

Mémoire

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CHATOR AUDE

BONOBOS' COOPERATION IN A FREE GROUP CHOICE EXPERIMENT

Thesis for the completion of a master's degree in biology of organization and ecology with an in-depth focus on ethology



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Abstract

Bonobos' cooperation in a free group choice experiment

2024 - Département de Biologie, Ecologie et Evolution – Winandy Laurane and Verspeek Jonas

The concept of cooperation has been explored and defined by various scholars across disciplines, revealing the complexity and nuanced nature of this fundamental behaviour. The aim of this work is to investigate the cooperative behaviours of bonobos (*Pan paniscus*) using a modified loose-string paradigm in a group context, alongside examining the relationship quality among bonobo dyads.

The study was conducted at the Planckendael Zoo in Mechelen, Belgium, focusing on a population of bonobos. The study included a total of 22 individuals, housed into two groups, with 11 adult or adolescent females, 6 adult or adolescent males, and 5 juveniles. Relationship quality was assessed based on eight behavioural variables, yielding scores for Relationship Value and Incompatibility. The results indicate that genetic sex combinations significantly influence relationship Value, with higher scores observed in female-female and mother-offspring dyads. In this study, the age difference did not affect the relationship quality.

The cooperation experiment involved 240 trials, with a 11% success rate. Individual performance varied, with factors such as motivation, task understanding, and social dynamics playing critical roles in successful cooperation. Additionally, behavioural inhibition and attention to partners were identified as crucial factors influencing cooperative success.

The findings did not fully support the self-domestication hypothesis but aligned with the cooperative breeding hypothesis, suggesting limited prosociality among bonobos due to their reproductive strategies. The empathy hypothesis also provided some insights, indicating that bonobos' ability to understand the needs and feelings of others might contribute to cooperative success. Bonobos exhibited difficulty in waiting for partners, often leading to premature actions and failure in cooperative tasks. This behaviour suggests a need to better understand the cognitive mechanisms underpinning cooperation.

In conclusion, this study provides insights into the cooperative behaviours of bonobos, emphasizing the importance of social relationships and individual differences. Future research should explore the long-term effects of cooperative tasks on social dynamics, incorporate methods to enhance motivation, and consider the impact of individual personality traits and past experiences on cooperation.

Résumé

Coopération entre bonobos dans le cadre d'une expérience de groupe à choix libre

2024 - Département de Biologie, Écologie et Évolution – Winandy Laurane and Verspeek Jonas

Le concept de coopération a été défini par divers chercheurs dans différentes disciplines, révélant la complexité et les nuances de ce comportement fondamental. L'objectif de ce travail est d'examiner les comportements coopératifs des bonobos (*Pan paniscus*) en utilisant une version modifiée du « loose-string paradigm » dans un contexte de groupe, ainsi que d'analyser la qualité des relations entre les dyades de bonobos.

L'étude a été réalisée au zoo de Planckendael à Malines, en Belgique, en se concentrant sur une population de bonobos. L'échantillon comprenait 22 individus répartis en deux groupes. La qualité des relations a été évaluée à partir de huit variables comportementales ce qui a permis d'obtenir des scores pour la valeur des relations et l'incompatibilité. Les résultats indiquent que les combinaisons génétiques de sexe influencent de manière significative la valeur de la relation, avec des scores plus élevés observés dans les dyades femme-femme et mère-fils. Dans cette étude, la différence d'âge n'a pas affecté la qualité de la relation.

L'expérience de coopération comprenait 240 essais, avec un taux de succès de 11 %. La performance individuelle varie et des facteurs tels que la motivation, la compréhension de la tâche et la dynamique sociale jouant un rôle crucial dans le succès de la coopération. L'inhibition comportementale et l'attention portée aux partenaires ont été identifiées comme des facteurs déterminants du succès coopératif.

Les résultats ne soutiennent pas l'hypothèse de l'auto-domestication, mais s'alignent sur l'hypothèse de la reproduction coopérative, suggérant une pro socialité limitée chez les bonobos en raison de leurs stratégies reproductives. Les bonobos ont éprouvé des difficultés à attendre leurs partenaires, ce qui a souvent conduit à des actions prématurées et à des échecs dans les tâches de coopération. Ce comportement suggère qu'il est nécessaire de mieux comprendre les mécanismes cognitifs qui sous-tendent la coopération

En conclusion, cette étude offre des perspectives sur les comportements coopératifs des bonobos, en soulignant l'importance des relations sociales et des différences individuelles. Les recherches futures devraient explorer les effets à long terme des tâches coopératives sur la dynamique sociale, intégrer des méthodes pour améliorer la motivation et prendre en compte l'impact des traits de personnalité individuels et des expériences passées sur la coopération.

