear (Langergraber *et al.,* 2007), but there seems to be an interaction between rank difference and kin. Related chimpanzees cooperate no matter their difference in rank (Suchak *et al.,* 2014). In addition, relationship quality might in some cases be a more important factor than the  capacity of the potential partner to solve a specific task (Suchak *et al.,* 2014). Monopolization must also be considered. Chimpanzees are less disposed to cooperate when food reward is monopolizable (Hare *et al.,* 2007; Suchake *et al*, 2014).

## 1.4 Social tolerance in great apes

Social tolerance plays an important role in cooperation and partner choice in primates (Cronin and Sánchez, 2012; Hare *et al.,* 2007; Melis *et al.*, 2006b; Molesti and Majolo, 2016; Suchak *et al.*, 2014). Understanding social tolerance, its evolution, and variation among different species, as well as between different populations of the same species, can advance the understanding of cooperation (Cronin *et al.,* 2015). Hence, I decided to explain further what social tolerance is and how it influences cooperation.

Social tolerance is a “concept that captures the probability that individuals will be in proximity to conspecifics around valuable resources with little or no aggression” (Cronin *et al.,* 2012). Individuals who are in close proximity while foraging and who show little aggression while doing so, have a high social tolerance (Cronin *et al.,* 2012). Social tolerance is necessary for the initiation of successful cooperative behaviour. Dyads with a high level of social tolerance will be in proximity around the resource, without aggression, which will give them more time to observe, manipulate and understand the problem they are trying to solve (Harrison *et al.,* 2021; Molesti and Majolo, 2016). They will learn how their behaviour, their partner’s behaviour, and the resources are connected, and hence, what they need to do to access it (Molesti and Majolo, 2016). Therefore, it is plausible to assume that social tolerance has been a crucial factor in the emergence of cooperation, as well as coordination (Molesti and Majolo, 2016).

Different ape species have different levels of social tolerance. The main theory explaining why social tolerance differs in great apes is based on their feeding ecology (Nolte and Call, 2021). For instance, bonobos (*Pan paniscus*) are often considered to be more socially tolerant than chimpanzees (Hare *et al.,* 2007; Nolte and Call, 2021; Wilson *et al.,* 2020; Yamamoto, 2020). Bonobos live in the humid forests in the Democratic Republic of Congo, south of the Congo River (IUCN) where food availability is large and stable throughout the year (Nolte and Call, 2021). Furthermore, bonobos depend on terrestrial herbaceous vegetation, which is available in large quantities, while chimpanzees rather depend on ripe fruit, which is temporally and spatially patchier (Wilson *et al.,* 2020). If food is patchier, the groups formed are smaller and there is more aggression against foreign individuals (Wilson *et al.,* 2020). If, on the other hand, food is widely distributed and abundant, larger groups will be formed and there will be less aggression against foreigners (Wilson *et al.,* 2020). In addition, living in taller groups with little aggression leads to a self-domestication process (Nolte and Call, 2021). Abundant food leads to healthier females with more frequent and longer fertility cycles, which again leads to fewer males per fertile female in the group, and less male aggression due to mating competition (Nolte and Call, 2021). Also, more frequent and longer fertility cycles mean more mating choice for females, which might then select less aggressive males and form coalitions against aggressive ones (Nolte and Call, 2021). Aggression in bonobos hence decreased while social tolerance increased and behaviours like non-conceptive sex, adult play, food sharing between strangers, and female gregariousness appeared (Yamamoto, 2020). This has also been observed in orangutans, with Sumatran orangutans (*Pongo* *abelii*) being more socially tolerant than Bornean orangutans (*Pongo pygmaeus*) (Meulman and van Schaik, 2010). It is generally assumed that plant productivity is higher in Sumatran than in Bornean forests and that Sumatran forests are of higher quality than Bornean ones (Marshall *et al.,* 2009).

Despite the relatively well-established idea that bonobos are more socially tolerant than chimpanzees, some studies with captive bonobos have shown that social tolerance might not be higher and that chimpanzees actually spend more time with their conspecifics around a resource (Cronin *et al.,* 2015; Jaeggi *et al.,* 2010). This could be explained by the fact that social tolerance is not the same in every population or group of the same species (Kaufhold and van Leeuwen, 2019), and not even in every individual of the same group (Chalmeau *et al.,* 1994; Melis *et al.,* 2006b; Molesti and Majolo, 2016; Suchak *et al.,* 2014). Social tolerance is characteristic of each individual and is part of the personality of each subject. Different individuals can be more or less socially tolerant and spend more or less time with conspecifics around a valuable resource, no matter their identity (Chalmeau *et al.,* 1994; Melis *et al.,* 2006b; Molesti and Majolo, 2016; Suchak *et al.,* 2014). Social tolerance is also influenced by the context and group composition (De Troy *et al.,* 2021). Because social tolerance influences cooperation and is variable between groups, cooperation may also be different in different groups or populations of apes (Kaufhold and van Leeuwen, 2019). Hence, it is important to take into account intergroup variation in every cooperation study. If possible, different populations should be compared, and conclusions that have been taken with one population only should not be generalized (Kaufhold and van Leeuwen, 2019).

## 1.5 In this study…

With this study, we wanted to assess which social factors influence partner choice for a coordinated cooperation problem in chimpanzees. We focused on how social tolerance, social rank, maternal relatedness, age, sex, and relationship quality influence partner choice. We hypothesize in a first step that dyads with high social tolerance and which are close in rank will cooperate more often. Second, high differences in rank and in age will negatively affect cooperation. Third, maternally related dyads will cooperate more often even when difference in rank and in age are high. Fourth, relationship quality will positively influence cooperation. Even if they are less successful in accessing the food, dyads with high relationship quality will keep cooperating, because for chimpanzees it might be more important to maintain the social relationship than to be successful at this specific task (Suchak *et al.,* 2014). We also hypothesize that males will cooperate more often than females. And finally, monopolization of the resource influences cooperation negatively.

To test these hypotheses we tried a new experimental design, named the “Cooperation Box”. This experiment consists of a metal box containing peanuts. The peanuts can only be accessed if two individuals simultaneously lift the baited platform within the box all the way to the top of the box. Because of the previously mentioned advantages of studying chimpanzees in a social environment, and because partner choice is a social skill that can only be observed in a social setting, the box was placed in the chimpanzee enclosure. The chimpanzees were free to approach the box and cooperate to access the food whenever and with whom they wanted to. After the peanuts were made available by two individuals, all chimpanzees could join and eat them. Because much of human cooperation is actually collaboration (Melis *et al.,* 2006a; Tomasello *et al.,* 2004), which combines both cooperation and coordination (Boesch and Boesch, 1989), and because we know that chimpanzees are capable of coordination (Matzusawa, 2018; Yamamoto, 2020) we wanted to test the extent of this capacity. Therefore, the tray with the peanuts needed to be lifted horizontally. If the tray tilted too much, the peanuts spilled and remained inaccessible, forcing the chimpanzees to coordinate their movements.

Social tolerance was determined using the “Peanut Plot” (van Leeuwen *et al.,* 2021), which consists of a rectangle drawn on the floor containing peanuts. The aim was to observe which chimpanzees entered the plot, next to whom they entered the plot, and whether they shared food or showed aggression. With this data social tolerance was rated for each dyad. Relationship quality was determined by doing daily behavioural observations of the chimpanzees and of their proximity to others. Information about social rank, kin and sex of the chimpanzees were obtained from the WKPRC staff.

The Cooperation Box experiment did not work as expected. The chimpanzees did not manage to access the peanuts. The reason for this will be further analysed in the discussion. Thanks to fellow researchers the hypotheses could still be tested. Nolte, Sterck and van Leeuwen (henceforth NSL) reproduced Hare and colleagues’ (2007) experiment in 2019 (under review), where they compared the co-feeding and cooperation capacity of bonobos and chimpanzees using the loose-string paradigm developed by Hirata and Fuwa (2007). Hare and colleagues (2007) found that, when the food reward was monopolizable, bonobos co-fed more than chimpanzees (they were more socially tolerant). This experiment was repeated with a large number of dyads, and information about their rank, age, relationship quality, social tolerance, kin and sex was also collected. I could therefore use the data and test whether these variables influenced the outcome of the experiment. The main difference between this experiment and the Cooperation Box was that the chimpanzees were not free to choose their partner, and that the dyad was separated from the rest of the group when doing the task. Thus, we do not know how these individuals actually choose their partner in a more natural condition. Nevertheless, this data may already provide us with some more insight on how chimpanzees choose their partner for a coordinated cooperation problem.

# 2 Materials and Methods

The following materials and methods section will be divided into two parts. The first part will cover the experiments and observations I did during my stay at the WKPRC and the second will describe Nolte, Sterck and van Leeuwen's (NSL) replication of Hare *et al.* (2007).

### *Ethical statement*

All the experiments described in this master's thesis, were non-invasive and strictly adhered to the legal requirements of Germany. The studies were ethically reviewed and approved by an internal committee with members of the Max Planck Institute for Evolutionary Anthropology and the Zoo Leipzig, namely: department director Prof. D. Haun, research coordinator Dr. D. Hanus, veterinarian Dr. A. Bernhard, head keeper D. Geissler and assistant head keeper M. Lohse. The chimpanzees were fed regularly, they had access to enrichment devices including shaking boxes and poking bins, and had access to water ad lib. At no point during the experiments and observations were they deprived of any of these. In addition, subjects voluntarily participated in the studies.

## 2.1 Part One – My Experiments and Observations

In this first part, we will start with a presentation of the chimpanzee group I worked with. We will then move on to the "Peanut Plot", the relationship quality observations, the statistical analysis of these two, and finally the "Cooperation Box" experiment.

### 2.1.1 Subjects

The experiments and observations took place at the Wolfgang Köhler Primate Research Centre (WKPRC) in Leipzig, Germany. The WKPRC has two captive chimpanzee groups (*Pan troglodytes verus*). The chimpanzee group the observations were done on (the A-chimpanzees) was composed of 14 adults (17 to 45 years old; 12 females, 2 males), 4 juveniles (3 to 6 years old; 1 female, 3 males), and 2 infants (< 3 years old; 1 female, 1 male). All chimpanzees were reared in zoos and are accustomed to doing behavioural experiments. Table 1 summarises all the information on the chimpanzee group.

The subjects have an inside and an outside enclosure. During the day, when no experiments are being done in the sleeping rooms, and when the weather allows it, all the chimpanzees are in the 1630 $m^2$ outside enclosure. All the experiments in this first section were done in the outside enclosure, and no direct interaction with the chimpanzees was possible.

*Table 1 Information on the A-chimpanzees at the Wolfgang Köhler Primate Research Centre. Maternal relatedness regroups mothers with their offspring and maternal siblings. Rank in Hierarchy gives the rank as assessed by the ape-keepers. The two infants Carola and Frank did not yet have a fixed rank, hence the NA values. Ape keepers did not agree on whether Bambari and Sandra were on rank 5 or 6, hence the value of 5.5.*

| Name | Sex | Date of Birth | Maternal relatedness | Rank in Hierarchy |
|---|---|---|---|---|
| **Azibo** | M | April 14, 2015 | Swela | 12 |
| **Bambari** | F | December 8, 2000 | NA | 5.5 |
| **Carola** | F | May 01, 2020 | Fraukje | NA |
| **Changa** | F | March 3, 2011 in | NA | 11 |
| **Corrie** | F | December 12, 1976 | Youma | 7 |
| **Dorien** | F | October 22, 1980 | NA | 6 |
| **Frank** | M | Dezember 25, 2019 | Kisha, Ohini | NA |
| **Fraukje** | F | April 06, 1976 | Carola | 9 |
| **Frodo** | M | November 28, 1993 | Natascha, Makeni | 1 |
| **Kisha** | F | March 04, 2004 | Frank, Ohini | 8 |
| **Maja** | F | May 01, 1986 | NA | 10 |
| **Makeni** | M | March 14, 2018 | Natascha, Frodo | 14 |

| | | | | |
|---|---|---|---|---|
| **Natascha** | F | March 28, 1980 | Frodo, Makeni | 5 |
| **Ohini** | M | March 25, 2016 | Kisha, Frank | 13 |
| **Riet** | F | November 11, 1977 | Sandra, Tai | 3 |
| **Robert** | M | December 01, 1975 | NA | 2 |
| **Sandra** | F | June 09, 1993 | Riet, Tai | 5.5 |
| **Swela** | F | Oct 19, 1995 | Azibo | 7 |
| **Tai** | F | August 12, 2002 | Riet, Sandra | 4 |
| **Youma** | F | Mar 25, 2018 | Corrie | 14 |

### 2.1.2 Social rank and general information on the chimpanzees

The social rank or dominance hierarchy was collected by a fellow researcher, who every two weeks would ask the responsible chimpanzee keeper to fill in a form where he would associate each chimpanzee to one rank.  The data of July and August 2021 was kindly forwarded. The raters agreed on all the ranks, except for Bambari and Sandra where they hesitated between rank 5 or 6. Hence they were given the rank 5.5.

Other information on the chimpanzees (kin, age and sex) were kindly given by the WKPRC staff.

### 2.1.3 Social tolerance (ST): the Peanut Plot Experiment

#### *2.1.3.1 Experimental setup*

To measure the social tolerance (ST) for each dyad in the chimpanzee group the Peanut Plot method (van Leeuwen, 2021) was used. This method consists of a rectangle, which was laid out on the ground in the outside enclosure (see Figure 1). The length of the rectangle is group dependent and is determined by attributing 20 cm to each chimpanzee without considering the infants. Here, the rectangle was 3.6 meters long and 1 meter wide. The plot was delimited by and filled with 216 peanuts in total. This amount is also group-dependent and was obtained by calculating 12 peanuts per chimpanzee, without considering the two infants. The peanuts were spread in lines over the entire plot, by a mean of 60 peanuts per square meter. Peanuts were chosen because they are the preferred food of all the chimpanzees of the group.

*Figure 1 The Peanut Plot*

*Figure 2 Image from video showing some chimpanzees in the Peanut Plot.*

#### 2.1.3.2 Protocol

The experiment was conducted four times a week, for three weeks (from the 19th of July to the 6th of August 2021). Whenever possible, a day was skipped between two sessions, so that the chimpanzees would not get used to finding peanuts in their enclosure, lose interest, and stop approaching the plot right after entering the outside enclosure. The experiment started right when the chimpanzees went to the outside enclosure. The exact time each session took place varied, because the chimpanzees went outside at different times every day. First, chimpanzees would not go out if it was raining too much, or if temperatures were too low. Second, if experiments were conducted by other researchers in the sleeping rooms in the morning, the chimpanzees would only go outside after the experiments were done, which was mostly around noon.

Before leaving the inside enclosure, one ape keeper, familiar to the chimpanzees, would show them a bag of peanuts, to catch the group’s attention to the experiment. The session started as soon as the first chimpanzee was within reach of the peanuts, which was at approximately 1m distance from the plot. The experiment finished when no peanuts were left, or every chimpanzee had left the plot. This took about 4 minutes on average. The experiment was filmed from two different angles, and data was coded from the videos.

#### 2.1.3.3 Coding

Coding was done in two steps. First, scan sampling was done every 15 seconds to assess the identity of every chimpanzee present in the Peanut Plot. All the possible dyads were noted. If the two individuals of one dyad were within one meter of one another, they were said to be in proximity.

In a second step, each chimpanzee was followed individually and it was noted whether the observed individual was showing aggression, positive food sharing, negative food sharing, or support towards a second individual. Aggression involved every type of aggressive behaviour. These were actual attacks on others and directed display. Positive food sharing was the act of voluntarily giving food to another, or of collecting peanuts directly in front of another chimpanzee, without any agonistic or fearful reaction of the second chimpanzee. Negative food sharing on the other hand, was when one chimpanzee stole food directly from the hand or from the space just in front of his fellow chimpanzee, leading usually to an agonistic reaction. Shielding peanuts from somebody else was also considered negative food sharing. Finally, support was the act of hugging or putting an arm around somebody.

#### 2.1.3.4 The data

The final data were composed of nine different variables, which are explained in the following table (Table 2). An overview of the data can be found in Appendix 1. For the frequency of the different behaviours which were noted throughout the trial and not just during the scans, the number of times each behaviour was observed was divided by the number of scans this dyad was present in the Peanut Plot to get the “proportion of scans”.

*Table 2 Data structure for the Peanut Plot experiment*

| **Variable** | **Explanation** |
|---|---|
| **Dyad** | Each possible dyad of chimpanzees |
| **Proportion together** | Proportion of the total number of scans each dyad was observed inside the Peanut Plot |
| **Proportion no-proximity** | Proportion of scans each dyad was together in the Peanut Plot and more than a meter apart |
| **Proportion proximity** | Proportion of scans each dyad was together in the Peanut Plot and less than a meter apart |
| **Frequency of aggression** | Proportion of scans each dyad was together in the Peanut Plot and showing aggression towards each other |
| **Frequency of positive food sharing** | Proportion of scans each dyad was together in the Peanut Plot and sharing food |
| **Frequency of negative food sharing** | Proportion of scans each dyad was together in the Peanut Plot and showing negative food sharing |

| | |
|---|---|
| **Frequency of support** | Proportion of scans each dyad was together in the Peanut Plot and showing support towards each other |
| **Frequency of “neutral” behaviour** | Proportion of scans each dyad was together in the Peanut Plot and not showing any of the behaviours above |

### 2.1.4 Relationship quality (RQ)

#### *2.1.4.1 Protocol*

To assess the relationship quality of every possible dyad of chimpanzees, behavioural observations were conducted every day for two hours (except on weekends), from the 16th of July to the 26th of August 2021, resulting in 62 hours of observation. During these two hours, every 15 minutes, a scan was made of all the chimpanzees who were in proximity of one another (less than one meter apart). Every 5 minutes a scan was made of the chimpanzees who were absent from the field of vision. During the whole two hours all occurrence sampling was done for the behaviours aggression, play, grooming and sex. Aggression comprised any type of aggressive behaviour whether they were actual attacks on others or directed display. Play involved any playful behaviour like wrestling, chasing and tickling each other, which were mostly accompanied by a play face and play panting. Sex included copulatory and non-copulatory sexual behaviours. The duration of the behaviour was not considered. For example, grooming with one partner could last for 2 or 10 minutes but would be counted as 1 single interaction. However, if one behaviour lasted over many 15-minutes-scans, it would be noted down once for each scan. When dyads stopped their behaviour for less than a minute and continued afterwards, the interaction was counted as one. When they stopped for longer and continued afterwards, they were counted as many interactions. When two individuals groomed each other back and forth, the interaction would count as two separate interactions. The direction of the interactions was not considered.

The observations were done in the outside enclosure, except on days where the chimpanzees would not go outside due to bad weather conditions, in which case the observations were done in the inside enclosure.

#### *2.1.4.2 The data*

The final data was composed of nine different variables, which are explained in the table below (Table 3). An overview of the data can be found in Appendix 2.

*Table 3 Data structure for the Relationship quality observations 2021*

| Variable | Explanation |
|---|---|
| **Dyad** | Each possible dyad of chimpanzees |
| **Present** | Number of 5-minute-scans each dyad was in the field of vision (deducted from the individuals who were absent) |
| **Proximity** | Number of 15-minute-scans each dyad was less than a meter apart |
| **No-proximity** | Number of 15-minute-scans each dyad was more than a meter apart |
| **Aggression** | Number of times each dyad showed aggression towards each other |
| **Grooming** | Number of times each dyad groomed each other |
| **Play** | Number of times each dyad played together |
| **Sex** | Number of times each dyad had sex |
| **Neutral** | Number of times each dyad was present but not showing any of the behaviours above |

### 2.1.5 Statistical analysis for social tolerance (ST) and relationship quality (RQ)

The data was analysed with a fuzzy correspondence analysis (FCA) using the package ade4 in Rstudio. For ST, the FCA was weighted by “proportion together”. The data was separated into two categories: one indicating proximity, and the other ape behaviour. For RQ, the FCA was weighted by the presence of the individuals in the field of vision, and two categories were used; proximity, and ape behaviour. Grooming, sex and play were added into one column (“positive behaviour”) because each single behaviour was not observed often enough. In both cases, axes which were positively correlated with “positive” behaviour and proximity and negatively correlated with agonistic behaviour (i.e. aggression and negative food sharing) and non-proximity were added. Axes which were negatively correlated with “positive” behaviour and proximity and positively correlated with agonistic behaviour and non-proximity were multiplied by – 1 before adding them to the other axes. In cases where “positive” behaviour and proximity, or agonistic behaviour and non-proximity were anti-correlated, and both were equally well represented (had a similar $\cos^2$), the axis was excluded to facilitate further interpretation of ST and RQ.

### 2.1.6 The Cooperation Box

#### 2.1.6.1 Experimental setup

The Cooperation Box is a metal, indestructible cage, with a movable tray and an automated peanut-dispenser (see Figure 3 and 4). The peanut-dispenser can be activated from afar with a remotecontroller, thus minimizing interaction with the human observer. When the dispenser is activated, peanuts fall on top of the tray. The chimpanzees can access the peanuts by manipulating the protruding ends of the tray (the handles) on opposite sides of the box. More precisely, only if they lift the tray to the top of the box can they seize the peanuts. The chimpanzees also have to coordinate their movements, because, if they tilt the tray too much, the peanuts spill and remain inaccessible.

The Cooperation Box was designed by E. van Leeuwen and S. Schütte. The cage itself was built by the firm Metallbau & Schlosserei Uwe Metzner. The inside-parts of the box were built by S. Schütte, research coordinator and technical engineer at the comparative cultural psychology group of the MPI-EVA. He kindly helped me throughout the experiment. Changes that I decided to make on the box were all discussed with and implemented by him.

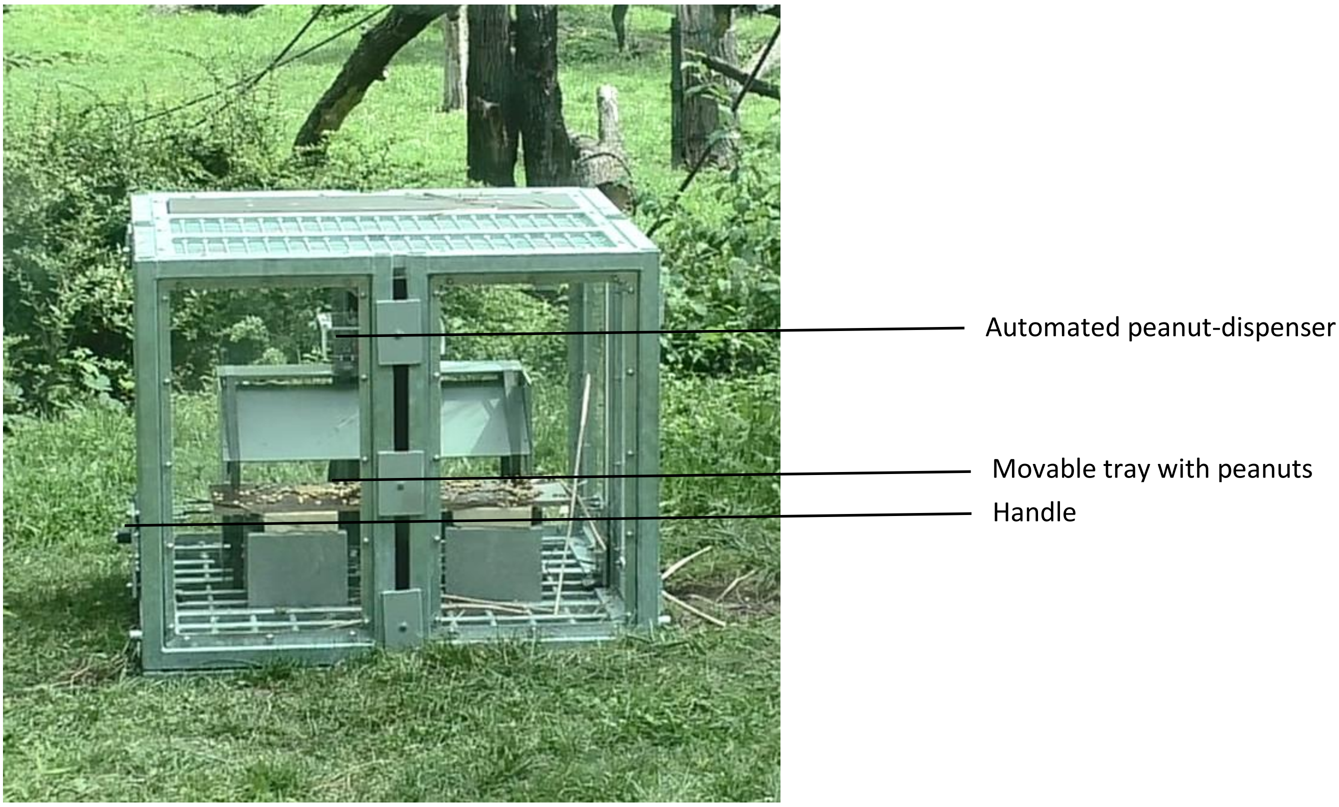

*Figure 3 The Cooperation Box*

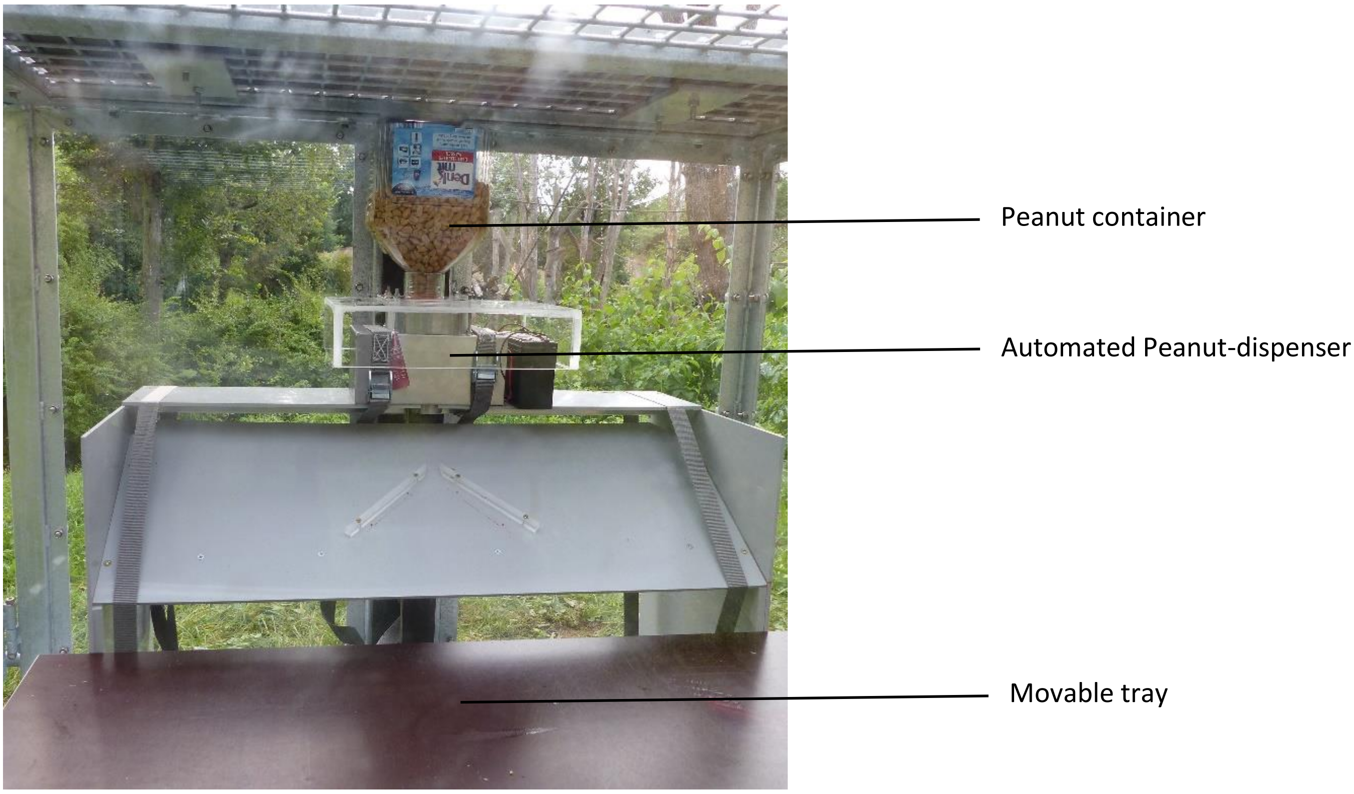

*Figure 4 The Cooperation Box (inside)*

#### 2.1.6.2 Protocol

The chimpanzees were free to access the box whenever and with whom they wanted to. The expected development of the experiment is described in Figure 5. The experiment was supposed to last two hours each day, during which, each time the chimpanzees were successful, the tray would be reloaded with peanuts.

The observed variables should have been:

- The identity of each chimpanzee
- Whether they cooperate or not:
    - Cooperation: both chimpanzees reach for the handles and lift them while the partner is doing the same
    - No cooperation: the chimpanzees do not reach for the handle when the other chimpanzee is next to the second handle, but they both cooperated in the past with other chimpanzees
- Whether they are successful or not:
    - Success: the chimpanzees coordinate their movements and access the peanuts
    - No success: the chimpanzees do not coordinate their movements and the peanuts fall off the tray
- Whether the peanuts where shared or monopolized

- Other interesting observations like:
    - The chimpanzees who are observing the cooperating chimpanzees without participating themselves
    - Communication between two chimpanzees (recruitment of a second chimpanzee)
    - Agonistic or amicable behaviour

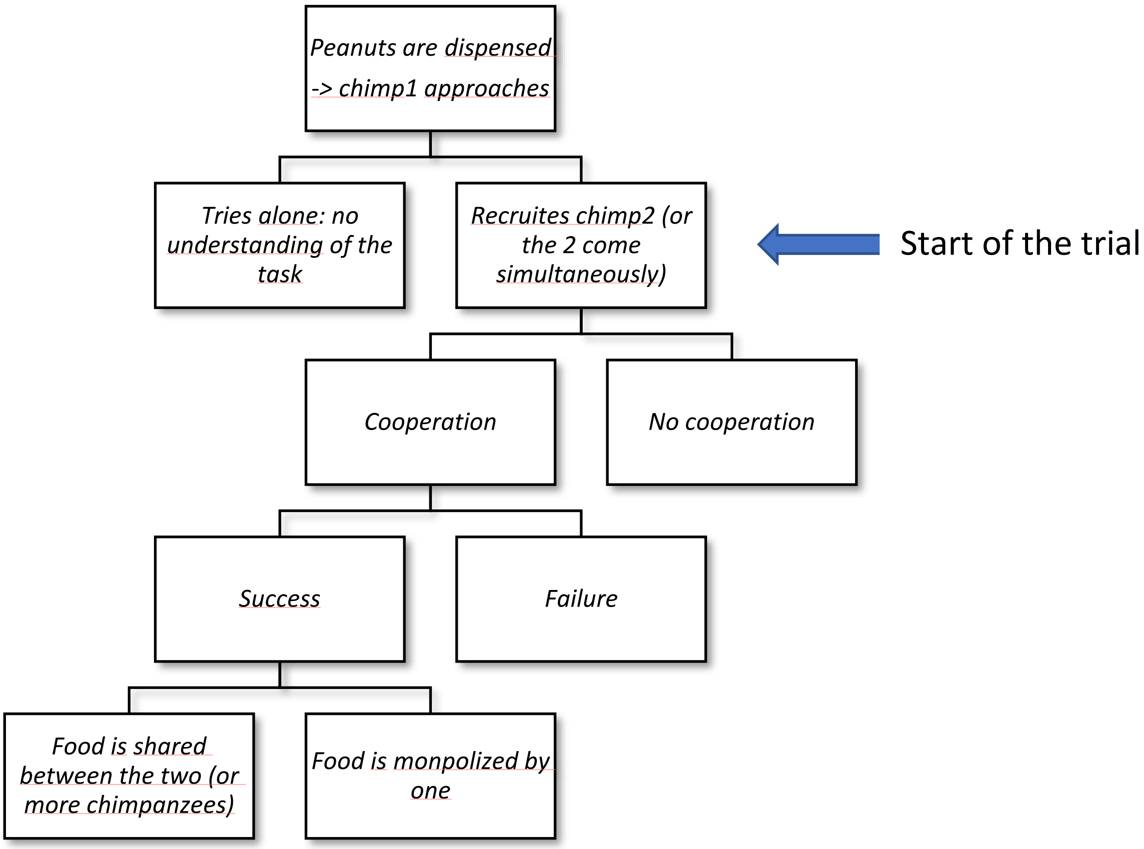

*Figure 5 Main points of the expected development of the experiment*

### 2.1.6.3 The data

The final data were supposed to have 11 variables plus one comment section. The variables are explained in Table 4.

*Table 4 Planned data structure for the "Cooperation Box" experiment*

| **Variable** | **Explanation** |
|---|---|
| **Dyad** | Each dyad of chimpanzees who cooperated (successfully or not) |
| **Cooperation** | If they cooperate or not |
| **Success** | If they cooperate successfully (1) or not (0) |
| **Kinship** | If they are related or not |
| **Rank difference** | The difference in rank |
| **Age difference** | The difference in age |
| **Sex** | Male-male, female-female, male-female dyads |
| **ST** | The social tolerance of the dyad |
| **RQ** | The relationship quality of the dyad |
| **Previous monopolization** | If there was food monopolization in the previous successful attempt of the same dyad |
| **Previous success** | If the dyad cooperated successfully in previous attempts |
| **Comments** | Other interesting observations |

#### 2.1.6.4 Unexpected problems

The construction of the Cooperation Box took longer than expected. The box was ready to be used on the 20th August 2021. Unfortunately, my stay at the WKPRC ended on the 10th of September 2021. Thus, I could only do the experiment for three weeks. Due to bad weather conditions, the chimpanzees did not go to the outside enclosure each day, and I could only do the experiment for 14 days in total, and some days for not more than an hour.

A similar Cooperation Box was placed in the Chimfunshi Wildlife Orphanage in Zambia, in the year 2015 by E. van Leeuwen and S. Schütte. Here the chimpanzees learned within a day how to use the box and managed to cooperate (S. Schütte, personal communication, August 2021). The chimpanzees at the WKPRC being used to doing experiments, it was expected that they would quickly solve the task as well. Therefore, no previous training or teaching was planned. However, the chimpanzees at the WKPRC did not lift the tray, and time was too short to find a way to teach them how to do it.

#### 2.1.6.5 Modifications of the setup

At the first contact with the Cooperation Box, the peanut-dispenser was not yet installed. The Cooperation Box was just a metal box. To catch the chimpanzees' attention and make them approach the box without fear, orange pieces were distributed on top of it. The presence of this metal box did not cause any trouble among the chimpanzees, despite its resemblance with a transportation box, of which the chimpanzees are often scared (D. Geissler, personal communication, August 2021). Two female chimpanzees directly climbed on it without further reticence. No chimpanzees showed any signs of fear, except for one juvenile who started screaming.

Once the peanut-dispenser was installed and the peanuts were laid out on the tray, the chimpanzees were curious and approached the box often. The alpha female (Riet) was the only one to touch the handles a few times, but without moving them. Riet, as well as other chimpanzees tried to use sticks to reach the peanuts. Only one chimpanzee (Changa) was successful doing this. She used a hollow bamboo stick, adjusted the hole on one side of the stick to make it large enough for a peanut to fit, then clamped one peanut inside the hole and pulled it out. However, this stick method was not very handy, and needed a lot of time and patience. Except for Changa, no other chimpanzee managed to eat any peanuts. Therefore different ways to teach them how to use the box were tried during the limited time that was left. All the methods used were non-invasive, and they were about giving hints and making the chimpanzees notice that the tray moved, or about improving their curiosity. Hence, these small changes would not have influenced partner choice itself, and therefore also not the final data.

First, it was decided to paint the handles, which were grey in the beginning, so that they would be more visible for the chimpanzees. Due to the simple fact that red colour was not available anymore, we painted them purple, hoping that it would catch the chimpanzees' attention. A second thing that was tried out at the same time, was lifting the tray to the top of the box, and supporting the handles with sticks (Figure 6). The chimpanzees could hence immediately access the peanuts that were on the tray. The sticks were easy to push away under the handles. As soon as they took away the sticks, the tray would fall down.

Natascha, a female chimpanzee, took away the first stick and then pulled the handle up and down a few times. The second time this end-state-method was tried, Natascha took away the second stick. This time, instead of falling down immediately, the tray got stuck at the top, and Natascha pushed it down. On the 30th of August, Natascha managed to lift the tray on her own (Figure 7). This was however not supposed to happen and was only possible because the tray got stuck on top when she lifted one side. The tray and the peanuts were humid and the peanuts therefore did not fall off the tray immediately. Natascha thus had the time to move to the other side of the box and lift the handle on that side as well. The tray got stuck on top for a few seconds, during which she could access the peanuts before it fell down again. For this not to happen again, the attachment between the handles and the tray were oiled regularly, the screws of the handles were loosened so that the handles would better slide up and down, and the tray was kept dry.

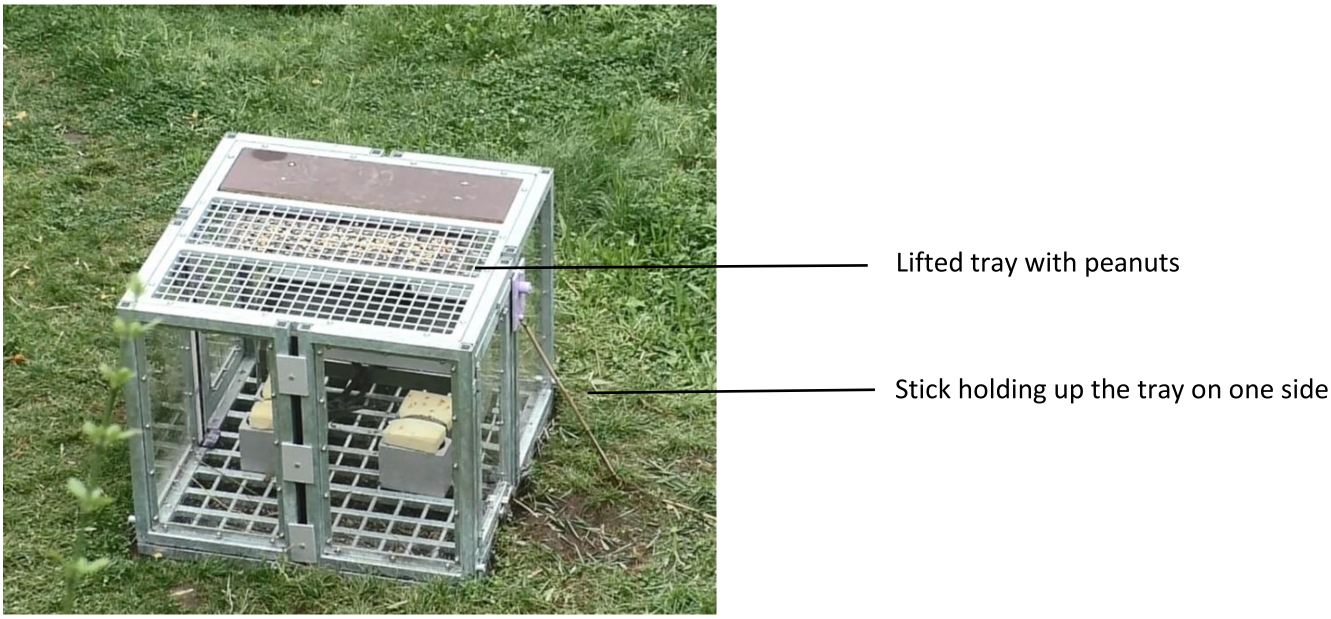

*Figure 6 End-state-method*

*Figure 7 Image from video of Natascha lifting the tray on her own*

Soon the chimpanzees lost interest in the box again and after 5 days it was decided to change the handles to make them bigger, more visible, and easier to grab (Figure 8).

*Figure 8 New handles*

The first day with new handles, we did not use the end-state-method. Instead the tray was down, and bananas were put on the tray with the peanuts for further motivation. Natascha lifted the tray immediately. While she did, Riet was on the other side of the box. She also lifted the handle, but never touched it at the same time as Natascha.

The two following days the end-state-method was tried again, however nothing happened, and the chimpanzees lost more and more interest in the Cooperation Box.

The last two days we tried using banana slices instead of peanuts. The idea behind it was that the banana slices would stick to the tray and would therefore not fall off immediately. This would give the chimpanzees the time to recruit a partner while lifting one side of the tray. The factor “coordination” would be taken out of the equation because the chimpanzees would not have to lift the handles on both sides simultaneously, but would have more time to do so. The new food woke the interest of the chimpanzees again, and more chimpanzees approached the Cooperation Box. However, again, Natascha was the only one to lift the tray on one side. She never showed any signs of communication to recruit a partner. Other chimpanzees started using sticks again to skewer the banana slices.

In conclusion, the Cooperation Box experiment failed. No chimpanzee, except for one female, repeatedly lifted the handles. Therefore, we cannot interpret anything in relation with chimpanzee cooperation.

## 2.2 Part two – Based on the data of Nolte et al. (under review)

In 2019, Nolte, Sterck and van Leeuwen (under review) (NSL) replicated the co-feeding and cooperation tests from Hare *et al.* (2007) with four captive and one semi-wild chimpanzee groups, among which the two chimpanzee groups at the WKPRC. The goal of the replication was to verify Hare and colleague's conclusion that bonobos are more tolerant of co-feeding than chimpanzees, and that when the food reward was highly monopolizable, bonobos would cooperate more often than chimpanzees. Cooperation was studied in a dyadic setting using the loose-string paradigm of Hirata and Fuwa (2007).