Table of content

1	Introduction	8
1.1	Cooperation in animals	9
1.1.1	Cooperation in naturalistic interactions.....	9
1.1.2	Cooperation in primates	11
1.1.3	How to measure cooperation	12
1.2	Study species: The Bonobo	15
1.2.1	Conflicting results.....	16
1.3	Objectives.....	19
2	Materials and methods.....	21
2.1	Study site.....	21
2.2	Observation protocol.....	23
2.3	Apparatus	25
2.3.1	Procedures	26
2.4	Data analysis.....	27
2.4.1	Determining Relationship Quality (RQ)	27
2.4.2	Cooperation experiment	29
3	Results.....	31
3.1	Components of relationship quality.....	31
3.2	Factors influencing relationship quality.....	31
3.3	Cooperation experiment.....	33
3.3.1	Number of Successes per Session.....	34
3.3.2	Number of Trials and Successes per Dyad.....	34
3.3.3	Breakdown of Interactions and Successes by Individual	35
4	Discussion	37

4.1	Relationship quality	37
4.2	Cooperation	38
4.2.1	Understanding the task and behavioural response	39
4.2.2	Factors Influencing Interaction with the Setup.....	39
4.2.2.1	Behavioural inhibition and attention to partners.....	39
4.2.2.2	Social structure and dominance hierarchy.....	41
4.2.2.3	Age effect.....	42
4.2.3	Limits of the study	42
5	Conclusion	44
6	Bibliography.....	46

Table of figures and tables

Figure 1 Layout of the inside enclosure. Layout of A) the entire enclosure with the tunnels connecting them and B) the areas visible for visitors.	22
Figure 2 Experimental set-up. A. Photograph showing the set-up from the trainers' side. B. Schematic drawing of the set-up from above.	26
Figure 3 : Sociograms based on the outcomes from the (a) Compatibility and (b) Value components	31
Figure 4 Median relationship value of unrelated male-male (MM), unrelated female-male (FM), unrelated female-female (FF), mother-daughter (MD) and mother-son (MS) dyads.	33
Figure 5 Distribution of successes across the 12 sessions.....	34
Figure 6 Number of total trials and the number of successes for each dyad.....	35
Figure 7 Number of participations in the experiment (alone and with another individual), failures, and successes for each individual.....	36
Table 1 : Overview of the sex, year of birth, place of birth and parents of the 17 studied individuals.....	22
Table 2 : Behavioural variables entered in the Principal Component Analysis (Stevens et al., 2015).....	28
Table 3 : Effects of genetic sex combination and age difference on the components Value and Compatibility.	32
Table 4 : Data for each individual, including the number of interactions, successes, and failures, as well as the proportion of successes for all interactions and specifically for interactions with another individual.....	36

1 Introduction

The concept of cooperation has been explored and defined by various scholars across disciplines, revealing the nuanced nature of this fundamental behaviour. Hamilton offers a broad definition, framing cooperation as a phenomenon where the actor and recipients derive fitness benefits or, in some cases, only the recipient benefits at a cost to the actor (Hamilton, 1964). Accentuating on outcomes, Hayes (Hayes, 1925) encapsulates cooperation as “the relation between activities that contribute to a common result”.

Dugatkin (Dugatkin, 1997) delves deeper into the complexities by distinguishing between cooperative acts and cooperative efforts. He defines cooperation as an outcome that, despite potential costs to the individual, is "good" for the group members, requiring collective action. The term "to cooperate" is clarified to encompass both achieving cooperation at the group level and behaving cooperatively at the individual level, the latter contributing to the possibility of realizing cooperation within the group (Brosnan and De Waal, 2002).

Sachs et al. (2004) and Bergmüller et al. (2007) narrow down cooperation to acts “performed by one individual that increase the fitness of another”. West et al. (2007) refine this perspective by defining cooperative behaviour as that “which provides a benefit to another individual and is selected for due to its beneficial effect on the recipient”. They stress that this selection is not solely based on the recipient's benefit, allowing for a more nuanced understanding of cooperative evolution (Connor, 2010).

Ecologist Bronstein (2003) introduces an ecological dimension, categorizing cooperation, mutualism, and symbiosis as mutually exclusive. Cooperation, in this context, is a mutually beneficial interaction among conspecifics, setting it apart from relationships between members of different species (Noë, 2006).

In essence, the varying definitions reflect a spectrum of perspectives, with some viewing cooperation as a recognizable type of interaction, others as a strategy within an interaction, and still others as a defining characteristic of long-term relationships. As we explore these dimensions, it becomes evident that cooperation is a multi-faceted and dynamic concept, essential for understanding social dynamics and ecological interactions.

For the sake of this thesis, we choose to follow the definition of Brosnan & de Waal (Brosnan and De Waal, 2002) “The voluntary acting together of two or more individuals that brings about, or could potentially bring about, an end situation that benefits one, both, or all of them in a way that could not have been brought about individually”.

1.1 Cooperation in animals

1.1.1 Cooperation in naturalistic interactions

Evolutionary theories, such as Darwin's and Fisher's Natural Selection, initially suggest a prevalence of selfish behaviours over cooperation. However, West et al. underlines that a fascinating counter-narrative unfolds in the animal kingdom, where cooperation prevails across biological hierarchies : genes cooperate to form eukaryotic cells and then multicellular organisms, animals reproduce cooperatively, humans and insects cooperate to build societies (West et al., 2007).

Cooperation is not only present between individuals of the same species but extends to unlikely collaborations between different species (Bergmüller et al., 2007). In essence, the evolutionary exploration of cooperation intricately weaves together ultimate and proximate causes, revealing a variety of regulatory mechanisms and diverse cooperative interactions that shape the intricate dynamics of the animal kingdom.

Cooperative interactions have been reported across different taxa, showing its adaptive value in diverse ecological niches and shedding light on the intricate dynamics of collaborative behaviour. One prominent example is group hunting behaviour, where cooperation provides fitness benefits to individuals, even with temporary costs. Bailey et al. (Bailey et al., 2013) underscore this phenomenon, reporting intra-specific cooperative hunting across 40 carnivora species, including otters, canids, hyenas, felids, and viverrids. Also, studies in African lions (*Panthera leo*) and harbour porpoises (*Phocoena phocoena*) have revealed significant insights into their hunting behaviours. In the Serengeti National Park, research on African lions showed nuanced variations in individual participation, with males often refraining from hunts. This research suggests that the degree of cooperation among the lions varies depending on how easily they can capture different prey species, indicating an adaptive flexibility in their hunting strategies. Similarly, studies on harbour porpoises have uncovered role specialization during group hunts, demonstrating the complexity of their collaborative efforts, even though they are generally considered asocial (Torres Ortiz et al., 2021). Dolphins, exemplified in both Shark Bay, Australia, and Laguna, Brazil, showcase cooperative behaviours like herding females or interacting with fishermen for mutual benefit (Connor et al., 1992; Daura-Jorge et al., 2012).

Beyond mammals, cooperation also extends to the aquatic realm, illustrated by the three-spined sticklebacks engaging in cooperative nest raiding. Nest raiding in sticklebacks involves coordinated efforts by groups of females to overpower males guarding conspecific eggs, showcasing the adaptive value of cooperative behaviours in facilitating reproductive success. Birds, too, exhibit cooperative behaviours, such as cliff swallows and great tits engaging in group foraging and mobbing predators, (Dugatkin, 1997).

Reciprocal altruism stands as a cornerstone concept in understanding cooperation among non-human animals. This theory suggests that individuals may engage in costly acts of cooperation with the expectation of receiving reciprocal benefits in the future. Trivers framed this concept within the framework of the Prisoner's Dilemma, highlighting the dilemmas individuals face in balancing self-interest with cooperation (Trivers, 1971; West et al., 2007). Studies have further explored the dynamics of reciprocal altruism, emphasizing the importance of partner choice and the existence of contingencies between actions and reciprocation (Brosnan and De Waal, 2002; Dugatkin, 2002). Reciprocal allogrooming in impala, as studied by Hart and Hart, and blood sharing in vampire bats, as explored by Wilkinson, provide compelling evidence of cooperation through reciprocal altruism (Hart and Hart, 1992; Wilkinson, 1984). These cooperative strategies, shaped by factors such as prey availability, habitat structure, cognitive abilities, and social dynamics, play pivotal roles in enhancing survival and reproductive success across diverse animal populations (Dugatkin, 1997).

Cooperative breeding, driven by kin selection, represents another crucial mechanism promoting cooperation among several animal species. In species where individuals forego reproduction to help raise the offspring of close relatives, inclusive fitness benefits are enhanced. Studies that have explored the cognitive consequences of cooperative breeding, suggest that it may lead to specific socio-cognitive performances like for example higher levels of social tolerance, increased prosocial tendencies and thus more successful cooperation (Dugatkin, 1997; Jennions, 1994a). Cooperative breeding is particularly prevalent among callitrichid primates and several bird species, such as tamarins and marmosets and corvids respectively, where individuals engage in extensive caregiving behaviours and active food sharing with offspring (Burkart and Van Schaik, 2010; Horn et al., 2020; Jennions, 1994a).

In summary, studies and theories on cooperation among animals offer a comprehensive understanding of the evolutionary origins of social behaviours and the adaptive strategies employed by these animals to navigate their social worlds. From reciprocal altruism to biological markets and cooperative breeding, these frameworks illuminate the diverse array of mechanisms driving cooperation in animal societies, enriching our understanding of social evolution and behaviour.

1.1.2 Cooperation in primates

As in many animals, cooperation in primates highlights their complex social structures, essential for survival, and offers insights into the evolution of social behaviours and strategies for navigating intricate social environments. Moreover, the close phylogenetic relationship between humans and primates underscores the importance of studying these species. Within the vast array of primate species, including New World monkeys, Old World monkeys, and great apes, lies a wealth of evolutionary history, offering invaluable parallels to human social evolution. The array of cooperative behaviours among primates showcases a complex suite of social interactions essential for their survival and societal organization. This complexity is evidenced across diverse species through distinct forms of cooperation, including coalitionary behaviours, alarm calling, and food sharing. Despite the significant role of kinship in forming bonds, many of these cooperative pairs consist of unrelated individuals, illustrating a sophisticated social structure where kinship is just one of multiple factors influencing alliances (Langergraber et al., 2007).

In contexts such as territorial defence, male chimpanzees engage in coalitionary behaviour, where they aggressively patrol their territories and confront neighbouring communities. These interactions can intensify into lethal conflicts, highlighting the critical nature of their cooperative strategies (Muller and Mitani, 2005). Species like vervet monkeys, along with Diana monkeys and Campbell's monkeys, have developed intricate alarm call systems that vary with the type of predator. These calls not only aid in group survival but also promote interspecies communication, demonstrating a high level of cooperative communication where different species recognize and react to each other's alarm calls (Seyfarth et al., 1980; Snowdon, 2020; Struhsaker, 1967; Zuberbühler, 2000).