The data of this replication study were kindly forwarded, so that we could try to answer our research questions. The main difference between NSL's experiment and the Cooperation Box was that the chimpanzees were not free to choose their partner, and that the dyad was separated from the rest of the group when doing the task. The high number of tested dyads, however, made it possible to see whether social tolerance, rank difference, age difference, sex and kinship influenced the cooperative capacity of a dyad. ST of the dyads was assessed using a "co-feeding" task, in which it was noted whether the dyad would co-feed, whether they would stay close to each other or at a certain distance while retrieving the food, and whether food would be shared or monopolized. Furthermore, NSL collected relationship quality (RQ) data from the two chimpanzee groups at the WKPRC in the same way as was done in 2021. I was kindly given the permission to use this data as well. Therefore, it was also possible to see the effect of RQ on cooperation. Since this RQ information was only available for the two WKPRC groups, only the data for these two chimpanzee groups was analysed.

Chimpanzee and bonobo cooperation will not be compared, since this would not be in line anymore with the initial master's thesis topic. However, comparing which social factors influence cooperation in bonobos and in chimpanzees, could be an interesting topic for future research, allowing to dive even deeper into the evolution of human cooperation.

### 2.2.1 Subjects

The A-chimpanzee group at the WKPRC changed between 2019 and 2021. Two male chimpanzees (Lome and Lobo) were present in 2019 and later left the group. Three other individuals were not yet present, namely Changa, a ten-year-old female, and the two infants Carola and Frank who were not yet born.

16 chimpanzees of the A-chimpanzee group (10 females, 6 males, $M_{\text{age}}$= 25.9) in 89 unique dyads (41 female, 6 male, and 42 mixed dyads) participated in the co-feeding task. Other dyads could not be tested due to high levels of aggression, fear by one partner, or fighting.

The number of A-chimpanzees that participated in the cooperation experiment was a subset of 11 chimpanzees (7 females, 4 males, $M_{\text{age}}$= 30.4) in 53 unique dyads of chimpanzees (19 female, 6 male, and 28 mixed).

The B-chimpanzee group was composed of 6 adult individuals (5 females, 1 male, $M_{\text{age}}$= 35.3) which formed 12 dyads (7 female and 5 mixed) for the co-feeding task. For the cooperation task, only 3 dyads (1 female, 2 mixed) were tested. See Table 2 for further information on the B-chimpanzees. The table does not contain any information on kinship, because none of the B-chimpanzees are related to each other.

*Table 5 Information on the B-chimpanzees at the Wolfgang Köhler Primate Reasearch Centre*

| **Name** | **Sex** | **Date of Birth** | **Rank in Hierarchy** |
|---|---:|---:|---:|
| **Alex** | M | March 10, 2001 | 1 |
| **Daza** | F | 1986 | 6 |
| **Frederike** | F | 1974 | 5 |
| **Hope** | F | December 14, 1990 | 2 |
| **Jeudi** | F | 1966 | 4 |
| **Zira** | F | June 3, 1997 | 3 |

### 2.2.2 Dominance Hierarchy

The dominance hierarchy was assessed using a method developed by NSL. They used a questionnaire with four questions which was answered by four different ape keepers of the Leipzig Zoo. Each question had to be answered for each chimpanzee dyad. The questions were the following: In this dyad,

- Who would take all the food?
- Who would fight back?
- Who would flee?
- Who would leave?

For each questions the chimpanzees would gain points. If a chimpanzee was expected by the ape keepers to take the food or to fight back, he would gain one point. If the chimpanzee was expected to flee or to leave, the opponent chimpanzee would gain one point. When both chimpanzees were thought to react in similar ways, or the ape keepers were not sure about how the chimpanzees would react, none of the chimpanzees received a point. Subsequently, the ranks were calculated with David's score using the function DS with the method Pij from the package EloRating in Rstudio.

### 2.2.3 Experimental setup

The apparatus was a wooden platform of 17 cm x 2.7 m, with three wooden dishes on top, each 17 cm x 27 cm. One dish was placed in the middle of the platform, and two on either side of it. On each side of the platform, a metal loop was fixed through which a rope could be threaded for the loose-string experiment.

For both the co-feeding and the cooperation experiment, the platform was placed one meter outside of the chimpanzee cage. Food was either placed at both ends of the platform, or in the middle of it, depending on the experimental condition. The different conditions are illustrated in Figure 9. In the condition “dispersed divisible”, two dishes, one on each side of the platform, were filled with two 1.5 cm thick pieces of banana. The “clumped-divisible” condition consisted of one single dish in the centre of the platform containing four 1.5 cm thick pieces of banana. Finally, the “clumped” condition was one single dish in the centre of the platform, with two 3 cm thick pieces of banana. For the cooperation task, only the “dispersed divisible” and the “clumped divisible” conditions were tested, as was also the case in Hare *et al.* (2007).

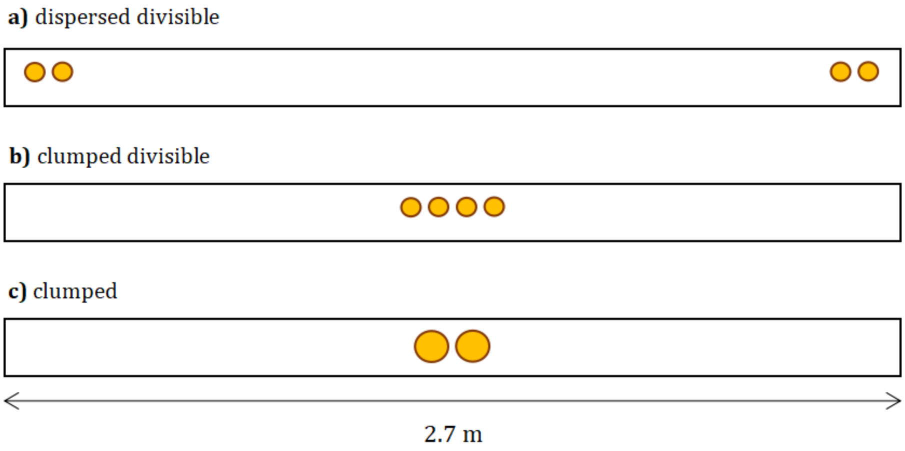

*Figure 9 “Conditions used in the two experiments. Following Hare* et al. *(2007), all three conditions were included in the co-feeding experiment, while only a) and b) were included in the cooperation experiment. Circles symbolize banana pieces of size 1.5 cm in a) and b) and 3 cm in c).” Taken from Nolte* at al. *(under review)*

In the co-feeding task, the chimpanzees did not have to do anything specific. Once the two chimpanzees were present at equal distances right and left of the platform, the platform was pushed towards the mesh by two experimenters. The chimpanzees could then immediately reach the food (Figure 10a).

In the cooperation task, a rope was threaded through the loops, and 20 cm of both ends of the rope were placed inside the chimpanzees’ cage at a distance of 2.7 m. In this task, the chimpanzees had to pull at both ends of the rope simultaneously, or one end of the rope would slide through the loops, and the platform would remain out of reach (Figure 10b).

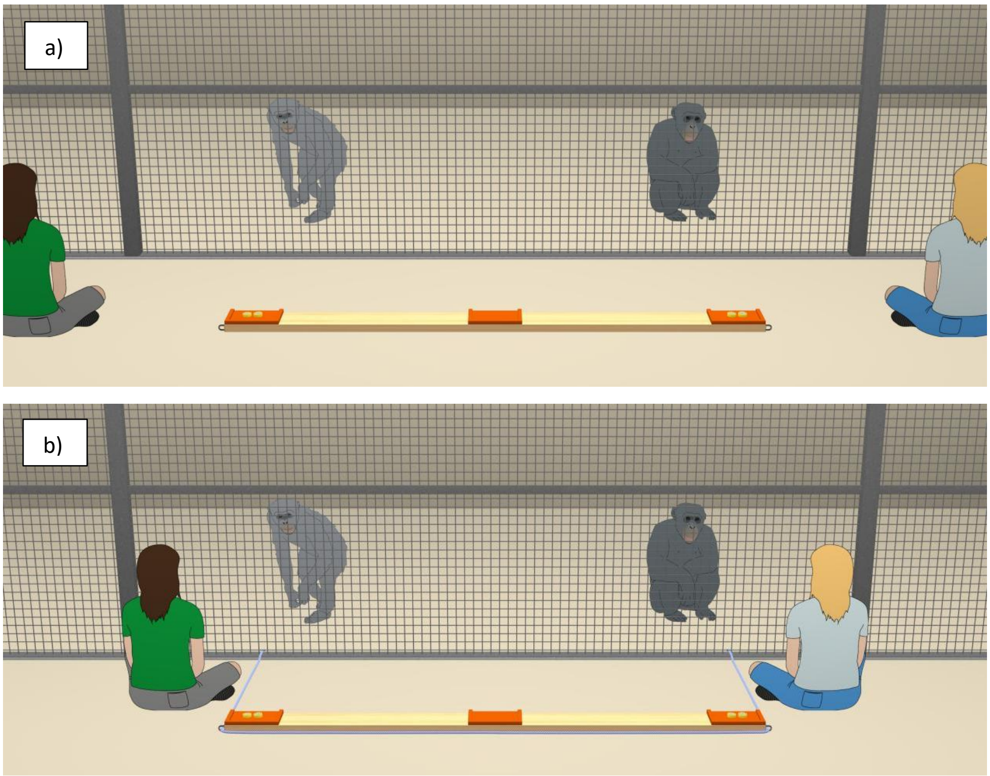

*Figure 10 “In the co-feeding task (a) no rope was used and, instead, two experimenters pushed the platform towards the mesh. In the cooperation task (b), the two apes had to pull at both ends of the rope to pull in the platform.” Taken from Nolte et al., 2021 (under review).*

### 2.2.4 Protocol

#### *2.2.4.1 Co-feeding task*

The first experiment, the co-feeding task, was used to assess social tolerance levels of each dyad. Each dyad participated in six trials, that were all done on the same day (session). Before each trial, the platform was baited and placed at a one-meter distance of the chimpanzee-cage, so that the food remained out of reach until the beginning of the trial. Both chimpanzees were then called by the experimenters to place themselves at equal distances, right and left of the platform, so that both chimpanzees were at the same distance of the food and had equal chances of accessing it. Once the chimpanzees were at their respective starting positions, the platform was pushed towards the mesh by the experimenters, and the chimpanzees could grab the food. A trial ended when the food was consumed, or until one minute had passed.

All sessions were video-recorded, and the number of banana pieces each chimpanzee obtained was noted, as well as playful, socio-sexual, and aggressive interactions that occurred before or during the trials. Interrater reliability was obtained by asking one research assistant who was blind to the procedure and the hypotheses to code 20% of the data. Cohen’s K was used to evaluate if the two raters agreed in their way of interpreting the chimpanzees’ interactions and the trials’ outcome (co-feeding or not). K was higher than 0.7 in each case.

After finishing the co-feeding task, the dyad would move on to the cooperation task.

#### 2.2.4.2 The Cooperation task

Before starting the experimental trials for the cooperation task, each chimpanzee was trained to learn how the loose-string paradigm worked. Only individuals that understood the task were also tested during the experimental trials. Each chimpanzee was trained individually. A longer rope was used, so that one chimpanzee could reach both ends of it at the same time. One dish with two small pieces of banana was placed at either side of the platform. The platform was placed at one meter of the chimpanzee cage. Each chimpanzee participated in a maximum of five training sessions that lasted each 15 minutes at the most. If an individual successfully pulled in the platform on more than six consecutive trials during one session, he or she could move on to the cooperative sessions. 14 A- and 3 B-chimpanzees passed this training. Eventually, due to husbandry reasons, only 11 out of the 14 A-chimpanzees were actually tested.

During the dyadic test procedure, only dyads of which both partners had finalized the co-feeding sessions and had passed the training sessions were tested. During the cooperation task, the rope was threaded through both loops on the platform. The platform was placed at a one-meter distance from the chimpanzee cage, and baited with banana slices. Two experimenters, one on each side of the platform, called the two chimpanzees by their names. Once both apes were in front of their respective experimenter, or after 20 seconds if only one or no chimpanzee approached, the experimenters simultaneously placed their side of the rope inside the cage, at a distance of 2.7 meters of the opposite end of the rope. Two different conditions were compared during this experiment; the dispersed-divisible, and the clumped-divisible (Figure 9), as was also the case in Hare *et al.* (2007).

A trial could end in three different ways. First, the trial could end when the chimpanzees pulled in the platform successfully; second, when they pulled the rope out of either loop, or third, when the chimpanzees did not do anything for more than a minute. Each dyad participated in each condition and 6 trials were conducted per condition. The six trials for one dyad were conducted during one day.

The sessions were video recorded. The same behaviours were coded as during the co-feeding task (number of banana pieces each chimpanzee obtained, playful, socio-sexual and aggressive behaviour), as well as whether the two chimpanzees cooperated by pulling both ends of the rope at the same time, or if one chimpanzee pulled one end while the second chimpanzee held the other end of the rope. Interrater reliability was obtained for each variable (K=0.7 for the interpretation of chimpanzees' behaviour, and K=0.93 for whether the dyads cooperated successfully).

When the co-feeding and the cooperation task were done, each chimpanzee would change partners and do the experiments again. All naive chimpanzees were first paired with another naive partner, to ensure that no partner had a disadvantage due to a lack of experience with the experimental setting. The apes were tested in a dyadic setting in their sleeping rooms.

### 2.2.5 Social tolerance (ST) and relationship quality (RQ)

Social tolerance (ST) was assessed using the co-feeding data (see Table 6 for the structure of the data). The value was calculated in the same manner as in section 2.1.5 (*2.1.5 Statistical analysis for ST and RQ)* by computing a fuzzy correspondence analysis (FCA). In the FCA, the data were not weighted because each dyad participated the same amount of times, and the two categories were whether food was monopolized or not, and the distance between the individuals. The behaviour of the chimpanzees (play, sex, grooming or aggression) was not considered, because of a very small amount of observations. See Appendix 3 for an overview of the data.

*Table 6 Data structure for the co-feeding experiment.*

| Variable | Explanation |
|---|---|
| **Group** | Group A or group B |
| **Dyad** | Each possible dyad of chimpanzee |
| **Monopolization** | Number of times food was monopolized in the dyad, no matter who monopolized the food. |
| **Non-monopolization** | Number of times food was shared between the dyad |
| **Close** | Number of times the individuals were less than 1 meter apart while retrieving the food |
| **Approach** | Number of times the individuals were less than 3 meters apart while retrieving the food |
| **Distance** | Number of times the individuals were more than 3 meters apart until food was retrieved |

To assess the RQ, behavioural observations were conducted every day for two hours, in the same way as in *2.1.4 Relationship quality (RQ),* for a total of 24 hours for the A-chimpanzees and 25 hours for the B-chimpanzees. In short, every 15 minutes, a scan was made of all the chimpanzees who were in proximity of one another (less than one meter apart). Every 5 minutes a scan was made of the chimpanzees that were absent from the field of vision. During the whole two hours all occurrence sampling was done for the behaviours aggression, play, grooming and sex. The duration of the behaviour was not considered, nor was its direction. Positive behaviour patterns (grooming, sex and play) were added into one column called “positive behaviour”, because each single behaviour was not observed often enough to use them separately. See Table 3 for the structure and Appendix 4 for an overview of the RQ data. The value was calculated in the same way as in section 2.1.5. In FCA, the data were weighted by the presence of the individuals in the field of vision, and the two categories were proximity and ape behaviour.

For ST and RQ, in the same way as in *2.1.5 Statistical analysis for social tolerance (ST) and relationship quality (RQ),* axes which were positively correlated to “positive” behaviour (or non-monopolization in the case of ST) and proximity, and negatively correlated with agonistic behaviours (i.e. monopolization for ST) and non-proximity were added. Axes which were negatively correlated to “positive” behaviour (non-monopolization for ST) and proximity, and positively correlated with agonistic behaviour (monopolization for ST) and non-proximity, were multiplied by – 1 before adding them to the other axes. In cases where “positive” behaviour (non-monopolization) and proximity, or agonistic behaviours (monopolization) and non-proximity were anti-correlated, and both were equally well represented (had a similar $\cos^2$), the axis was excluded to facilitate further interpretation of ST and RQ.

### 2.2.6 Data for the cooperative task

The dataset contains the same variables as the ones that should have been collected for the Cooperation Box, except for two variables. First, previous success is not considered, and second, there is no differentiation of the variables “Cooperation” and “Success”. The difference between this dataset and the expected “Cooperation Box” dataset will be further examined in the discussion. The final data are recapitulated in Table 7. The first few lines of the dataset can be found in Appendix 5.

A few problems were encountered in this dataset. The first was the very different number of replicates for certain variables. There were only 6 maternally related dyads out of the 56 tested dyads. There were also only 6 male dyads. Furthermore, in both cases the 6 dyads were in group A and none were in group B.

Another problem was the fact that one dyad had a very high RQ. This dyad was composed of Fraukje, a low-ranking, female chimpanzee, and Frodo, the alpha male. The RQ value was compared with the RQ value collected in 2021. In both cases Fraukje and Frodo have a higher RQ than the average. In the 2021 data however, RQ was half as high as in the NSL data. In the data from 2021, the only dyads which had a higher RQ than Fraukje and Frodo, were the mother-infant dyads Fraukje and Carola and Kisha and Frank, as well as Riet and Tai who had the second highest RQ in 2019. Hence, the RQ value for Fraukje and Frodo does not seem to be wrong, just exceptional. They were therefore kept for the statistical analysis.

*Table 7 Data structure for Nolte* et al.*'s cooperation experiment (under review)*

| Variable | Explanation |
|---|---|
| **Dyad** | Each dyad of chimpanzees who cooperated (successfully or not) |
| **Group** | Group A or group B |
| **Success** | If they cooperate successfully or not |
| **Condition** | The two experimental conditions (clumped-divisible and dispersed-divisible) |
| **Trial** | The experimental trial (there were 6 per dyad and per condition) |
| **Order** | The order in which the two experimental conditions were applied |
| **Maternal relatedness** | If the subjects are maternally related or not |
| **Rank difference** | The difference in rank |
| **Age difference** | The difference in age |
| **Sex** | Male-male, female-female, male-female dyads |
| **ST** | The social tolerance of the dyad |
| **RQ** | The relationship quality of the dyad |
| **Previous monopolization** | If the previous trial was successful and if there was food monopolization |

### 2.2.7 Statistical analyses

In a first step, the continuous variables of the data were scaled and checked for correlations using the package *PerformanceAnalytics* and the method “spearman”. ST was significantly negatively correlated with rank and age difference. However, the correlation was only of -0.16 and -0.21 respectively. Age difference and rank difference were negatively correlated by a factor -0.12. Rank difference and previous monopolization were positively correlated by a factor 0.16. Because these correlations are not very strong it was decided to keep all the variables in the model. See Appendix 6 for the correlation matrix.

The results for the cooperation task were analysed using a generalized linear mixed model (GLMM) with a binomial family and a logit link. The response variable was “success”. Fixed variables were the experimental condition, sex and maternal relatedness as factors, and age difference, rank difference, ST and RQ as continuous variables. Interactions between age difference and maternal relatedness and between rank difference and maternal relatedness were omitted due to the lack of replicates for maternally related dyads. Interactions between ST and rank difference, as well as RQ and rank difference were added to the model. Dominance hierarchy influences many aspects of chimpanzees’ interactions. Therefore we wanted to know whether rank difference could influence some of the previous mentioned effects. Random factors that were included in the model were the trial, the dyad nested in the group as well as the individuals nested in the group.

To solve non-convergence issues, “Bobyqa”, “Nelder_Mead” and “L-BFGS-B” optimizers were implemented in the model. Akaike information criterion (AIC) (a model selection criterion) was used to compare the models with different optimizers. “Bobyqa” and “L-BFGS-B” showed the same AIC which was slightly lower than the one for the “Nelder_Mead” optimizer. It was decided to go on with the “Bobyqa” optimizer. This was not yet enough to solve non-convergence warnings. Thus, the number of adaptive Gauss-Hermite quadrature points (nAGQ) was set to 0. On top of solving any non-convergence issues, nAGQ=0 decreased the computation time considerably. By adding this argument to the model, the random factors were only taken into account partially. The difference with nAGQ=1 (the default) is often fairly small (Stegmann *et al.*, 2018). In our case, the difference was negligible. The difference in AIC was 1.32. Usually, differences in AIC smaller than 2 are considered acceptable (Stegmann *et al.,* 2018). The *drop1* function from the package *stats* was used to check which interactions were non-significant. Both interactions (ST with rank difference and RQ with rank difference) were significant and were thus kept in the model. The *drop1* function also delivered p-values based on Chi-square test. These were used to interpret the results, except for variables which were not calculated by the function because they were integrated in the interactions (ST, RQ and rank difference). For these values the p-value given by the basic *summary* function was used. This p-values in the summary function are computed using z-values. Another variable for which the p-value from the *summary* function were used was sex, because the *drop1* function would not calculate a p-value for each factor (female, male or mixed dyads), but only a general value for the variable.

Because of the skewness in the dataset, it was decided to do a model stability check, which was obtained by rerunning the model with each time one dyad removed from the dataset (with replacement). This was done to see if some dyads influence the results more than others and check whether the estimates of the full model were robust against dyad omissions.

The interactions between continuous variables (ST and rank difference, and RQ and rank difference) were further analysed by doing simple-slopes analyses and calculating Johnson-Neyman intervals. For this, we used the *slim_slopes* function from the package *interactions*. We adjusted for false discovery rates by using the argument *control.fdr = TRUE.*

To see if food monopolization influenced future cooperation, a second GLMM was computed. This time with success as response variable and no other fixed effects than previous monopolization. Only trial and group were kept as random factors because other factors had an effect close to zero, and adding them resulted in a singular fit. Previous monopolization was not included into the previous

GLMM because of the numerous NA-values. Indeed, when there was no cooperation, there could also not be any monopolization. On one hand, creating two different models increases the Type I error rate. On the other, including the variable into the full model led to the deletion of all the NA values, and therefore of most of the data being lost. It was therefore decided to create two distinct models. This model will, based on if a dyad is successful in one trial and whether the food reward was monopolized in this trial, predict if the dyad will be successful in the following trial as well.

Dispersion was checked for both models and no overdispersion was detected.

# 3 Results

## 3.1 Part One – My Experiments and Observations

### 3.1.1 Social tolerance (ST) and relationship quality (RQ) 2021

After calculating the ST and RQ, two different social network structures were obtained (Figure 11). We can see that in both cases there are three different communities in the group. Members of each community share higher ST or RQ with each other than with chimpanzees outside of the community. RQ was especially strong between mother and infants, like between Fraukje (fa) and her infant child Carola (cl), who together with the alpha male Frodo (fo), form their own community. When taking Carola and the other infant Frank (fk) out of the analysis for RQ, there are only two communities left. One community is composed of all the juveniles who often played together, as well as Kisha (ki), the mother of Ohini (oh) and Frank, who was always having an eye on her children. Bambari (ba) and Maja (mj) would also often be seen interacting with the juveniles, while the other adults form their own community.

For ST, the communities are very different. Some individuals were much keener to go inside the Peanut Plot no matter who else was present. For example, Bambari (ba), Frodo (fo), Tai (ta) and Maja (mj) were most often in the plot (green community). Others would go less often inside the Peanut Plot, and when they did, they were always with the same individuals. This would be the case for the pink and blue communities. They avoided the green community, which was much more hectic, with more screaming, aggression and display, especially coming from Frodo and Bambari.

Figure 11 also shows that Individuals who have a high RQ do not necessarily have a high ST. For example, Fraukje and Frodo who have a very high RQ, were almost never together in the Peanut Plot and have therefore a low ST.

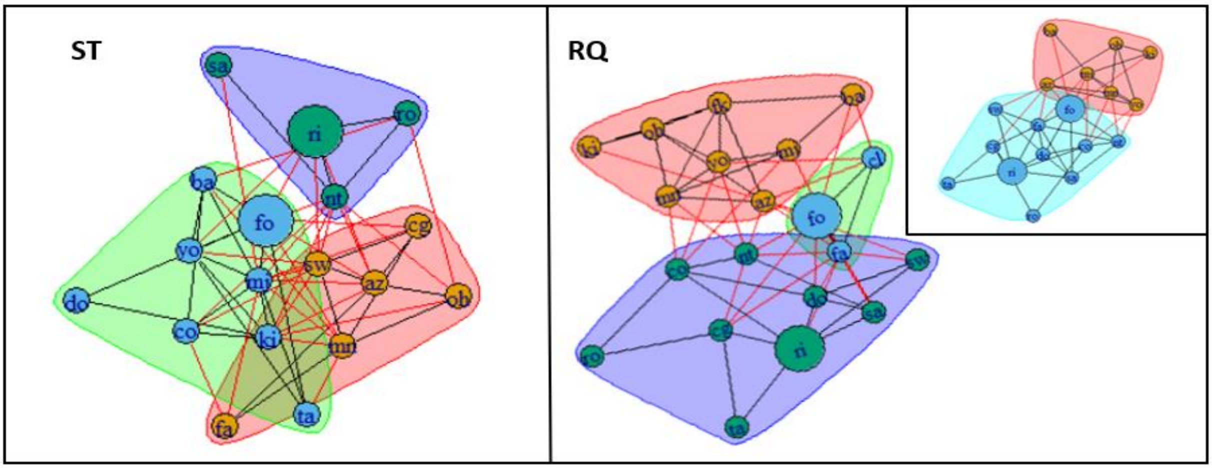

*Figure 11 Social networks for social tolerance (ST) (left) and relationship quality (RQ) (right) for the A-chimpanzee group in 2021. The small network on the top right indicates the network for RQ without the infants Carola (cl) and Frank (fk). The larger*

*circles indicate the alpha male Frodo (fo) and alpha female Riet (ri). Different coloured surfaces indicate different communities inside the chimpanzee group. Individuals inside a community share a stronger ST or RQ with each other than with chimpanzees outside their community. Links indicate all the interactions that were stronger than the average. Weaker interactions were omitted from the figure to avoid overfitting. Black links indicate interactions inside a community, red links indicate interactions between communities. For ST measurements the two infants Carola and Frank were not considered and are therefore not depicted.*

## 3.2 Part two – Based on the data of Nolte *et al.* (under review)

### 3.2.1 Social tolerance (ST) and relationship quality (RQ)

Figure 12 shows the different communities for ST and RQ for group A and B in 2019. We can see for both groups that the communities for ST and RQ are different, as was also observed in 2021 (see section 3.1.1.). For ST, there is a group with Frodo (fo), the alpha male, the three other males of the group Lome (lm), Lobo (lb) and Robert (ro), as well as two very high-ranking females Tai (ta) and Natascha (nt). Sandra (sa) and Fraukje (fa) who are very low ranking are also in this community. A second community is formed by the other females of the group, and a third group is composed of Swela (sw) and her juvenile child Azibo (az). For the RQ in group A, in the small network on the top right corner of Figure 10, we can see that when the dyad Fraukje-Frodo is included in the analysis, they form their own community with the rest of the group forming a second one. This indicates that Fraukje and Frodo share a very high RQ. When this dyad is excluded from the analysis, two equally large communities can be observed. One community is formed around Riet, the alpha female, and includes all the males except Frodo. The second community seems to be composed of individuals who do not share strong relationships with others.

In group B, we can see that ST is higher among the three top ranking individuals Alex (ax) (alpha male), Hope (hp) (alpha female) and Zira (zi). For RQ however, Hope and Alex are in two different communities. Hope has a strong relationship with the second ranking female Zira, while Alex forms a community with the other females.

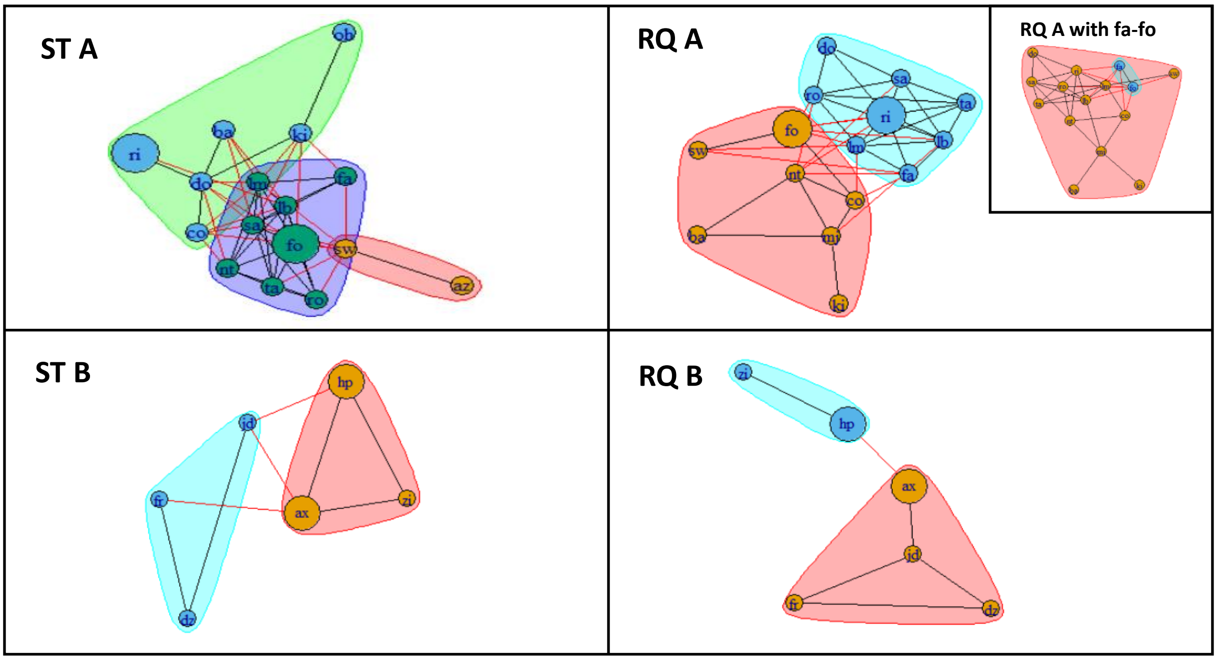

*Figure 12 Social networks for social tolerance (ST) (left) and relationship quality (RQ) (right) for the A-chimpanzee group (top) and the B-group (bottom) in 2019. Only individuals who were tested in the co-feeding test are depicted in the ST network. The juveniles and infants were not considered for the RQ assessment. The dyad Fraukje(fa)-Frodo(fo) was excluded from the RQ network for the A-chimpanzees. They are included however in the small network on the top right. The larger circles indicate the alpha male Frodo (fo) and alpha female Riet (ri). Different coloured surfaces indicate different communities inside the chimpanzee group. Individuals inside a community share stronger ST or RQ with each other than with members of other communities. Links indicate all the interactions that were stronger than the average. Weaker interactions were omitted from the figure to avoid overfitting. Black links indicate interactions inside a community, red links indicate interactions between communities.*

### 3.2.2 Factors influencing cooperation

The generalized linear mixed model revealed four significant effects (Table 8). These were the effect of the experimental condition (p-val < 2.2e-16), ST (p-val = 0.049), the interaction between ST and rank difference (p-val = 0.015), and the interaction between RQ and rank difference (p-val = 0.005). The intercept of the model was also significant, which means that when we use the clumped-divisible condition, when only females cooperate, and all the continuous variables are 0 (which corresponds to their mean), the probability of success is invlogit(-2.77) = 0.059. See Appendix 7 for the whole summary of the GLMM, and Appendix 8 for the output of the *drop1* function with which the p-values were calculated.

*Table 8 Summary of the generalized linear mixed model. Estimates were computed using the logit link and need to be backtransformed for interpretation. P-values were calculated using Chi-square test for condition, age difference, ST:rank_difference and RQ:rank_difference. The p-values for the intercept, maternal relatedness, ST, RQ, rank difference and sex were calculated using z-score. See Appendix 7 for the whole summary of the GLMM.*

| Factor | Estimate | Std. Error | P-val |
|---|---|---|---|
| **Intercept** | -2.77028 | 0.98809 | **0.00505 **** |
| **Condition (disp.div)** | 3.37610 | 0.28254 | **<2.2e-16 ***** |
| **Maternal relatedness (1)** | 0.46276 | 1.11025 | 0.701299 |
| **Age difference** | -0.53749 | 0.34303 | 0.122842 |
| **ST** | 0.79082 | 0.40156 | **0.0489 *** |
| **RQ** | -0.36676 | 0.56145 | 0.51360 |
| **Rank difference** | -0.04363 | 0.42789 | 0.91878 |
| **Sex (female-male)** | 0.02543 | 0.94788 | 0.97860 |
| **Sex (male-male)** | 1.96979 | 1.78706 | 0.27035 |
| **ST:rank_difference** | 1.07736 | 0.46630 | **0.014784 *** |
| **RQ:rank_difference** | 0.73161 | 0.30090 | **0.004524 **** |

The effect of the condition is very clear (Figure 13) (p-val < 2.2e-16). In the dispersed-divisible condition chimpanzees would cooperate about 29 times more often than in the clumped-divisible condition.

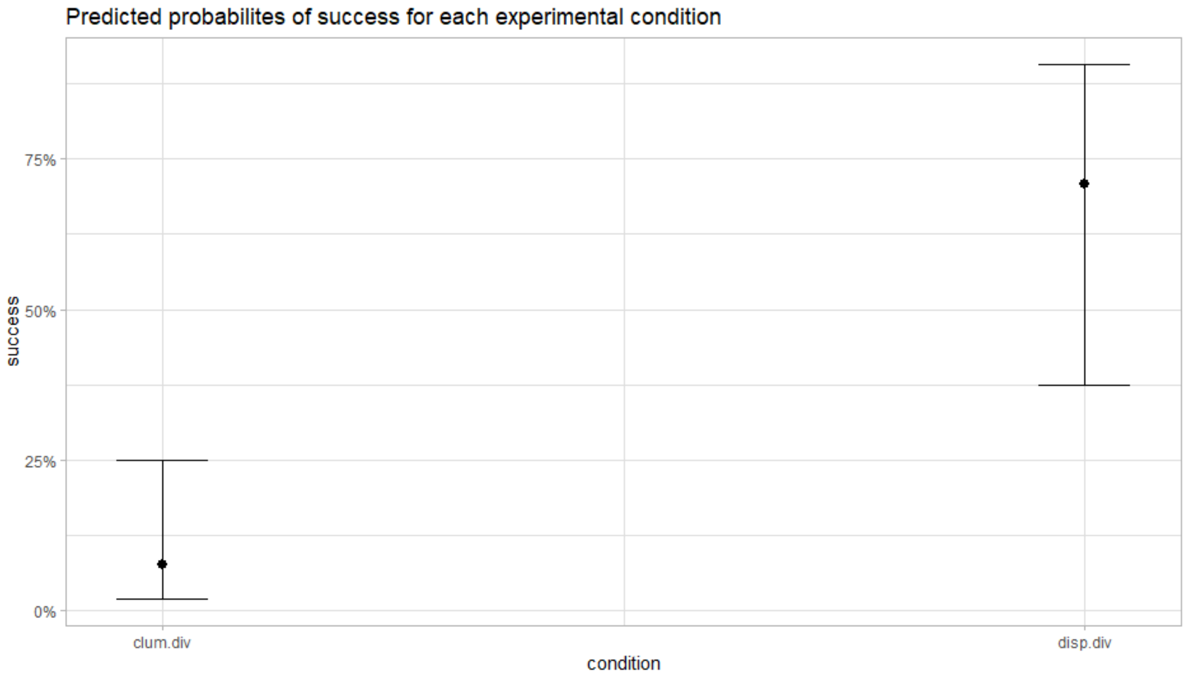

*Figure 13 Predicted probabilities of success for each experimental condition. The two conditions are clumped-divisible (clum.div) and dispersed-divisible (disp.div). For clumped-divisible one dish was placed in the middle of the platform with four 1.5 cm thick banana slices. For dispersed-divisible two dishes were placed on opposite ends of the platform and each was filled with two 1.5 cm thick banana slices. Error bars represent 95% confidence intervals. Effects were calculated with the function ggeffect from the package ggeffect, which averages the effects of the variable of interest over the levels of the other variables.*

The *summary* of the model indicates a significant effect of ST. To check if this variable has indeed a significant effect on its own, on top of the effect of the interaction between ST and rank difference, the model is re-run without the interaction. The new model gives a p-value of 0.094 using Chi-square and an estimate of 0.70178 ± 0.41177 (Figure 14). Hence, the effect is not significant but remains close to the 0.05 threshold.

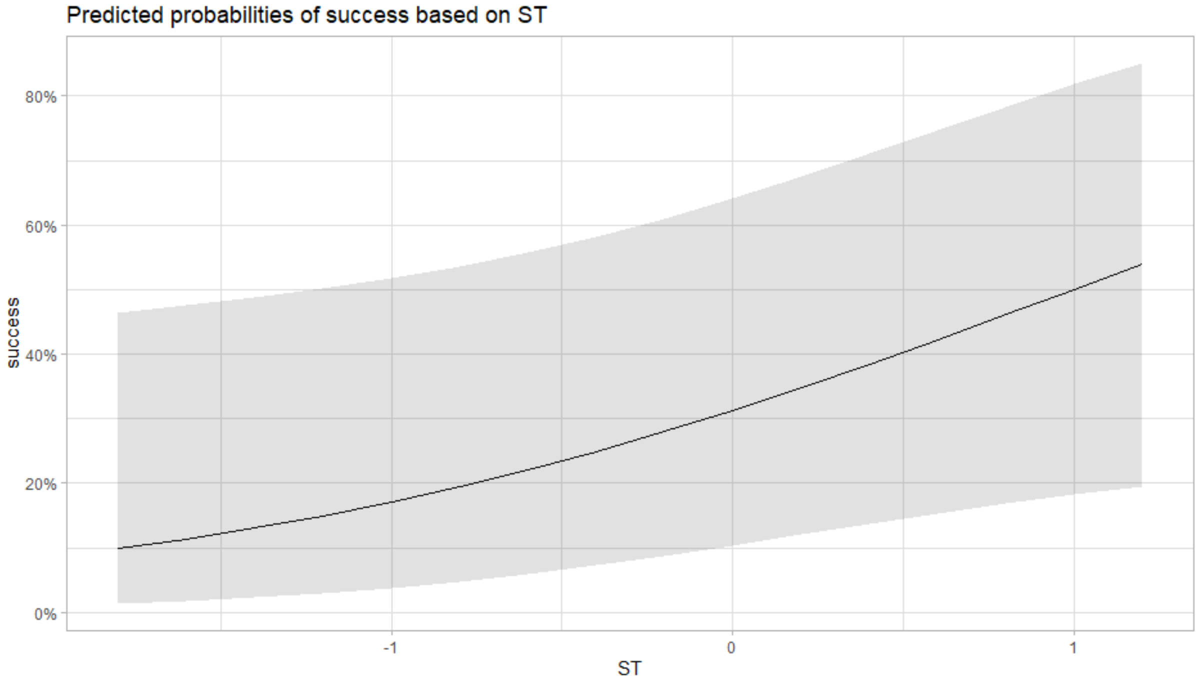

*Figure 14 Predicted probabilities of success based on social tolerance (ST). The grey area represents 95% confidence intervals. Probabilities of success were calculated with the function ggeffect from the package ggeffect, which averages the effects of the variable of interest over the levels of the other variables.*

Furthermore, ST interacts with rank difference (p-val = 0.015). Figure 15 splits the data into three approximately equal sized groups; the lower, middle, and upper thirds of the observed values for rank difference. For the middle third, success increases linearly with social tolerance. For the upper third, success increases almost exponentially with social tolerance. On the contrary, for the lower third, success decreases when social tolerance increases. We can also see in Figure 15 that when ST is low, there is more cooperation when rank difference is low than when it is high. The opposite is true when ST is high. To understand this interaction in more detail, a simple slopes analysis was done and Johnson-Neyman intervals were calculated (Figure 16).