Food sharing is another essential cooperative behaviour observed in a diverse array of primate species, highlighting its widespread evolutionary significance. Among chimpanzees (*Pan*

troglydytes), food sharing often involves meat from hunts, where individuals share the spoils with others who may provide support in future conflicts or hunts, demonstrating a complex form of reciprocity and alliance-building (Mitani, 2009; Muller and Mitani, 2005). Capuchin monkeys (*Cebus capucinus*) are also known for their food-sharing behaviours, which are thought to reinforce social bonds within their groups and play a crucial role in social hierarchy and cooperation (Jaeggi and Gurven, 2013). Intriguingly, in tamarins (*Saguinus* spp.) and marmosets (*Callithrix jacchus*), food sharing even extends beyond simple parental care, involving entire groups where adults and even older siblings share food with juveniles, supporting the cooperative breeding system that is characteristic of these species (Feistner and Price, 1990; Guerreiro Martins et al., 2019) and helps maintain group cohesion and ensures all members are nourished (Feistner and Price, 1990).

In the realm of primate sexual relationships, social trade and cooperation also play a pivotal role. A study in long-tailed macaques found evidence of a grooming-mating trade, where male-to-female grooming was associated with increased rates of sexual activity (Gumert, 2007)

These examples highlight the adaptive value of cooperation in primates, showing how it is intricately woven into the fabric of their social lives, affecting everything from daily survival to complex social dynamics and intercommunity relationships. These behaviours are critical not only for the immediate benefits they provide but also for the long-term stability and evolutionary success of primate groups. Through detailed empirical studies, researchers continue to unravel the intricacies of cooperation among primates, shedding light on the evolutionary origins of social behaviour in these fascinating animals.

1.1.3 How to measure cooperation

The study of cooperation in animals has long been a central focus in comparative psychology, where experimental designs have evolved to highlight the complex mechanisms underlying collaborative behaviours. String-pulling experiments, a cornerstone of comparative psychology, test the ability of animals to coordinate actions to solve cooperative tasks (Jacobs and Osvath, 2015). The loose-string paradigm is the most popular task, where participants must simultaneously pull on a string attached to a reward-laden tray. In this experiment, two animals are required to pull simultaneously on both ends of a string to bring a platform, which is baited with food rewards, within reach. If only one end of the string is pulled, the other end moves out of reach, rendering the baited platform inaccessible (Heaney et al., 2017). Such tasks are

designed to be impossible for an individual to accomplish alone, emphasizing the necessity of cooperation.

Originally developed over a century ago, this paradigm has evolved into numerous variations, known as string patterns, and has been employed in studies involving more than 163 species of mammals and birds. This diversity underscores the method's versatility and its importance in studying behavioural psychology (Jacobs and Osvath, 2015). The loose-string version is particularly notable for testing how animals synchronize their efforts both spatially and temporally, offering insights into the cognitive and social dynamics underpinning cooperative behaviour (Massen et al., 2019).

For instance, Meredith Crawford's 1936 study with chimpanzees pioneered this line of inquiry, demonstrating that cooperation could be induced through experimenter intervention (Nissen and Crawford, 1936). In this study, chimpanzees were tasked with pulling ropes connected to a heavy box to access food. Initially unable to solve the task solo, they learned to coordinate their efforts following guidance, illustrating not only their ability to cooperate but also their capacity to learn from situational cues (Hirata and Fuwa, 2007; Nissen and Crawford, 1936). Further exploring avian intelligence, research on keas, a parrot species endemic to New Zealand, revealed their exceptional cooperative capabilities. In experiments assessing cooperative cognition, keas displayed the ability to delay gratification significantly longer than previously observed in other non-human animals, waiting for over a minute for a cooperative partner when necessary (Heaney et al., 2017). Elephants, too, have shown cooperative skills in the loose-string paradigm. They can synchronize with a partner to simultaneously pull a rope to achieve a common goal. Notably, these elephants demonstrated patience, waiting up to 45 seconds for a partner to be ready to cooperate, which suggests a sophisticated level of social awareness and a deep understanding of the task's cooperative demands (Plotnik et al., 2011). In comparative studies involving wolves and dogs, wolves consistently outperformed dogs in the cooperative string-pulling task. This disparity likely stems from wolves' social dynamics that facilitate effective coordination and conflict management, allowing them to engage simultaneously without hesitation. These findings underscore the impact of social structure on the ability to coordinate actions in cooperative contexts, with wolves adapting quickly to complex cooperative tasks (Marshall-Pescini et al., 2018, 2017).