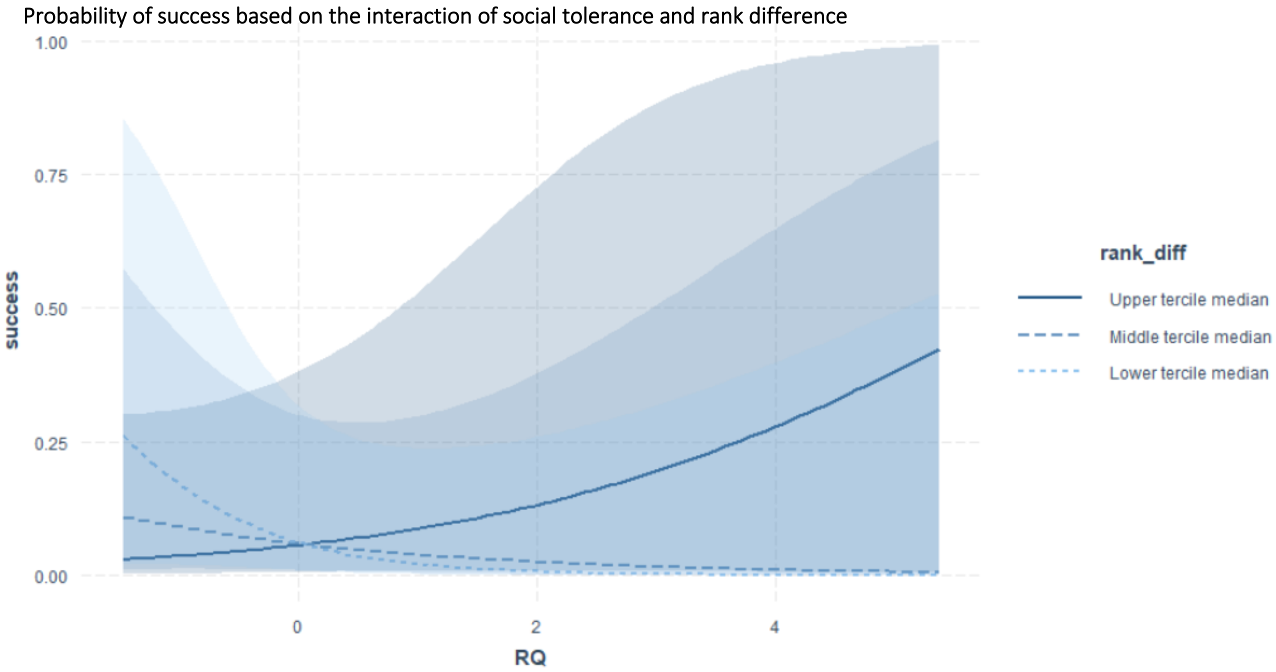

*Figure 15 Interaction of social tolerance (ST) and rank difference (rank_diff). Upper, middle, and lower tercile median indicate the upper, middle, and lower third of the observed values for rank difference respectively. Shaded areas indicate 95% confidence intervals. The y-axis indicates the probability of success.*

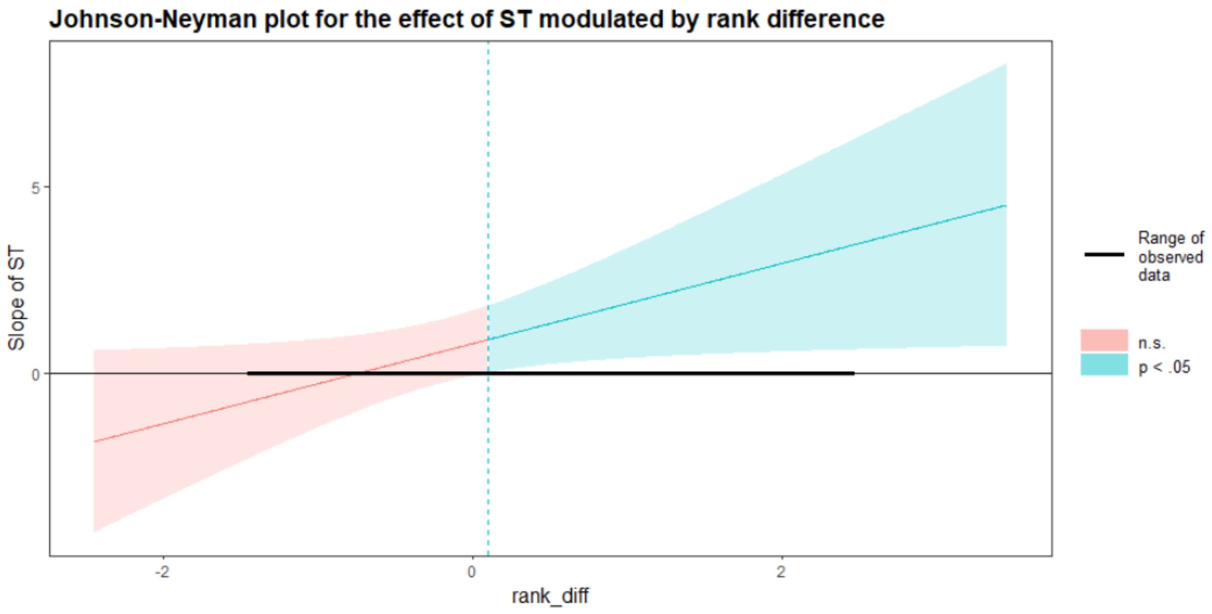

*Figure 16 Johnson-Neyman plot for the effect of social tolerance (ST) modulated by rank difference (rank_diff). Blue indicates the range for which the slope of ST is significant, and red the range for which the slope of ST is non-significant. The black line indicates the range of the observed values for rank difference. The dotted line indicates the rank difference value for which ST starts having a significant effect.*

When rank differences is higher than 0.1, the p-value is smaller than 0.05. This means that ST has only a positive effect on cooperation when rank difference is higher than 0.1. Since all the continuous variables were scaled, a value of 0.1 represents a rank difference slightly higher than the mean rank difference of the group. Furthermore, we can see that the slope of ST increases when rank difference increases, meaning that the effect of ST becomes larger when rank difference is larger, too. On the other hand, when rank difference is smaller than 0.1, the slope of ST is not significant. Hence, ST might not have an effect on cooperation anymore when rank difference is low, although, it seems that the effect of ST remains positive until rank difference is approximately -0.7. See Appendix 9 for details of the slim-slopes and Johnson-Neyman-interval analyses.

Next, slim-slopes and Johnson-Neyman-interval analyses were done for rank difference modulated by ST. Figure 17 indicates that when ST increases, the slope of rank difference increases, too. Because the p-value for rank difference is not significant we cannot say that rank has an effect on cooperation. We can observe however that the effect of rank difference seems to be negative until ST reaches approximately 0. Hence, ST and rank difference modulate each other's effects on cooperation.

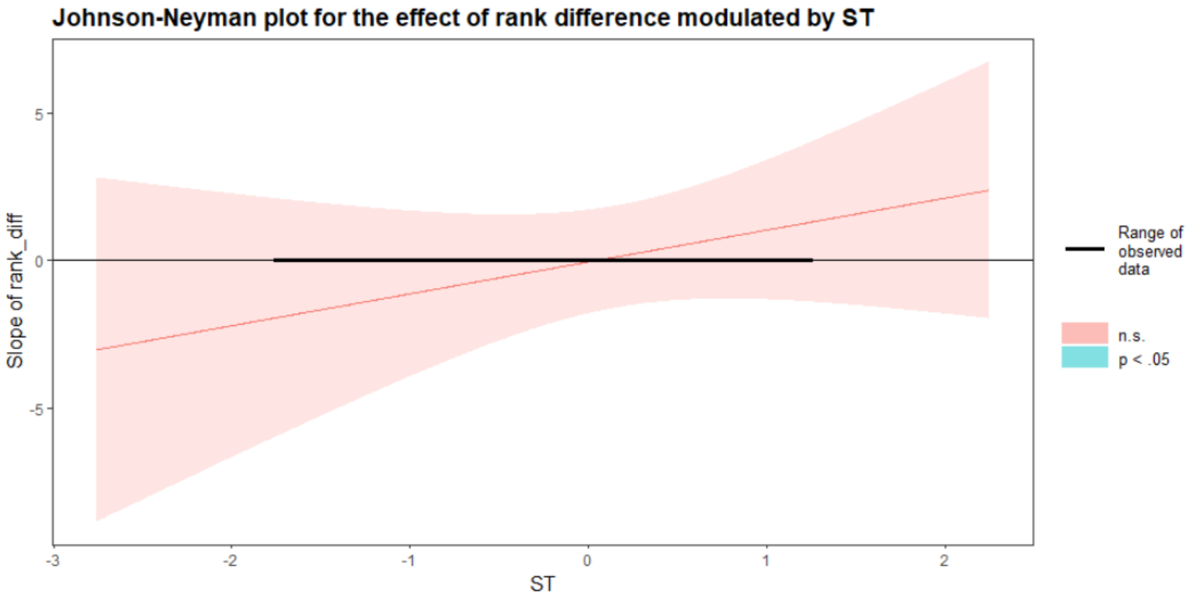

*Figure 17 Johnson-Neyman plot for the effect of rank difference (rank_diff) modulated by social tolerance (ST). Red shaded area indicates that the slope of rank difference is not significant. The black line indicates the range of observed values for ST.*

The same is true for the interaction between RQ and rank difference. In this case, both variables have a non-significant effect on cooperation. Both variables modulate each other's effect on cooperation, though (p-val = 0.0045). We can see on Figure 16 that for the middle and the lower third of the rank difference, success decreases when RQ increases. For the higher third of the rank difference, success increases with RQ.

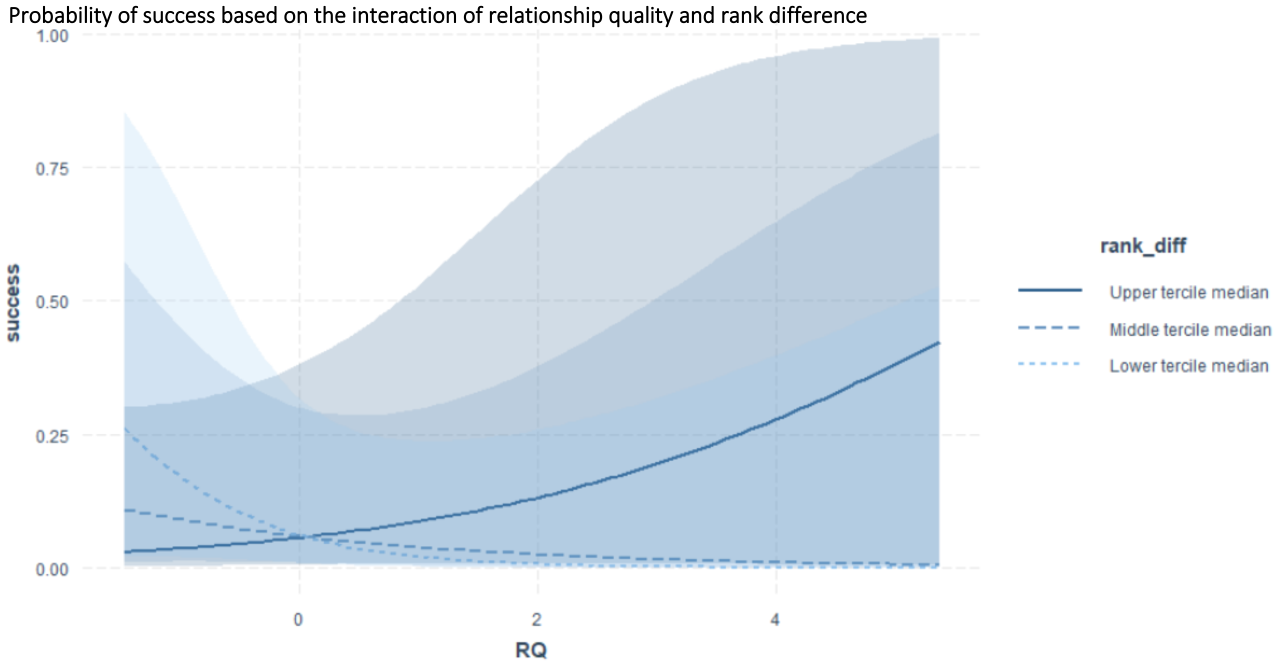

*Figure 18 Interaction between relationship quality (RQ) and rank difference (rank_diff). Upper, middle and lower tercile medians indicate the upper, middle, and lower third of the observed values of the rank difference respectively. Shaded areas indicate 95% confidence intervals. The y-axis indicates the probability of success.*

We know that RQ is very much influenced by the outlier-dyad Fraukje-Frodo. The model was therefore re-run without this dyad and indeed the interaction between RQ and rank difference was no longer significant (p-val = 0.66). The other before mentioned variables however stayed significant, except for ST which had a p-value of 0.061 instead of 0.049. The p-values and estimates for the interaction between ST and rank difference and for the experimental condition remained approximately the same. For a summary of this new model, please refer to Appendix 11.

To check whether other dyads influenced the model in such a strong manner, likelihood ratio tests (LRT) were done on each variable with each time one dyad omitted. The only strong effect observed was indeed the effect of Fraukje and Frodo on the interaction of RQ with rank difference. LRT yielded 0.661 in this case, while for all the other dyads the value remained lower than 0.05, confirming that the interaction between RQ and rank difference is only significant when the dyad Fraukje-Frodo is considered. For all the other variables no dyad stood out.

Next, a model stability check was done on the whole model where the model was reiterated with each time another dyad omitted. This gave us the estimate range for each variable (Figure 19).

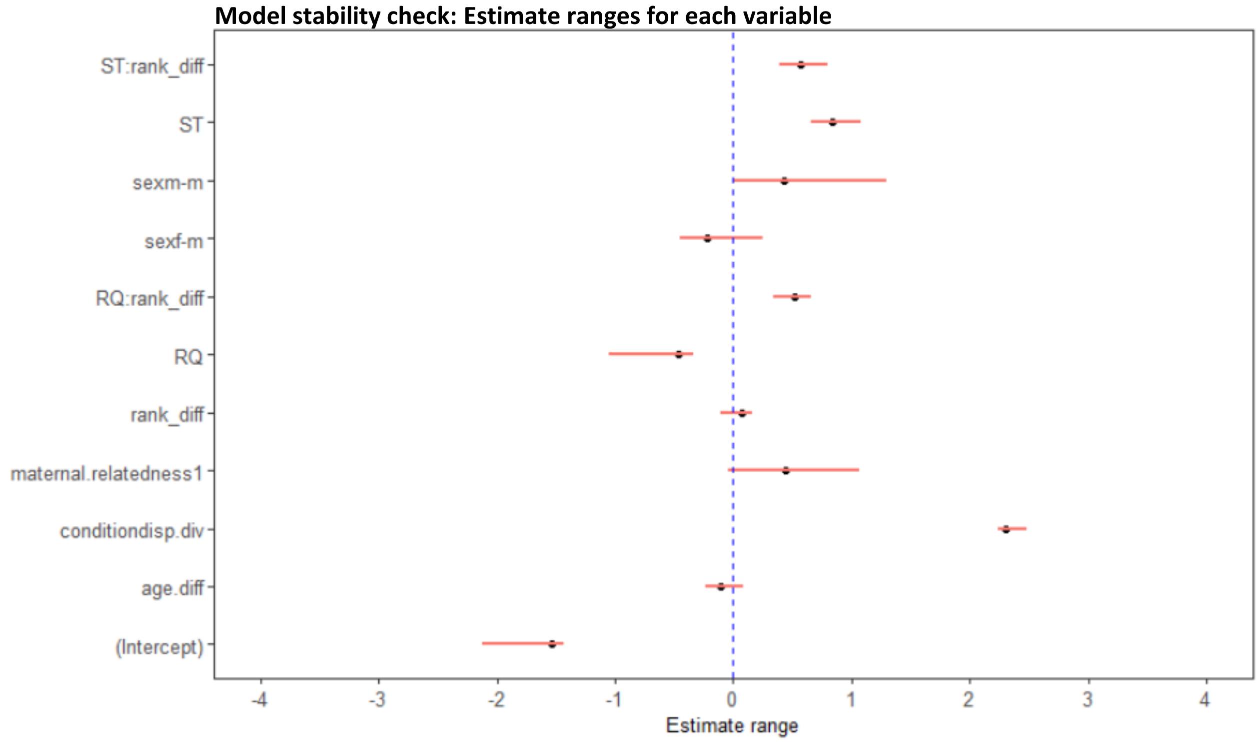

*Figure 19 Model stability. Black dots show the estimates for each variable with the full model. Red bars indicate the range of estimates obtained when reiterating the model with each time another dyad omitted. A larger red bar means that estimates vary a lot based on the dyads that are included or not. Small bars mean that the model is stable for this variable.*

We can see that the model seems to be relatively stable for the experimental condition, ST, the interaction between ST and rank difference, and the interaction between RQ and rank difference. These are also the variables with a significant p-value. They all have positive estimates. For ST and the experimental condition, this means that they influence cooperation positively, with the experimental condition having the strongest effect. For the interactions this means that when both variables increase, cooperation increases, too. The estimates for age and rank difference are stable as well, but close to zero. The estimates for maternal relatedness and sex are very unstable. They vary a lot depending on the dyads that are included in the model. These are also the variables that are badly represented in the dataset.

Because maternal relatedness and sex are badly represented, we cannot say whether they have a significant effect on cooperation. Nonetheless, in the following parts, some descriptive statistics are presented (Figure 20 and 21).

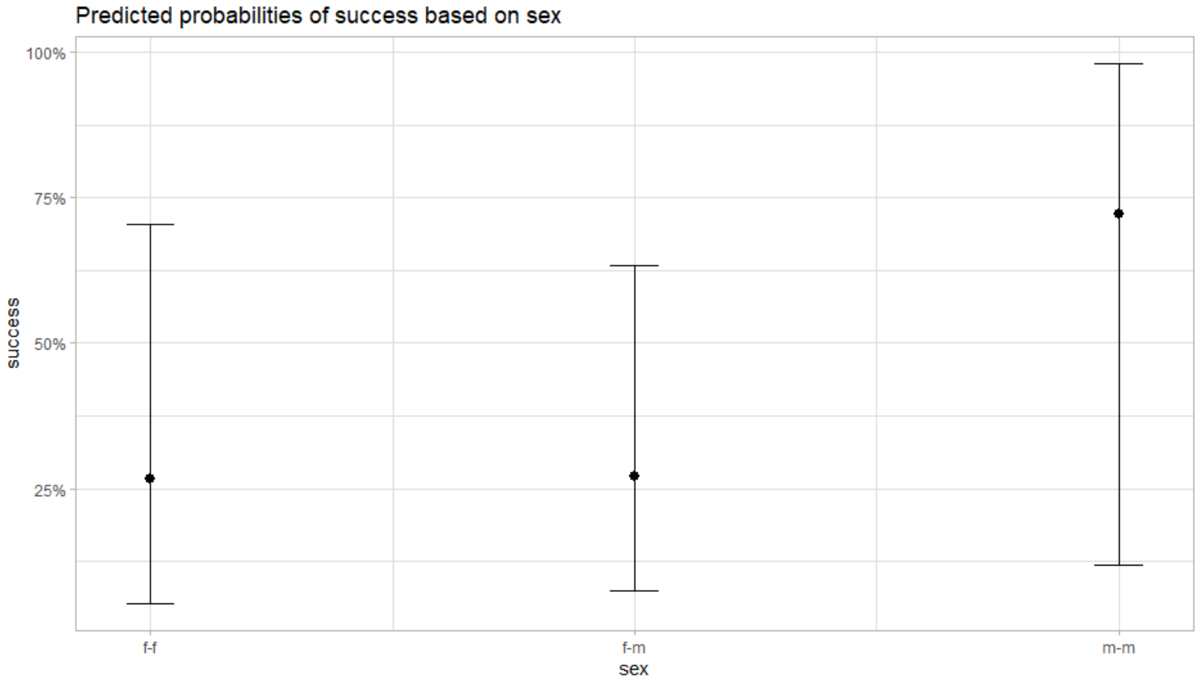

*Figure 20 Predicted probabilities of success based on sex. Effects were calculated with the function ggeffect from the package ggeffect, which averages the effects of the variable of interest over the levels of the other variables. Error bars represent 95% confidence intervals. f-f are female dyads, f-m are mixed dyads, and m-m are male dyads.*

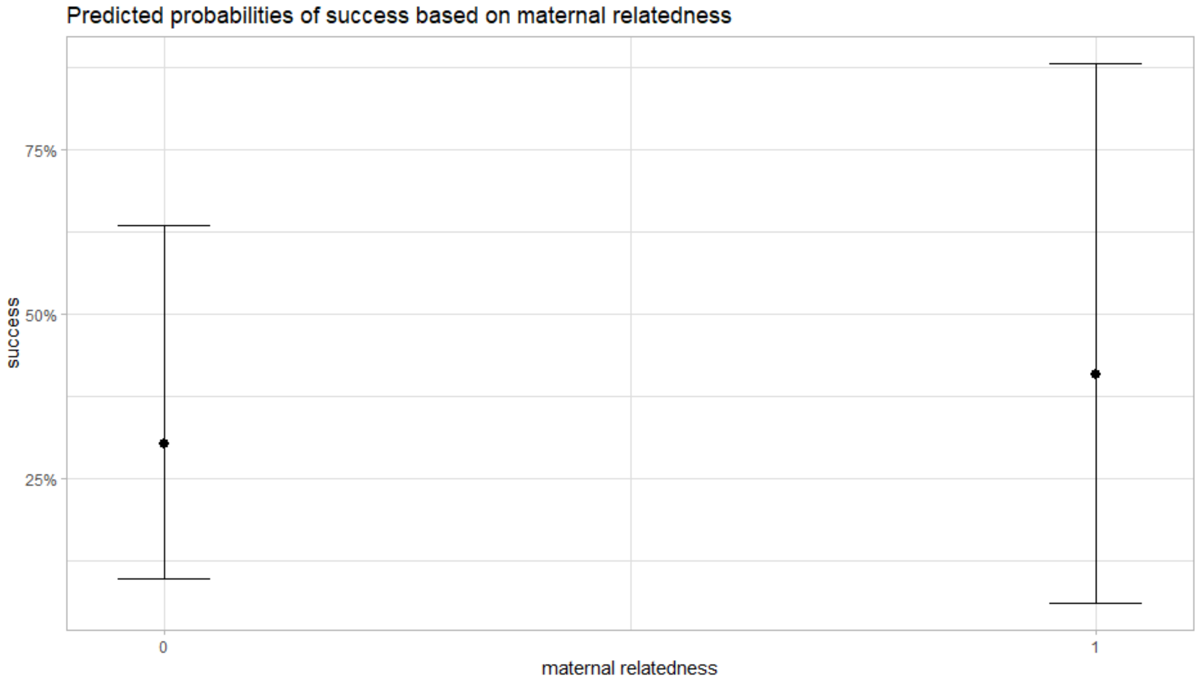

*Figure 21 Predicted probabilities of success based on maternal relatedness. Effects were calculated with the function ggeffect from the package ggeffect, which averages the effects of the variable of interest over the levels of the other variables. Error bars represent 95% confidence intervals. 1 corresponds to maternally related individuals. 0 corresponds to non-related individuals.*

Figure 20 shows that there is a tendency for males to cooperate more than female and mixed dyads. Figure 21 indicates that maternally related individuals seem to cooperate slightly more than non-related individuals. The confidence intervals are however very large, and p-values are not significant (p-val (Chisq) = 0.322 and 0.702 for sex and maternal relatedness respectively). The observed tendencies could be due to pure chance.

### 3.2.3 The effect of previous monopolization on success

The GLMM with only the effect of the monopolization of the food reward in the previous trial indicated that monopolization had a very significant (p-val = 3.08e-10) negative effect on success. The estimate was -2.3551 ± 0.3741. The predicted probabilities of success based on monopolization can be seen in Figure 22. The summary of the generalized linear mixed model can be found in Appendix 12.

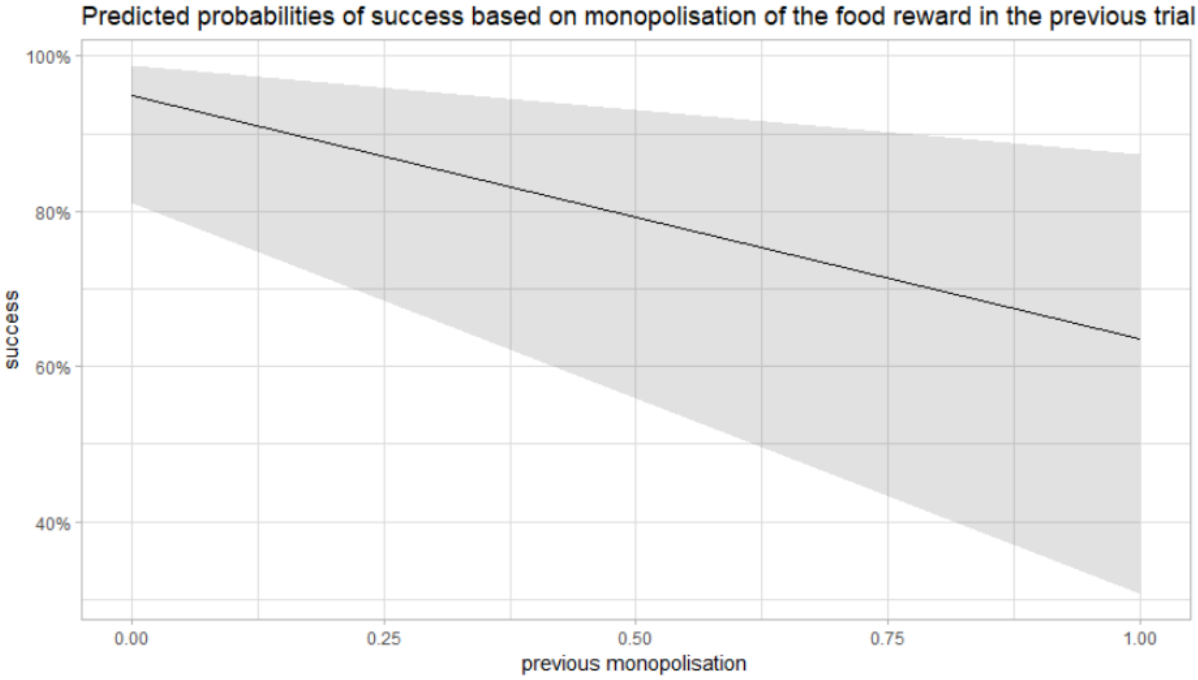

*Figure 22 Predicted probabilites of success based monopolization of the food reward in the previous trial. Shaded area represents 95% conifdence intervals. Effects were calculated with the function ggeffect from the package ggeffect, which averages the effects of the variable of interested over the levels of the other variables*

# 4 Discussion

## 4.1 Recapitulating the aim of the study

The aim of this research project was to identify the factors that influence partner choice for a coordinated cooperation problem in chimpanzees. The factors expected to influence partner choice were social tolerance (ST), relationship quality (RQ), rank difference, age difference, maternal relatedness, sex and monopolization of the food reward, as well as the interactions between maternal relatedness and rank, and maternal relatedness and age difference. The hypotheses were the following:

1. ST, RQ and maternal relatedness influence cooperation positively.
2. A high difference in age and rank, as well as monopolization in previous trials influence cooperation negatively.
3. Male dyads cooperate more frequently than female or mixed dyads.
4. Maternally related individuals cooperate more than non-related dyads, no matter their rank or age difference.

Moreover, because we know that the dominance hierarchy influences so many aspects of chimpanzees' lives, we wanted to know whether rank difference could influence some of the previous mentioned effects. We therefore decided to also test the interaction between ST and rank difference and between RQ and rank difference.

In the following section we will first discuss whether the Peanut Plot is a good way to assess ST. Then we will try to analyse why the Cooperation Box experiment did not work, and what its differences are with the NSL experiment. In the second part we will discuss and interpret the results from the NSL experiment and try to draw conclusions on which factors influence cooperation and partner choice in a cooperative task in chimpanzees.

## 4.2 Part one – My Experiments and Observations

### 4.2.1 Social tolerance (ST) and relationship quality (RQ)

We observed that group A is composed of different communities whose members share higher ST or RQ with each other than with chimpanzees outside their community. The communities are different depending on whether we look at ST or RQ. These results should have been used in a generalized linear mixed model with the results of the Cooperation Box experiment, to see whether ST and RQ influence partner choice for a cooperative and coordinated task. This was not possible, as will be discussed in the next section (section 4.2.2*).*

It is necessary to point out some critiques about the method used to assess ST. ST for each dyad was evaluated using the Peanut Plot experiment. This experiment has been used in previous studies to assess ST at the group level (Cronin *et al.*, 2015; van Leeuwen *et al.*, 2021). Only one study has used this method to assess dyadic ST so far (Vermeulen *et al.* (in preparation)). When using this group-level method for extracting dyadic ST some things need to be noticed. Individuals who are often together in the Peanut Plot without showing any aggression towards each other have a high ST, while individuals who are never seen together or show a lot of aggression towards each other, are said to have a low ST. The problem is that the beginning of each session was always very hectic with a lot of screaming, display and aggression. During this time, the same community, composed of Frodo (the alpha male) and Tai (the second ranking female) among others, were always in the plot. Once these individuals had eaten enough peanuts and calmed down or left the plot, other individuals, and other communities of chimpanzees would enter the plot. It is therefore possible that some chimpanzees who entered the plot once the situation in and around the plot was calmer, were never seen with the chimpanzees who were there in the beginning. This behaviour would result in our analysis in a low dyadic ST. Yet, the fact that these chimpanzees were never together in the plot could be due to one of the two chimpanzees not wanting to enter the plot while the situation was so hectic. For example, Fraukje and Frodo had a high RQ but a low ST. We could wonder whether Fraukje never entered the plot when Frodo was there because they had indeed a low ST or because this also corresponded to situations when other chimpanzees were screaming and being aggressive. Especially with her baby Carola, Fraukje would probably avoid these risky situations. Fraukje and Frodo would in this case have a low ST not because they are not tolerant of each other, but because the situation, and the presence of third parties, impeded them from ever being together in the plot. It is therefore possible with the Peanut Plot method to mix up low dyadic ST with shyness or carefulness of one of the two individuals forming a dyad.

The Peanut Plot nevertheless, has the advantage of being done in a social setting. As discussed in the introduction, experiments in social settings have the advantage of better assessing how behaviours would develop in a natural environment (Cronin *et al.,* 2017). Moreover, chimpanzees are social species, and the presence of others can strongly influence their behaviour. A solution to use the Peanut Plot and excluding the possibility of confusing low ST with shyness, could be to conduct the Peanut Plot experiment on consecutive days, and not leave a day out between two sessions. Conducting the experiment on multiple consecutive days might lead to the chimpanzees getting used to the presence of the peanuts in their enclosure. We could argue that this has two possible effects. The first effect is the one that made us decide to do the experiment every second day. It consists in that the chimpanzees could lose interest in the peanuts, and stop going near the plot straight after entering the enclosure.

However, the chimpanzees always seemed excited to have peanuts, even when the experiment was done on consecutive days. Hence, maybe, if they get used to the peanuts, they would still go to the Peanut Plot, but remain calmer in the beginning of the experiment, hence allowing also shyer individuals to come near the resource.

Another option to measure dyadic ST might be the co-feeding method used by NSL. In this method only two individuals are together in the experiment room and it is observed whether they co-feed or not, whether food is monopolized, and if they remain close to each other while feeding. The conditions are more controlled in this experiment and it is possible to assess only dyadic ST without the effect of third parties. This method on the other hand, has the problem, that not all the dyads can be tested, due to husbandry reasons, for instance, some chimpanzees not wanting to be together in the same room, or just not wanting to participate in the experiment. The dyad Fraukje-Frodo had a low ST with both the Peanut Plot and the co-feeding task. In general however, ST varied a lot and with no specific pattern between the two methods. This was however also due to the fact that the Peanut Plot was used in 2021 and the co-feeding method in 2019. First, the group changed a lot in these two years, and second, some chimpanzees were omitted from the ST measurement in 2019 due to husbandry reasons. We could therefore not compare the two methods.

### 4.2.2 The Cooperation Box

Initially it was planned to test chimpanzee partner choice with the Cooperation Box in their social environment. The aim was to observe how chimpanzees choose their partner when they are free to choose among many individuals and while being in their social group. By studying them in a social setting we would have been sure that this was their “natural” way of choosing a partner. Nevertheless, the experiment did not work. No chimpanzees, except for two female chimpanzees, ever lifted the handles of the Cooperation Box. Only one of them did it repeatedly. No chimpanzees ever cooperated to lift the tray. Therefore, we cannot interpret anything about cooperation and partner choice.

A similar Cooperation Box was installed in one of the chimpanzee groups at the Chimfunshi Wildlife Orphanage in Zambia in 2015. Here, chimpanzees started retrieving the peanuts from the box within one day (S. Schütte, personal communication, August 2021). This made us wonder what the difference between the two chimpanzee groups was which caused the difference in their capacity of using the Cooperation Box. The chimpanzees at the WKPRC are used to doing experiments and solving tricky tasks. Therefore, we excluded the idea that the chimpanzees at the WKPRC might not be intelligent or capable enough to understand how the Cooperation Box worked. We hypothesise that the difference between the two chimpanzee groups was their motivation. The chimpanzees at the WKPRC receive food throughout the day, approximately every two hours. Seeing that they were not able to access the peanuts, they quickly lost interest in trying to solve the task, because they knew that they would soon receive food anyway. Out of obvious ethical reasons, giving the chimpanzees less food, to see if they would then be more motivated to solve the task, was not possible. This could explain why in the wildlife sanctuary Chimfunshi, the chimpanzees found out quickly how the Cooperation Box worked. In this sanctuary, they receive less food than at the WKPRC (S. Schütte, personal communication, August 2021), and could therefore be more motivated to solve the Cooperation Box task and to cooperate to access the food.

For a future use of the Cooperation Box, it would be interesting to try to rebuild the Cooperation Box, or a similar mechanism inside the experiment rooms of the chimpanzees at the WKPRC. Here, they could first be taught individually, and in a second step, in dyads, that they need to lift the handles to access the peanuts in the box. Finally, after this, the chimpanzees could be again confronted with the Cooperation Box in the outside enclosure. Another option would be modifying the Cooperation Box for it to resemble the loose-string task, which the chimpanzees are already familiar with, maybe using ropes instead of handles. If the chimpanzees then know how the Cooperation Box works, they might also cooperate, despite the fact that they are fed regularly. Peanuts are the A-chimpanzees' favourite treat (D. Geissler, personal communication, August 2021) and they do not receive any with their regular meals. Hence, as soon as the chimpanzees understand their task, the peanuts might be motivation enough to trigger their participation.

### 4.2.3 Comparison between the Cooperation Box and the Loose-String Paradigm

Before moving on to the discussion about the results obtained with the NSL data, we will discuss the main differences between the Cooperation Box and the NSL experiment.

The NSL experiment was done in a dyadic setting, which can have advantages. For instance, in a social setting, some chimpanzees might monopolize the apparatus (here the Cooperation Box) impeding others from using it, as was for instance the case in Chalmeau (1994). In a dyadic setting this effect can be excluded and the number of chimpanzees participating might increase (Cronin *et al.,* 2017). Moreover, it is easier to control for the number of participations per dyad, hence facilitating statistical analyses (Cronin *et al.,* 2017). Studying chimpanzees in a dyadic setting can also have an advantage when wanting to observe one specific factor. A dyadic setting can be controlled and unwanted factors can be excluded (Cronin *et al.,* 2017).

However, the aim of the Cooperation Box was to study partner choice for a cooperative task in chimpanzees. Partner choice can only be observed in a social setting (Molesti and Majolo, 2016). Only in a social setting do chimpanzees actually have many potential partners from which they can pick. In a dyadic setting, as for instance in the NSL experiment, the chimpanzees do not have the choice. When comparing many dyads, like was the case here, we can observe certain preferences of the chimpanzees. These preferences can hint towards whom chimpanzees would pick as a partner if they had the choice, but they are different behaviours and we might not detect all the factors influencing partner choice by studying only dyadic settings. For example, in a social setting, some chimpanzees might refuse to cooperate with certain subject when they know that they have the possibility to cooperate with more suitable partners. In a dyadic setting, these same individuals might decide to cooperate because they do not have a better option and want to access the food. This becomes clearer when we picture it for instance with rank difference. In a social setting, subordinates can choose to not go near the apparatus for cooperation (in this case the Cooperation Box) when a dominant is present. The subordinate can just walk away or wait for another partner. In a dyadic setting, the subordinate chimpanzees might choose to cooperate with a dominant out of fear of his possible aggressive reaction. Another possibility, could be that a low-ranking individual would just not enter the experimental room with the dominant chimpanzee due to too much fear. There could also be too much aggression between the two, forcing the experimenters to exclude the dyad from the study. In fact, in the NSL study only 56 out of the 135 possible dyads were tested, mostly due to husbandry reasons, i.e. among others, certain dyads not being able to be together in the same room. Hence, many effects might not be detected in a dyadic setting.

Moreover, studying chimpanzees in a social setting increases the socio-ecological validity of the experiment (Cronin *et al.,* 2017). Chimpanzees are social animals and do not behave in the same way when they are in a group or separated from it. Only in a social setting do we get information about how chimpanzees behave in a more natural environment and hence, on which behaviours are actually subject to natural selection (Cronin *et al.,* 2017). This is especially true for cooperation, which is a social capacity, and is strongly influenced by the presence of conspecifics, their identity, and their relationship with the test subject (Cronin *et al.,* 2017).

On top of this, there is a research gap in chimpanzee cooperation in social settings. While cooperation in dyadic settings is easy to study, it is much more difficult to have the right conditions and infrastructure to study chimpanzees in a social setting. The Cooperation Box at the WKPRC would have been a great opportunity to conduct such an experiment.

Another point which differentiates the NSL experiment form the Cooperation Box is that we wanted to include the factor “coordination” in our study, because much of human cooperation is actually collaboration (Melis *et al.,* 2006a; Tomasello *et al.,* 2004), which combines both cooperation and coordination (Boesch and Boesch, 1989). We do know that chimpanzees are capable of coordination (Matzusawa, 2018; Yamamoto, 2020) and wanted to test the extent of it. In the loose-string paradigm, chimpanzees do not need to coordinate any movements. They do indeed need to wait for the partner to hold the rope before pulling it, but they do not need to adjust their movements with the partner's. In the Cooperation Box they would have to pay attention that the tray is always horizontal, thus really needing to fine-tune their movements with the partner's. Hence, no conclusion on chimpanzee coordination abilities was possible.

Finally, we wanted to see if previous successful cooperation would lead to more cooperation in the future. The idea behind this was to see if chimpanzees would choose the better collaborator (Melis *et al.,* 2006a) or if they would rather take into account their RQ with the partner, despite not being successful (Suchak *et al.,* 2014). Suchak and colleagues (2014) argue that chimpanzees will sometimes prefer cooperating with partners with whom they can share other social interactions like grooming, sex, play, or food sharing, and not necessarily cooperate with an individual with whom they might be successful. With the Cooperation Box this would have been easier to see, because chimpanzees could both try to cooperate, but fail to coordinate their movements and access the peanuts (Figure 4). With the NSL experiment, this was more difficult. The chimpanzees could only fail in this task if none pulled the rope (no cooperation) or if one pulled alone. In the latter case it is difficult to know whether the second chimpanzee wanted to cooperate and the first did not wait for him, or if the second individual just did not want to cooperate.

To put it in a nutshell, the Cooperation Box would have been a better option to study partner choice as we initially intended to. Nevertheless, since the experiment did not work, the NSL experiment was a good alternative, allowing us to identify many factors which might indeed influence partner choice. This would however need to be checked in a future study in a social setting.

## 4.3 Part two – Based on the data of Nolte *et al.* (under review)

### 4.3.1 Factors influencing cooperation

Out of all the factors tested, four appeared to actually influence cooperation. These were the experimental condition, with chimpanzees cooperating much more when food was dispersed; the interactions between ST and rank difference and between RQ and rank difference, with chimpanzees cooperating more when both rank difference and ST or rank difference and RQ were high; and the monopolization of the food reward in the previous trial, which influenced cooperation negatively.

#### *4.3.1.1 Experimental condition and previous monopolization*

The effect of the experimental condition was also identified by Hare and colleagues (2007), the study replicated by NSL. They found that chimpanzees cooperated less when food was clumped than when it was dispersed, because when food was clumped, it was easier for one chimpanzee to monopolize it and the second then stopped cooperating. More precisely, in Hare and colleagues' study, they found that chimpanzees and bonobos cooperated the same amount when the food reward was dispersed (i.e. sharable). When the food reward was clumped (i.e. monopolizable) chimpanzees would cooperate less than bonobos, indicating that bonobos have a higher social tolerance than chimpanzees. This is consistent with our second finding that previous monopolization of the food reward has a strong negative effect on cooperation. It is generally well established in the literature that monopolization and a monopolizable food reward are obstacles to cooperation in chimpanzees (Chalmeau, 1994; Hare *et al.,* 2007; Suchak *et al.,* 2014; Schmelz and Call, 2015). When the food reward is monopolizable, chances are high that one of the two chimpanzees will not receive any food. Chimpanzees are known to cooperate only when they obtain a higher benefit from doing so than from not cooperating (Bullinger *et al.,* 2011). In the wild for instance, chimpanzee cooperation is often based on reciprocity (Melis *et al.,* 2006a; 2010; Mitani, 2009). Chimpanzees who create coalitions reciprocate favours like grooming, meat sharing, and support in agonistic interactions with other group members, and they also trade social favours like grooming for support, or grooming for meat (Muller and Mitani, 2005). When there is no food sharing, or no reciprocation of a social favour, chimpanzees might prefer not to cooperate. It has therefore been advanced that to study cooperation it is generally better to use a non-monopolizable food reward if you want to maximize participation from the chimpanzees (Suchak *et al.,* 2014).

#### *4.3.1.2 ST and rank difference*

Cooperation was positively influenced by ST. This is a well-studied effect in the literature (Cronin and Sánchez, 2012; Cronin *et al.,* 2014; Hare *et al.,* 2007; Melis *et al.*, 2006b; Suchak *et al.*, 2014). In fact, as mentioned in the introduction, cooperation could not have evolved without ST. Individuals with a high ST will be more likely to be in proximity and without aggression around a resource. This provides them more time to observe, manipulate and understand the problem they are trying to solve (Harrison *et al.,* 2021; Molesti and Majolo, 2016). They are therefore more likely to learn how their behaviour, their partner's behaviour, and the resource are connected, and thus, what they need to do to access it (Molesti and Majolo, 2016).