While the loose-string paradigm has provided valuable insights into the mechanics of animal cooperation, its application has notable limitations. Specifically, most of these studies do not require animals to actively recruit a partner. This aspect of cooperation, which is more cognitively demanding than selecting a cooperative apparatus when a partner is already present, remains underexplored (Range et al., 2019). Moreover, although dyadic experiments reveal whether individuals are capable and motivated to cooperate, they primarily illuminate the cognitive mechanisms underpinning these interactions. However, they offer limited insights into the complexities of large group cooperation observed in wild animals. Cooperating with just one other individual involves certain abilities such as spatial and temporal coordination, yet the dynamics become increasingly complex as group sizes expand. This complexity suggests a need for studies that extend beyond the dyad to more accurately reflect the group-level cooperation seen in natural settings (Williams et al., 2022). Additionally, most experimental studies, including those on primates, elephants, and birds, limit the ability of subjects to choose their partners. This constraint is significant as it may impact the ecological validity of the findings, failing to replicate the nuanced social choices and strategies that animals employ in natural environments (Suchak et al., 2014). These limitations highlight the importance of designing experiments that more accurately simulate the natural conditions under which animal cooperation evolves and is maintained. Addressing the limitations of dyadic studies, recent research advocates for more ecologically valid approaches. These include studying cooperation within the natural social structures of animal groups, considering the influence of multiple individuals and their social dynamics (Marshall-Pescini et al., 2016).

One innovative method that addresses these concerns is the loose-string paradigm in a group context. This approach allows for free choice of participation and partners, capturing spontaneous and voluntary cooperation within a group context. For instance, studies on chimpanzees in large outdoor enclosures have shown that individuals can spontaneously engage in cooperative tasks, even without specific training, highlighting the potential of this paradigm to reveal naturalistic cooperative behaviours (Suchak et al., 2014).

In summary, while dyadic studies have contributed significantly to our understanding of cooperation, they are limited in capturing the complexity of natural interactions. The loose-string paradigm in a group context offers a promising alternative by enabling the study of cooperation within the dynamics of primate social groups, providing valuable insights into the evolution and mechanisms of cooperative behaviours.

1.2 Study species: The Bonobo

Bonobos (*Pan paniscus*), one of our closest living relatives, is a highly interesting species to study cooperative decision making because of several reasons. Sharing 98% of their DNA with humans, they serve as critical models for understanding our own development and behaviour (King et al., 1988). One of these, is their fission-fusion social structure, in which individuals form groups that frequently change in size and composition, often including members of both sexes and all age groups (Badrian and Badrian, 1984; White, 1986; Nishida, 1979; Kuroda, 1979). Bonobos are also characterized by a female centred and co-dominated social organization. Bonobos are a male philopatric species meaning that males stay in their natal group when reaching the age of sexual maturity while females disperse to neighbouring groups (Furuichi, 1989; Kano and Kano, 1992). Therefore, the social system of bonobos is distinctive because it includes a female-centered structure with extensive affiliative interactions between females even though females are not related. This heightened female sociality is likely linked to reduced competition for food, which not only allows for more stable and cohesive female groups but also provides a strategic advantage in defending food resources against other group members or rival communities (White, 1996).

In addition, mothers support their adult sons in agonistic conflicts, allowing their sons to obtain higher dominance positions (Furuichi, 1989; Furuichi and Ihobe, 1994; Kano and Kano, 1992; Surbeck et al., 2011). In bonobos, association patterns are mainly determined by mother-infant relationships (Surbeck et al., 2017b). This matriarchal structure is particularly evident in how females influence social interactions within the group, where newly immigrated females often seek the older adult females for integration and social guidance (Furuichi, 1989; Idani, 1991). These senior females not only command central roles in the daily social fabric of the group but also in the socio-political landscape, affecting the affiliations and status of males within the group, where a male's rank is significantly impacted by his maternal relationship (Kano, 1986; Furuichi, 1988b). Male-male dyads on the other hand do not form strong bonds or share food but do occasionally form coalitions against other males (Furuichi and Ihobe, 1994; Kano and Kano, 1992; Stevens et al., 2006; Surbeck et al., 2017a; Surbeck and Hohmann, 2015).

During periods of resource abundance bonobos display remarkable social cohesion, often congregating in large, stable groups to exploit these resources collectively. This contrasts with their closest relatives, the chimpanzees, who tend to disperse into smaller factions under similar

conditions (White and Chapman, 1994). Such cohesive behaviour is facilitated by social practices like grooming or socio-sexual interactions, which serves not only to reinforce social bonds but also to mitigate tension during high-stress situations. This behaviour, observed in both natural and captive settings, is often associated with feeding and is thought to ease group excitement and facilitate cooperative behaviours like food sharing and mating (de Waal and Luttrell, 1988; Kano, 1980).

Furthermore, bonobos have been suggested to exhibit a remarkable level of social tolerance, both within their own groups and when interacting with neighbouring communities (Cheng et al., 2022, 2021; Hohmann and Fruth, 2002; Kano and Kano, 1992; Sakamaki et al., 2018; Tokuyama et al., 2019), but Cronin et al (Cronin et al., 2015) actually show that their level of tolerance is not as high as usually suggested. This high level of tolerance facilitates the exchange of resources and fosters cooperative interactions, contributing to the resilience of bonobo societies.

1.2.1 Conflicting results

Described as among the most peaceful of primates, early studies suggested bonobos to exhibit a remarkable propensity for tolerance, prosociality and cooperation, setting them apart from other great ape species. However, more recent studies on bonobo behaviour provide a more varied perspective on this popular image of bonobos (Verspeek et al., 2022). Observations of voluntary food sharing among bonobos revealed a preference for sharing highly desirable food, even at a cost to themselves. This behaviour was not influenced by factors such as satiation or kinship, suggesting a potential altruistic motivation (Hare and Kwetuenda, 2010; Tan and Hare, 2013). However, studies implementing validated prosociality paradigms indicated that adult bonobos did not consistently exhibit prosocial behaviour (Tan et al., 2015; Verspeek et al., 2022) This suggests a lack of prosocial tendencies in controlled experimental settings. Conversely, other studies examining social tolerance among bonobos also yielded mixed results. While some studies suggested greater social tolerance compared to chimpanzees (Hare et al., 2007) our other closest living relatives, others found no significant difference or even lower social tolerance in bonobos (Cronin et al., 2017; Jaeggi et al., 2010). These conflicting findings indicate a complex interplay of social dynamics in different contexts. This may be influenced by age effects. Indeed, research that reports high levels of prosociality, such as helping and food sharing, predominantly involves subadults and juveniles (bonobos are categorized into different age groups: infants (0-1 year), juveniles (2-6 years), adolescents (7-

14 years), and adults) (Hare et al., 2007; Hare and Kwetuenda, 2010; Kano and Kano, 1992; Tan et al., 2015). However, in mixed-age groups, these high levels of social tolerance, cofeeding, and prosocial behaviours were not observed (Bullinger et al., 2013; Cronin et al., 2015; Jaeggi et al., 2010). Part of these conflicting conclusions is related to the use of different paradigms in highly controlled experimental paradigms. Dyadic studies with pre-selected participants have long been fundamental in unravelling the intricacies of cooperation among non-human primates, particularly in the realm of comparative psychology. One of the most prevalent methods, the string-pulling paradigm, has been extensively employed to probe into the cognitive abilities and social dynamics of various species (Jacobs and Osvath, 2015). However, despite their widespread application, these studies often lack clarity in reporting and fail to address the nuanced cognitive mechanisms underlying cooperative behaviours in a biological context (Marshall-Pescini et al., 2016).

The great variety of cooperative interactions across the animal kingdom involve reciprocal prosocial acts between partners. Therefore, prosociality is proposed as the proximate promoter of cooperation (Fletcher, 2008; Jaeggi, Burkart, & van Schaik, 2010; Silk, 2012). Several hypotheses have been proposed to explain how prosociality evolved and thus how cooperative interactions can be beneficial over the long term. They explain prosociality at different levels but are not mutually exclusive as prosociality has been suggested to multidimensional and flexible (review in Verspeek et al., 2022): self-domestication hypothesis, cooperative breeding hypothesis, empathy hypothesis.

The self-domestication hypothesis posits that certain species, including bonobos, have undergone a process akin to domestication during evolution. This process is believed to result in increased tolerance, decreased aggression, and a heightened propensity for cooperation (Hare, 2017). Bonobos have been identified as potential candidates for self-domestication due to their markedly reduced aggression compared to chimpanzees (Wrangham and Pilbeam, 2002). Unlike chimpanzees, bonobos exhibit minimal aggression within their groups, with no instances of lethal aggression recorded among them. This reduced aggression is attributed to selection for intragroup prosociality, driven by preferences for less aggressive mates.

Consequently, the self-domestication hypothesis predicts that bonobos will display high levels of tolerance, cooperation, and prosocial behaviour in tasks like the loose-string paradigm, reflecting their evolved inclination towards peaceful social interactions (Hare et al., 2012a).

The cooperative breeding hypothesis suggests that bonobos may not exhibit high levels of prosociality. Cooperative breeding, observed in various mammalian and bird taxa, entails individuals assisting in raising offspring that are not their own (Jennions, 1994a). While early explanations for such behaviours focused on kin selection, recent evidence emphasizes the importance of direct benefits in maintaining cooperation (Bergmüller et al., 2007a). Since bonobos are non-cooperative breeders, they are expected to show low levels of prosociality and might prioritize their own benefits over collaborative efforts, potentially leading to less successful cooperation. This hypothesis implies that bonobos may not demonstrate extensive prosocial behaviours due to competing reproductive interests (Bergmüller et al., 2007a; Jennions, 1994a).

The empathy hypothesis proposes that bonobos, with their elevated levels of empathy, are predisposed to engage in prosocial behaviours (Marshall-Pescini et al., 2016). Empathy, defined as the ability to share and understand the feelings of others, is considered a driving force behind cooperative interactions in both humans and non-human species (De Waal, 2018). Bonobos have shown evidence of empathy through behaviours like consolation and yawn contagion, indicating their capacity for emotional resonance with conspecifics (De Waal, 2018). Accordingly, the empathy hypothesis predicts that bonobos will exhibit high levels of cooperation in tasks like the loose-string paradigm, driven by their genuine concern for the well-being of others (De Waal, 2018; Marshall-Pescini et al., 2016).

In summary, these three hypotheses offer distinct perspectives on the expected cooperative behaviour of bonobos in the loose-string paradigm. By considering the influence of self-domestication, cooperative breeding tendencies, and empathy, researchers aim to gain a comprehensive understanding of the underlying mechanisms driving cooperation in this species.

1.3 Objectives

In this study, we aim to study cooperation in bonobos in a group context, complementing dyadic studies. Therefore, there is a need for cooperative paradigms in a more naturalistic setting to allow for more biologically relevant interactions. To enhance the relevance of our study, we will introduce two apparatuses in parallel, freely accessible to all individuals in the group.