In this study we found that ST had only a significant positive effect on cooperation, when rank difference was higher than the average rank difference in the group. The amount of cooperation increased when both ST and rank difference increased. Here, I suggest that this is because for a subordinate, cooperating with high-ranking individuals might lead to more social benefits in the future than cooperating with low-ranking individuals when ST is high. Cooperating with a high-ranking chimpanzee when ST inside the dyad is low, will not lead to any advantage, but rather the monopolization of the food reward by the high-ranking individual. We saw in the previous paragraph that cooperation in chimpanzees is based on reciprocity (Melis *et al.,* 2006a; 2010; Mitani, 2009). Chimpanzees cooperate with each other but expect something in return. It has been observed in wild chimpanzees that high-ranking individuals can cede matings to lower-ranking individuals to assure their help to maintain their position in the dominance hierarchy (Mitani, 2009). High-ranking individuals can also have more possibilities than low-ranking chimpanzees to provide another low-ranking with food when he is granted the subordinates' help (Mitani, 2009). On the other hand, when rank difference is low and ST increases, success is low and seems to decrease even further. However, this effect is not significant. There is not enough data in this low range of rank difference to establish whether there is an effect. We could hypothesize that when rank difference and ST are low, other factors will rather be considered to evaluate if there will be cooperation or not, for instance sex or maternal relatedness.

In addition, we should not forget that only 56 out of the 135 possible dyads were tested in the cooperation experiment. The reasons for the non-testing of theses dyads were high aggression or fear of one partner as well as other husbandry reasons. This could have influenced the results for ST and rank difference. Dyads who could not be in the same room might have had a low ST, or a high difference in rank. Not taking these dyads into account could have strongly influenced our results.

#### *4.3.1.3 RQ and rank difference*

RQ and rank difference modulated each other's effect on cooperation in the same way as ST and rank difference did. This effect was however only significant when the dyad Fraukje-Frodo was included. The explanation could be the same as for ST and rank difference. Chimpanzees might cooperate more with individuals with whom rank difference is high, only when their RQ is high, too. They might gain more social benefits from this than from cooperating with lower-ranking individuals. Cooperation with high-ranking individuals when RQ is low will not provide them any advantages either.

Nevertheless, even if this interaction goes in the same direction as the interaction between ST and rank difference, there is a difference. RQ and rank difference modulate each other's effect on cooperation, but the final effect that RQ or rank difference have on cooperation is not significant. In the case of RQ this could be explained by the fact that the chimpanzees were only observed for 24 and 25 hours, for the A and the B chimps respectively. This might not have been enough to correctly assess the RQ of all the dyads. Moreover, we have again the fact that only 56 dyads were tested out of the 135, which might have hidden many effects, especially for rank difference. Rank difference has been shown in laboratory studies as well as in social settings to negatively influences cooperation (Suchak *et al.,* 2014). We discussed before (section 4.2.3.) that in a social setting chimpanzees would have been freer to choose to cooperate or not with a high-ranking partner, because they could choose to not go near the Cooperation Box when a higher-ranking individual was present. In a dyadic setting, this effect would be hidden because the lower-ranking individual might cooperate with a dominant out of fear of aggression, because the dominant is forcing the subordinate to cooperate, or because the dyads which might have a high difference in rank and which showed too much aggression might just not be tested. Nevertheless, in both interactions with rank difference, we can see that the effect of rank difference goes in the direction that we predicted, namely success decreases when rank difference is high, but only when ST and RQ are low.

#### *4.3.1.4 Age difference*

Age difference did not influence cooperation in our study. The estimate for age difference is negative (-0.54 ± 0.34) although very close to 0. The negative estimate goes in the predicted direction, namely that chimpanzees would rather cooperate with partners of the same age, and that cooperation decreases when age difference increases. Again, in a social setting the result might have been different, we therefore do not exclude that age difference might have an effect on cooperation. We can hypothesize though, that its effect is less important than for example the effects of ST and food monopolization which are already significant in a dyadic setting.

#### *4.3.1.5 Sex and maternal relatedness*

Finally, sex and maternal relatedness were not well represented in the dataset. Due to too little replicates and too much variation, the power to detect any significant effects was probably too low. Despite, we can see tendencies that go in the predicted directions. Males were predicted to cooperate more often than females due to male philopatry, even though in places where females do not disperse, for instance in captivity, females seem to form strong coalitions as well (Gilby and Wrangham, 2008; Melis *et al.*, 2010). According to our results, we do not exclude that they might still tend to cooperate less than males, albeit we cannot say anything with certainty. We can also not conclude on the effect of kinship on cooperation, albeit we did see that there was a slight tendency for related dyads to cooperate more than non-related ones. The effect of kinship is however not well established in the literature. It seems that other factors like ST or rank are much more important for cooperation than kinship (Langergraber *et al.*, 2007 ; Langergraber, 2012; Mitani *et al.*, 2002; Mitani, 2009).

#### *4.3.1.6 To sum up*

In summary, we saw that monopolization and whether the food reward is monopolizable influence cooperation negatively. These were the strongest effects that we identified, which are in line with the literature. Social tolerance has a positive effect on cooperation, especially when rank difference is high. Chimpanzees cooperate more when both rank difference and ST are high, probably due to the higher amount of social benefits subordinates can obtain by cooperating with dominants when their ST is high. The interaction between RQ and rank difference shows the same idea, even though this interaction is strongly influenced by one single dyad.

Furthermore, we did not identify any effect of age difference. Males, as well as maternally related individuals, seem to cooperate more than females and non-related dyads, but due to the small sample size we could not identify any significant effect and need to be careful when interpreting these results.

More research with a better sample size will be needed to take further conclusions on these factors. To assess all the variables affecting partner choice it is indispensable to do experiments in social settings.

## 4.4 Conclusion

In this research project we wanted to identify the factors that influence partner choice for a coordinated cooperation problem in chimpanzees. We could not test partner choice because our new experimental design, the Cooperation Box, did not yield any results due to limited time and possibly a lack of motivation from the chimpanzees. We used the data by Nolte, Sterck and van Leeuwen (under review), which was collected in a dyadic setting using the loose-string paradigm by Hirata and Fuwa (2007) to assess which factors might affect cooperation, and might play a role in partner choice. We found that monopolization limits cooperation, that a high social tolerance increases cooperation only when rank difference is high as well, and that relationship quality might have a positive effect on cooperation when rank difference is high.

Concerning our initial hypotheses, the ones for social tolerance and monopolization were verified. Chimpanzees did cooperate more when ST was high and when there was no monopolization. The effect of ST was however only significant when rank difference was higher than the mean rank difference in the group. The hypothesis that relationship quality would also positively influence cooperation was only partially verified. Cooperation rates seemed to increase when RQ was high, but only when rank difference was high as well. Furthermore, this effect was only observed when one specific dyad (Fraukje-Frodo) was included in the analyses. The hypothesis that rank difference influences cooperation negatively was partially verified as well. Rank difference modulated the effect of ST and RQ on cooperation, and cooperation increased when both rank difference and ST, or rank difference and RQ, were high. Hence, rank difference seemed to have a rather positive effect on cooperation. When ST and RQ were low, the effect of rank difference followed our predictions, namely that cooperation decreased when rank difference increased, but this effect was not significant.

We could not conclude anything about the effect of maternal relatedness nor sex difference, due to the low amount of replicates, though tendencies were observed that went in the predicted direction, namely with male dyads and maternally related dyads cooperating slightly more often than female and non-related dyads. We could not test our hypotheses about the interactions between maternal relatedness and rank difference, as well as maternal relatedness and age difference due again to the small sample size.

We could not conclude on the extent of the coordination capacity of chimpanzees since coordination was not tested in the NSL experiment and the Cooperation Box did not work.

More research is needed to better understand what lies at the basis of chimpanzee partner choice. Chimpanzees share very complex social interactions and it is impossible to resume them with just a small amount of variables, especially when the chimpanzees are studied in dyadic settings which exclude all the interactions with the group. Studying chimpanzees in social settings, increasing the sample size and comparing a large amount of chimpanzee groups, to control for inter-group variation, will provide us with a better overview of what influences chimpanzee partner choice and allow us to infer information about the evolution of human cooperation.

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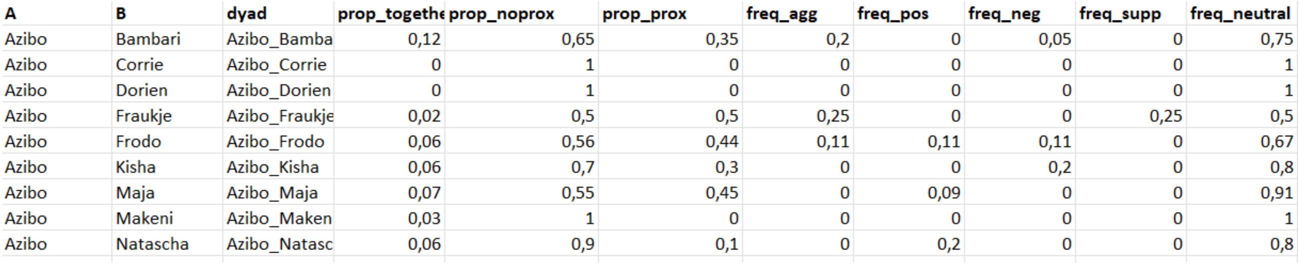
# 6 Appendix

## 6.1 Appendix: Materials and methods

### 6.1.1 Part one : My Experiments and Observations

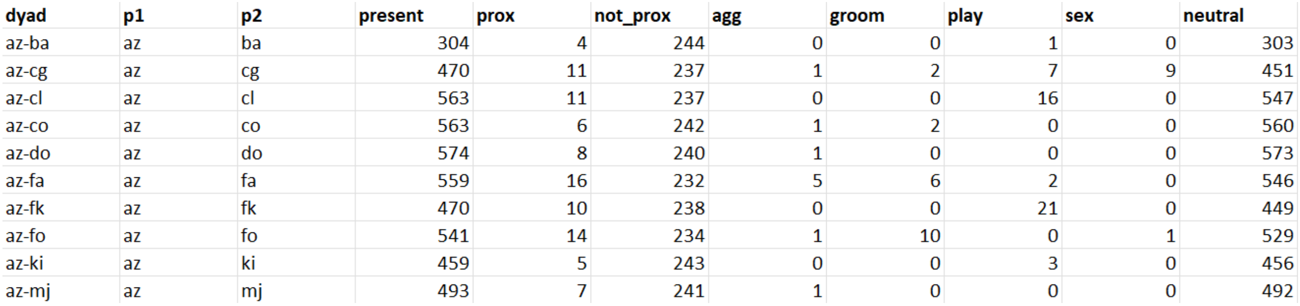
#### *6.1.1.1 Appendix 1: Peanut Plot*



| A | B | dyad | prop_togethe | prop_noprox | prop_prox | freq_agg | freq_pos | freq_neg | freq_supp | freq_neutral |
|---|---|---|---|---|---|---|---|---|---|---|
| Azibo | Bambari | Azibo_Bamba | 0,12 | 0,65 | 0,35 | 0,2 | 0 | 0,05 | 0 | 0,75 |
| Azibo | Corrie | Azibo_Corrie | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Azibo | Dorien | Azibo_Dorien | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Azibo | Fraukje | Azibo_Fraukje | 0,02 | 0,5 | 0,5 | 0,25 | 0 | 0 | 0,25 | 0,5 |
| Azibo | Frodo | Azibo_Frodo | 0,06 | 0,56 | 0,44 | 0,11 | 0,11 | 0,11 | 0 | 0,67 |
| Azibo | Kisha | Azibo_Kisha | 0,06 | 0,7 | 0,3 | 0 | 0 | 0,2 | 0 | 0,8 |
| Azibo | Maja | Azibo_Maja | 0,07 | 0,55 | 0,45 | 0 | 0,09 | 0 | 0 | 0,91 |
| Azibo | Makeni | Azibo_Maken | 0,03 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Azibo | Natascha | Azibo_Natasc | 0,06 | 0,9 | 0,1 | 0 | 0,2 | 0 | 0 | 0,8 |

File: PeanutPlot.xlsx, sheet: Final

#### *6.1.1.2 Appendix 2: Relationship quality 2021*

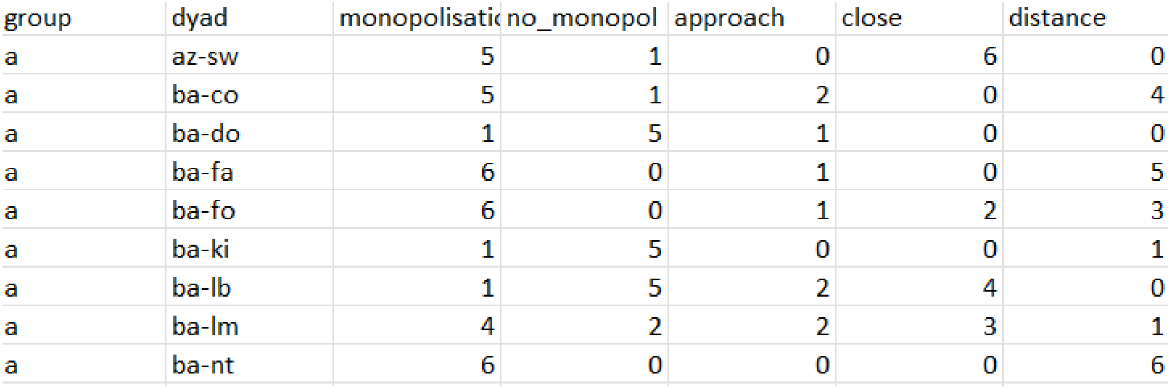


| dyad | p1 | p2 | present | prox | not_prox | agg | groom | play | sex | neutral |
|---|---|---|---|---|---|---|---|---|---|---|
| az-ba | az | ba | 304 | 4 | 244 | 0 | 0 | 1 | 0 | 303 |
| az-cg | az | cg | 470 | 11 | 237 | 1 | 2 | 7 | 9 | 451 |
| az-cl | az | cl | 563 | 11 | 237 | 0 | 0 | 16 | 0 | 547 |
| az-co | az | co | 563 | 6 | 242 | 1 | 2 | 0 | 0 | 560 |
| az-do | az | do | 574 | 8 | 240 | 1 | 0 | 0 | 0 | 573 |
| az-fa | az | fa | 559 | 16 | 232 | 5 | 6 | 2 | 0 | 546 |
| az-fk | az | fk | 470 | 10 | 238 | 0 | 0 | 21 | 0 | 449 |
| az-fo | az | fo | 541 | 14 | 234 | 1 | 10 | 0 | 1 | 529 |
| az-ki | az | ki | 459 | 5 | 243 | 0 | 0 | 3 | 0 | 456 |
| az-mj | az | mj | 493 | 7 | 241 | 1 | 0 | 0 | 0 | 492 |

File: Relationship quality.xlsx, sheet: Final

### 6.1.2 Part two: Nolte *et al.* (under review)

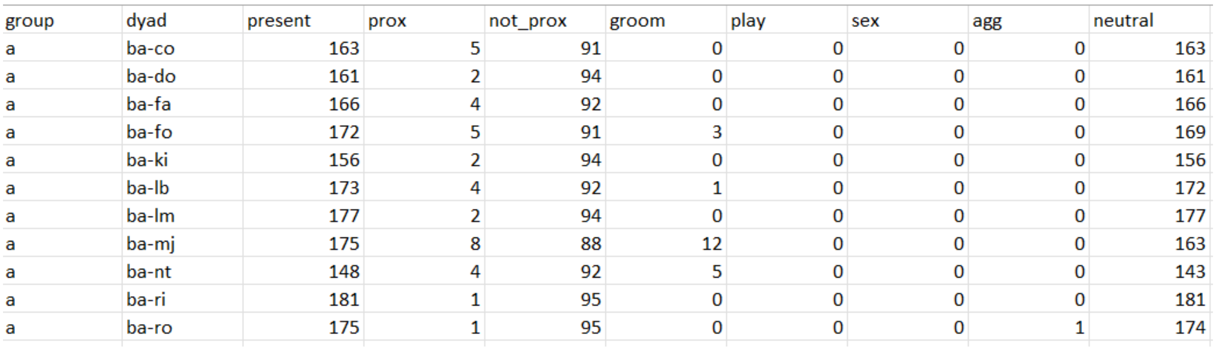
#### *6.1.2.1 Appendix 3: The co-feeding data (Social tolerance)*



| group | dyad | monopolisati | no_monopol | approach | close | distance |
|---|---|---|---|---|---|---|
| a | az-sw | 5 | 1 | 0 | 6 | 0 |
| a | ba-co | 5 | 1 | 2 | 0 | 4 |
| a | ba-do | 1 | 5 | 1 | 0 | 0 |
| a | ba-fa | 6 | 0 | 1 | 0 | 5 |
| a | ba-fo | 6 | 0 | 1 | 2 | 3 |
| a | ba-ki | 1 | 5 | 0 | 0 | 1 |
| a | ba-lb | 1 | 5 | 2 | 4 | 0 |
| a | ba-lm | 4 | 2 | 2 | 3 | 1 |
| a | ba-nt | 6 | 0 | 0 | 0 | 6 |

File: cofeed_for_FCA.xlsx

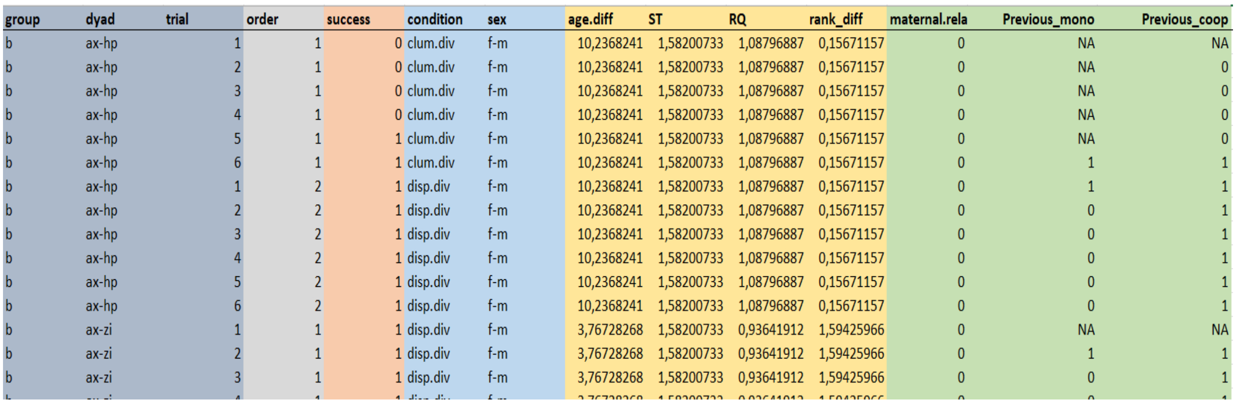
### 6.1.2.2 Appendix 4: Relationship quality



| group | dyad | present | prox | not_prox | groom | play | sex | agg | neutral |
|---|---|---|---|---|---|---|---|---|---|
| a | ba-co | 163 | 5 | 91 | 0 | 0 | 0 | 0 | 163 |
| a | ba-do | 161 | 2 | 94 | 0 | 0 | 0 | 0 | 161 |
| a | ba-fa | 166 | 4 | 92 | 0 | 0 | 0 | 0 | 166 |
| a | ba-fo | 172 | 5 | 91 | 3 | 0 | 0 | 0 | 169 |
| a | ba-ki | 156 | 2 | 94 | 0 | 0 | 0 | 0 | 156 |
| a | ba-lb | 173 | 4 | 92 | 1 | 0 | 0 | 0 | 172 |
| a | ba-lm | 177 | 2 | 94 | 0 | 0 | 0 | 0 | 177 |
| a | ba-mj | 175 | 8 | 88 | 12 | 0 | 0 | 0 | 163 |
| a | ba-nt | 148 | 4 | 92 | 5 | 0 | 0 | 0 | 143 |
| a | ba-ri | 181 | 1 | 95 | 0 | 0 | 0 | 0 | 181 |
| a | ba-ro | 175 | 1 | 95 | 0 | 0 | 0 | 1 | 174 |