First, to be able to link the levels of successful cooperation to relevant social factors, we aim to determine the relationship quality among all bonobo dyads of the study group. Next to validate our findings, we aim to compare our results to published results by investigating the effects of age difference and genetic sex combination on the components of relationship quality. Furthermore, to visualize our findings on relationship quality, we aim to generate sociograms for each of the relationship quality components.

- We aim to use the model described by Stevens et al (2015) and Verspeek et al (2019). Using the same method and behavioural variables, we expect to find the same two components: Relationship Value and Incompatibility. We also expect that these components will be influenced by genetic-sex-combination, with mother-child dyads having a higher Value and lower Incompatibility compared to other dyads (Stevens et al., 2015; Verspeek et al., 2019).

Second, we aim to explore bonobo cooperation in a group context using a modified version of the loose-string paradigm (Hirata and Fuwa, 2007; Melis et al., 2006).

- Following the self-domestication hypothesis, bonobos are expected to be very tolerant, cooperative and prosocial; and thus, would behave highly cooperative, also in this group context.
- Based on the cooperative breeding hypothesis, bonobos are not expected to behave very prosocial and thus not cooperate that successfully.
- Based on the empathy hypothesis, bonobos are expected to behave prosocially according to their high levels of empathy, which would result in high levels of cooperation.

Finally, we aim to explore which of the following factors influence cooperative interactions and presence around the set-up: social relationship, genetic-sex-combinations and age difference between the participating subjects.

- Social relationship: based on the two components of relationship quality, we predict that dyads with higher Value and lower Incompatibility will cooperate more.
- Genetic-sex-combination: based on as the socio-ecology of bonobos where females engage in agonistic coalitions, we predict that female-female dyads may be more likely to cooperate. We also predict that mother-offspring dyads are successful cooperators as association patterns are mainly determined by mother-infant relationships (Surbeck et al., 2017b).
- Age: based on age effect hypothesis, we aim to see if young individuals are more likely to interact with the set-up.

2 Materials and methods

2.1 Study site

The study was conducted at the Planckendael Zoo in Mechelen, Belgium, focusing on a population of bonobos. The study included a total of 22 individuals, housed into two groups, with 11 adult or adolescent females, 6 adult or adolescent males, and 5 juveniles. The composition of these groups varied over the course of this study due to management purposes.

Observations were only carried out on individuals that were older than 7 years ($n = 17$), listed in Table 1. The bonobos were housed in an enclosure consisting of 10 interconnected rooms covering (422) m², along with an outdoor area spanning 3000 m² (figure 1). Specific rooms were allocated to each group to maintain separation, and rooms were enriched with climbing structures, ropes, nets, and other environmental enhancements. The bonobos were given the choice between accessing the indoor and outdoor areas, with a daily rotation between the two groups. On any given day, one group had access to the outdoor area while the other remained indoors, and this configuration was reversed the following day. This rotation ensured that each group had equal access to both environments.

The bonobos received three meals daily at 9:00 am, 1:00 pm, and 3:50 pm, consisting of a variety of vegetables, with *ad libitum* access to water. Additional smaller food items are provided in enrichment items once or twice a day. The observation period spanned 8-10 weeks, totalling 50 days. Observations were conducted between 8:30 am and 5:00 pm on average.

Table 1 : Overview of the sex, year of birth, place of birth and parents of the 17 studied individuals.

Individual	Abbreviation	Sex	Year of birth	Born	Parents
<i>Hortense</i>	HO	F	1978	DRC	Unknown
<i>Vifjo</i>	VI	M	1994	Planckendael	Kidogo II x <u>Hortense</u>
<i>Zamba</i>	ZA	M	1998	Planckendael	Kidogo II x <u>Hortense</u>
<i>Kikongo</i>	KK	M	2014	Apenheul	Bolombo x <u>Hortense</u>
<i>Djanao</i>	DJ	F	1995	Berlin Zoo	Santi x Yala
<i>Habari</i>	HB	M	2006	Planckendael	<u>Vifjo</u> x <u>Djanao</u>
<i>Busira</i>	BS	F	2004	Wuppertal	Birogu x Eja
<i>Sanza</i>	SA	F	2017	Planckendael	Lucuma x <u>Busira</u>
<i>Banya</i>	BY	F	1990	Keulen	Clyde x Bonnie
<i>Mokonzi</i>	MZ	M	2013	Twycross	Luo x <u>Banya</u>
<i>Kianga</i>	KG	F	2005	Stuttgart	Diwani x Kombote
<i>Moko</i>	MK	M	2016	Twycross	Keke x <u>Kianga</u>
<i>Nayembi</i>	NA	F	2006	Apenheul	Mobikisi x Liboso
<i>Nila</i>	NL	F	2015	Stuttgart	Kasai x <u>Nayembi</u>
<i>Binti</i>	BT	F	1995	Frankfurt	Bono x Ukela
<i>Bina</i>	BN	F	2015	Cologne	Clyde x <u>Binti</u>
<i>Swahili</i>	SW	F	Unknown	Vallée des singes	David x Lingala