File: Table_for_FCA_RQ.xlsx

### 6.1.2.3 Appendix 5 : Final data

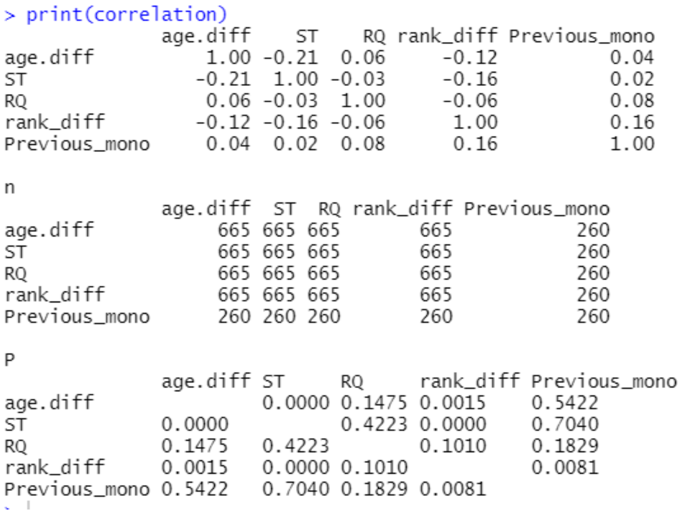


| group | dyad | trial | order | success | condition | sex | age.diff | ST | RQ | rank_diff | maternal.rela | Previous_mono | Previous_coop |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| b | ax-hp | 1 | 1 | 0 | clum.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | NA | NA |
| b | ax-hp | 2 | 1 | 0 | clum.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | NA | 0 |
| b | ax-hp | 3 | 1 | 0 | clum.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | NA | 0 |
| b | ax-hp | 4 | 1 | 0 | clum.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | NA | 0 |
| b | ax-hp | 5 | 1 | 1 | clum.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | NA | 0 |
| b | ax-hp | 6 | 1 | 1 | clum.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | 1 | 1 |
| b | ax-hp | 1 | 2 | 1 | disp.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | 1 | 1 |
| b | ax-hp | 2 | 2 | 1 | disp.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | 0 | 1 |
| b | ax-hp | 3 | 2 | 1 | disp.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | 0 | 1 |
| b | ax-hp | 4 | 2 | 1 | disp.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | 0 | 1 |
| b | ax-hp | 5 | 2 | 1 | disp.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | 0 | 1 |
| b | ax-hp | 6 | 2 | 1 | disp.div | f-m | 10,2368241 | 1,58200733 | 1,08796887 | 0,15671157 | 0 | 0 | 1 |
| b | ax-zi | 1 | 1 | 1 | disp.div | f-m | 3,76728268 | 1,58200733 | 0,93641912 | 1,59425966 | 0 | NA | NA |
| b | ax-zi | 2 | 1 | 1 | disp.div | f-m | 3,76728268 | 1,58200733 | 0,93641912 | 1,59425966 | 0 | 1 | 1 |
| b | ax-zi | 3 | 1 | 1 | disp.div | f-m | 3,76728268 | 1,58200733 | 0,93641912 | 1,59425966 | 0 | 0 | 1 |

File: definitive_Table.xlsx

## 6.2 Appendix: Results

### 6.2.1 Appendix 6: Correlation matrix



```
> print(correlation)
              age.diff    ST    RQ rank_diff Previous_mono
age.diff          1.00 -0.21  0.06     -0.12          0.04
ST               -0.21  1.00 -0.03     -0.16          0.02
RQ                0.06 -0.03  1.00     -0.06          0.08
rank_diff        -0.12 -0.16 -0.06      1.00          0.16
Previous_mono     0.04  0.02  0.08      0.16          1.00

n
              age.diff  ST  RQ rank_diff Previous_mono
age.diff           665 665 665       665           260
ST                 665 665 665       665           260
RQ                 665 665 665       665           260
rank_diff          665 665 665       665           260
Previous_mono      260 260 260       260           260

P
              age.diff ST     RQ     rank_diff Previous_mono
age.diff               0.0000 0.1475 0.0015    0.5422
ST            0.0000          0.4223 0.0000    0.7040
RQ            0.1475   0.4223        0.1010    0.1829
rank_diff     0.0015   0.0000 0.1010           0.0081
Previous_mono 0.5422   0.7040 0.1829 0.0081
```

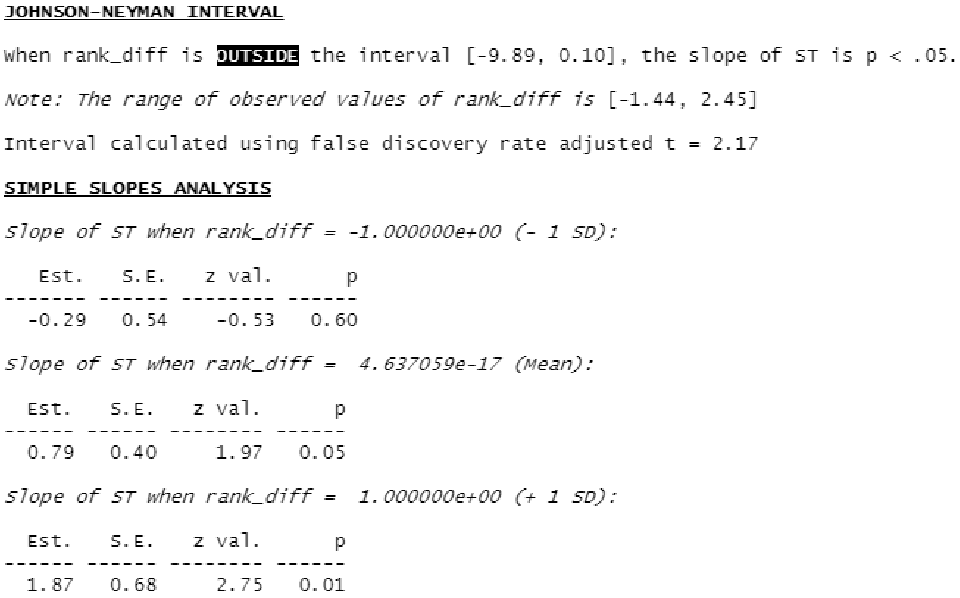
### 6.2.2 Appendix 7: Summary of the model

```
> summary(GLMM1)
Generalized linear mixed model fit by maximum likelihood (Adaptive Gauss-Hermite Quadrature, nAGQ = 0) [
glmerMod]
 Family: binomial  ( logit )
Formula: success ~ condition + maternal.relatedness + age.diff + ST +
    RQ + rank_diff + sex + RQ:rank_diff + ST:rank_diff + (1 |
    dyad/group) + (1 | trial) + (1 | X1/group) + (1 | X2/group)
   Data: apes
Control: glmerControl(optimizer = "bobyqa")

     AIC      BIC   logLik deviance df.resid
     564      645     -264      528      647

Scaled residuals:
    Min      1Q  Median      3Q     Max
-5.5977 -0.4189 -0.0521  0.3289  3.8895

Random effects:
 Groups     Name        Variance Std.Dev.
 dyad       (Intercept) 1.4904   1.2208
 group:dyad (Intercept) 0.9802   0.9901
 X2         (Intercept) 0.9186   0.9585
 group:X2   (Intercept) 0.9366   0.9678
 X1         (Intercept) 1.2165   1.1030
 group:X1   (Intercept) 1.1616   1.0778
 trial      (Intercept) 0.0000   0.0000
Number of obs: 665, groups:  dyad, 56; group:dyad, 56; X2, 12; group:X2, 12; X1, 12; group:X1, 12; trial, 6

Fixed effects:
                      Estimate Std. Error z value Pr(>|z|)
(Intercept)           -2.77028    0.98809  -2.804  0.00505 **
conditiondisp.div      3.37610    0.28254  11.949  < 2e-16 ***
maternal.relatedness1  0.46276    1.11025   0.417  0.67682
age.diff              -0.53749    0.34303  -1.567  0.11714
ST                     0.79082    0.40156   1.969  0.04891 *
RQ                    -0.36676    0.56145  -0.653  0.51360
rank_diff             -0.04363    0.42789  -0.102  0.91878
sexf-m                 0.02543    0.94788   0.027  0.97860
sexm-m                 1.96979    1.78706   1.102  0.27035
RQ:rank_diff           0.73161    0.30090   2.431  0.01504 *
ST:rank_diff           1.07736    0.46630   2.310  0.02086 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) cndtn. mtrn.1 ag.dff ST     RQ     rnk_df sexf-m sexm-m RQ:rn_
cndtndsp.dv -0.169
mtrnl.rltd1 -0.188  0.037
age.diff     0.114 -0.051 -0.045
ST           0.077  0.071 -0.164  0.147
RQ           0.115 -0.011 -0.275 -0.077  0.117
rank_diff    0.204 -0.004 -0.181  0.164  0.219 -0.103
sexf-m      -0.657  0.010  0.115 -0.047 -0.227 -0.054 -0.407
sexm-m      -0.528  0.037  0.001 -0.202 -0.123 -0.268  0.107  0.583
RQ:rank_dff -0.113  0.077  0.153 -0.090  0.211 -0.636 -0.021 -0.015  0.241
ST:rank_dff -0.018  0.083 -0.089 -0.330  0.221  0.099 -0.172 -0.033  0.161  0.478
```

### 6.2.3 Appendix 8: p-values of the model using the *drop1* function

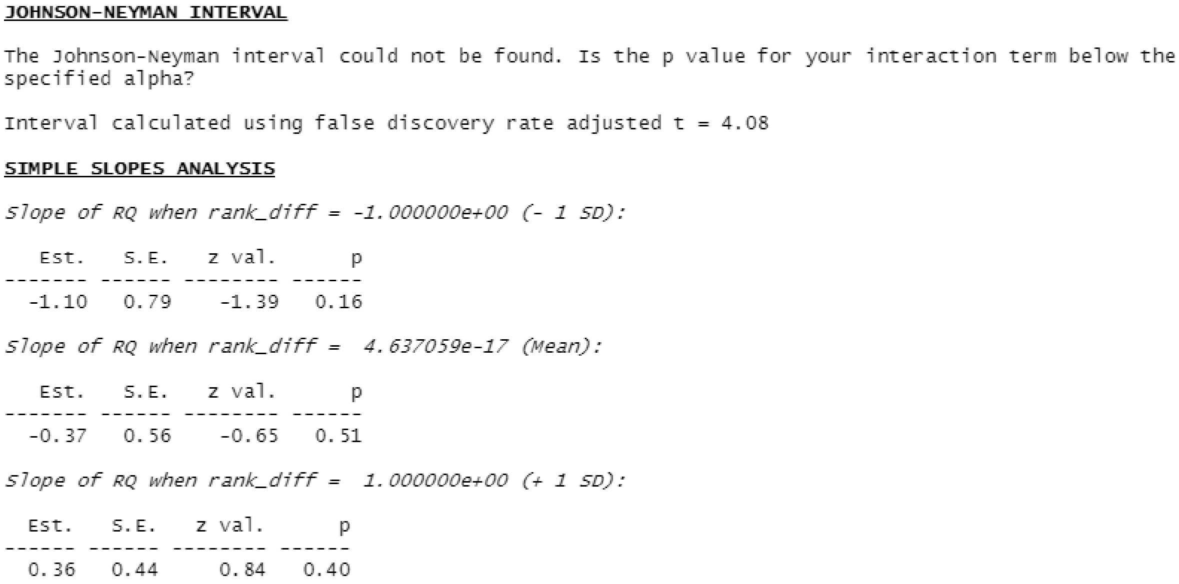
```
> drop1(GLMM1, test="Chisq")
Single term deletions

Model:
success ~ condition + maternal.relatedness + age.diff + ST +
    RQ + rank_diff + sex + RQ:rank_diff + ST:rank_diff + (1 |
    dyad/group) + (1 | trial) + (1 | X1/group) + (1 | X2/group)
                     npar    AIC     LRT   Pr(Chi)
<none>                    564.00
condition               1 785.47 223.474 < 2.2e-16 ***
maternal.relatedness    1 562.14   0.147  0.701299
age.diff                1 564.38   2.381  0.122842
sex                     2 562.26   2.264  0.322418
RQ:rank_diff            1 570.06   8.061  0.004524 **
ST:rank_diff            1 567.94   5.942  0.014784 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

### 6.2.4 Appendix 9: Johnson-Neyman interval and slim-slopes analysis results for ST:rank_difference



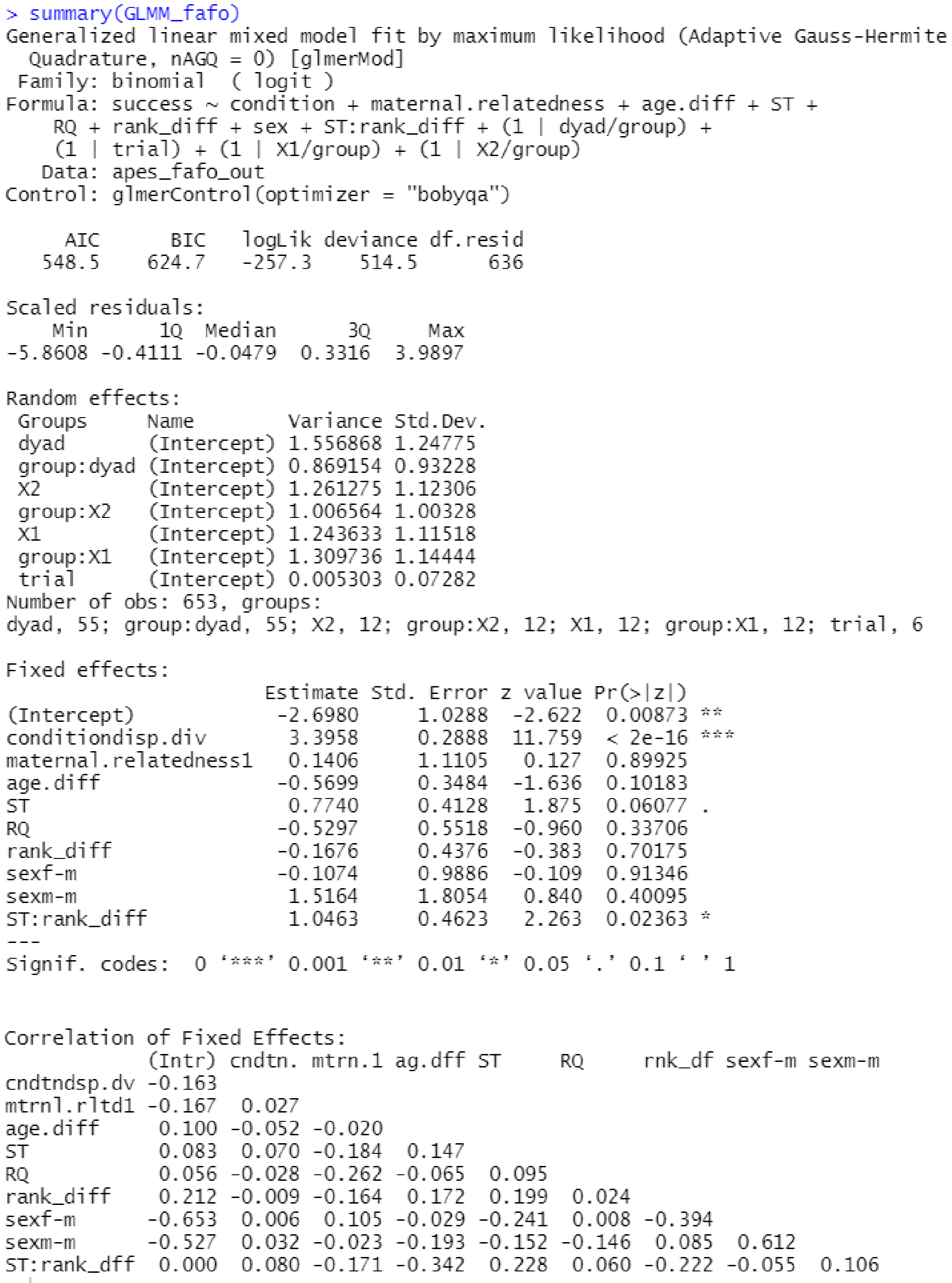
```
JOHNSON-NEYMAN INTERVAL

When rank_diff is OUTSIDE the interval [-9.89, 0.10], the slope of ST is p < .05.

Note: The range of observed values of rank_diff is [-1.44, 2.45]

Interval calculated using false discovery rate adjusted t = 2.17

SIMPLE SLOPES ANALYSIS

Slope of ST when rank_diff = -1.000000e+00 (- 1 SD):

   Est.   S.E.   z val.      p
------- ------ -------- ------
  -0.29   0.54    -0.53   0.60

Slope of ST when rank_diff =  4.637059e-17 (Mean):

  Est.   S.E.   z val.      p
------ ------ -------- ------
  0.79   0.40     1.97   0.05

Slope of ST when rank_diff =  1.000000e+00 (+ 1 SD):

  Est.   S.E.   z val.      p
------ ------ -------- ------
  1.87   0.68     2.75   0.01
```

### 6.2.5 Appendix 10: Johnson-Neyman interval and slim-slopes analysis results for RQ:rank_difference



```
JOHNSON-NEYMAN INTERVAL

The Johnson-Neyman interval could not be found. Is the p value for your interaction term below the
specified alpha?

Interval calculated using false discovery rate adjusted t = 4.08

SIMPLE SLOPES ANALYSIS

Slope of RQ when rank_diff = -1.000000e+00 (- 1 SD):

   Est.   S.E.   z val.      p
------- ------ -------- ------
  -1.10   0.79    -1.39   0.16

Slope of RQ when rank_diff =  4.637059e-17 (Mean):

   Est.   S.E.   z val.      p
------- ------ -------- ------
  -0.37   0.56    -0.65   0.51

Slope of RQ when rank_diff =  1.000000e+00 (+ 1 SD):

  Est.   S.E.   z val.      p
------ ------ -------- ------
  0.36   0.44     0.84   0.40
```

### 6.2.6 Appendix 11: Summary Table for the GLMM excluding the dyad Fraukje-Frodo



```
> summary(GLMM_fafo)
Generalized linear mixed model fit by maximum likelihood (Adaptive Gauss-Hermite
  Quadrature, nAGQ = 0) [glmerMod]
 Family: binomial  ( logit )
Formula: success ~ condition + maternal.relatedness + age.diff + ST +
    RQ + rank_diff + sex + ST:rank_diff + (1 | dyad/group) +
    (1 | trial) + (1 | X1/group) + (1 | X2/group)
   Data: apes_fafo_out
Control: glmerControl(optimizer = "bobyqa")

     AIC      BIC   logLik deviance df.resid
   548.5    624.7   -257.3    514.5      636

Scaled residuals:
    Min      1Q  Median      3Q     Max
-5.8608 -0.4111 -0.0479  0.3316  3.9897

Random effects:
 Groups     Name        Variance Std.Dev.
 dyad       (Intercept) 1.556868 1.24775
 group:dyad (Intercept) 0.869154 0.93228
 X2         (Intercept) 1.261275 1.12306
 group:X2   (Intercept) 1.006564 1.00328
 X1         (Intercept) 1.243633 1.11518
 group:X1   (Intercept) 1.309736 1.14444
 trial      (Intercept) 0.005303 0.07282
Number of obs: 653, groups:
dyad, 55; group:dyad, 55; X2, 12; group:X2, 12; X1, 12; group:X1, 12; trial, 6

Fixed effects:
                      Estimate Std. Error z value Pr(>|z|)
(Intercept)            -2.6980     1.0288  -2.622  0.00873 **
conditiondisp.div       3.3958     0.2888  11.759  < 2e-16 ***
maternal.relatedness1   0.1406     1.1105   0.127  0.89925
age.diff               -0.5699     0.3484  -1.636  0.10183
ST                      0.7740     0.4128   1.875  0.06077 .
RQ                     -0.5297     0.5518  -0.960  0.33706
rank_diff              -0.1676     0.4376  -0.383  0.70175
sexf-m                 -0.1074     0.9886  -0.109  0.91346
sexm-m                  1.5164     1.8054   0.840  0.40095
ST:rank_diff            1.0463     0.4623   2.263  0.02363 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1


Correlation of Fixed Effects:
            (Intr) cndtn. mtrn.1 ag.dff ST     RQ     rnk_df sexf-m sexm-m
cndtndsp.dv -0.163
mtrnl.rltd1 -0.167  0.027
age.diff     0.100 -0.052 -0.020
ST           0.083  0.070 -0.184  0.147
RQ           0.056 -0.028 -0.262 -0.065  0.095
rank_diff    0.212 -0.009 -0.164  0.172  0.199  0.024
sexf-m      -0.653  0.006  0.105 -0.029 -0.241  0.008 -0.394
sexm-m      -0.527  0.032 -0.023 -0.193 -0.152 -0.146  0.085  0.612
ST:rank_dff  0.000  0.080 -0.171 -0.342  0.228  0.060 -0.222 -0.055  0.106
```

### 6.2.7 Appendix 12: Summary of the GLMM with previous monopolization

```
> summary(mono)
Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: success ~ Previous_mono + (1 | trial) + (1 | group)
   Data: apes

     AIC      BIC   logLik deviance df.resid 
   217.2    231.4   -104.6    209.2      256 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-4.6074  0.2021  0.2881  0.3454  1.7124 

Random effects:
 Groups Name        Variance Std.Dev.
 trial  (Intercept) 0.5280   0.7266  
 group  (Intercept) 0.4364   0.6606  
Number of obs: 260, groups:  trial, 6; group, 2

Fixed effects:
              Estimate Std. Error z value Pr(>|z|)    
(Intercept)     2.9121     0.7415   3.927 8.60e-05 ***
Previous_mono  -2.3551     0.3741  -6.295 3.08e-10 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr)
Previous_mn -0.361
```