*Underlined individuals are present in the study group

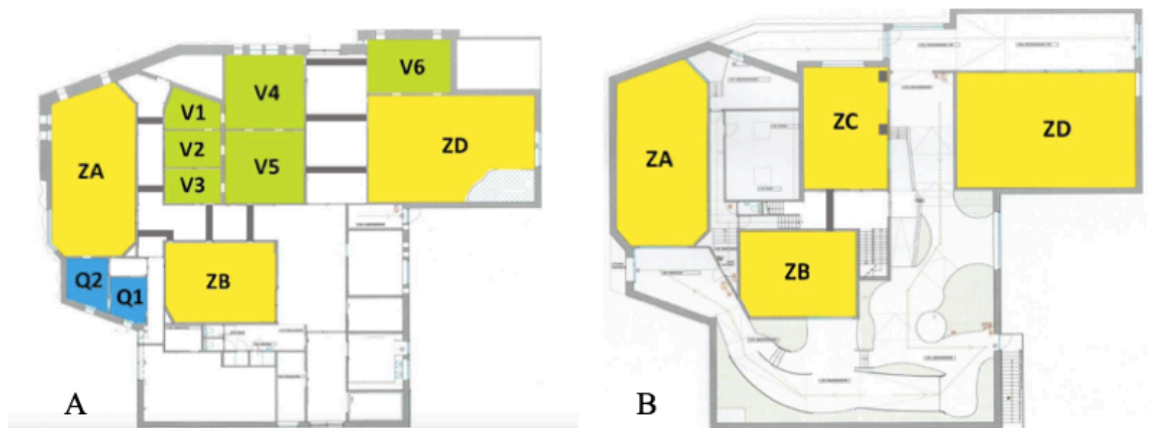


Figure 1 Layout of the inside enclosure. Layout of A) the entire enclosure with the tunnels connecting them and B) the areas visible for visitors.

2.2 Observation protocol

Data collection was carried out by a sole observer, the author of this study. Prior to initiating data collection, the observer underwent a comprehensive training period lasting three weeks. This training involved the acquisition of essential skills and knowledge necessary for accurate and consistent observations. To validate proficiency, the observer was required to pass an inter-observer-reliability test, achieving a minimum score of 70%.

Throughout the observation period, a standardized ethogram was employed (Stevens et al., 2023). This ethogram served as a structured guide, ensuring uniformity in the recorded behaviours across all observations. The use of a standardized ethogram enhances the reliability and comparability of the data collected during the study.

Three observation methods were employed: continuous focal sampling, continuous group sampling, and group scan sampling (Altmann, 1974). Continuous focal sampling was used during ten-minute sessions randomly focusing on individual bonobos, recording all of their behaviours... This method involves recording all specific interactions of an individual during each observation period. We captured not only the focal animal's actions but also behaviours directed towards it by others. Continuous group all occurrence sampling was applied during feeding sessions to capture prevalent interactions, with a particular emphasis on aggressions and sexual actions observed ad libitum, providing the advantage of observing all animals simultaneously. Group instantaneous scan sampling was implemented before each focal sample to record behaviours and proximities of all individuals, providing a snapshot of the group's dynamics. Proximities are noted as "sit alone," "sit with close," "sit with near," or "sit with touch" depending on the distance to another individual (touch: body of subject and receiver touch each other; close: body of subject and receiver are within one meter (or one arm length); near: body of subject and receiver are within 2 meters (or 2 arm lengths)).

Observations were recorded using Noldus 'The Observer' software, version XT14. The data collection process involved the use of a camera system installed within the bonobos' enclosures, enabling both live and recorded observations. This system provided the flexibility to monitor the bonobos' behaviours in real-time as well as to review recorded footage at a later time. The selection of focal individuals can be randomized using a table of random numbers, with individuals chosen randomly from the entire group. This randomization process was employed in our data collection procedure. We collected a total of 93.54 hours of focal observations (mean

5.50 hours per individual), 484 group scans (mean 28 per individual) and 36.60 h of all occurrence observations during feedings (16.26 for group 1 and 20.34 for group 2).

2.3 Apparatus

In our study, we implemented a modified version of the loose-string paradigm to investigate cooperative behaviours among bonobos (Hirata and Fuwa, 2007; Melis et al., 2006). The apparatus featured a simple yet effective design: a movable board on which a rope was laid around two anchoring points such that each end of the rope extended to either side of the board. At both sides of the board, grapes were strategically placed as food reward. These grapes were set far enough from the mesh that they could not be reached by the bonobos directly through the mesh, thus necessitating an element of cooperation for retrieval (see Figure 2). The core mechanism of the apparatus required that two individuals pull on each side of the rope simultaneously. This action would cause the board to slide closer, allowing the grapes to come within reachable distance. The design of the ropes and the placement of the board were such that a single bonobo could not perform both roles — pulling both ends of the rope — simultaneously. If an individual attempted to pull the rope alone, the slack in the rope would simply draw it closer to them without moving the board, thus failing to bring the grapes any closer.

The testing occurred in a group setting, with the bonobos having access to a subset of interconnected indoor rooms. This arrangement allowed them to interact with the setup in a semi-naturalistic environment, promoting natural behaviours while under observation. This setup not only facilitated the study of cooperative dynamics in a controlled environment but also allowed for the observation of social interactions and problem-solving strategies within the group. In this study, two identical versions of the loose-string apparatus were presented at the same time and were placed in front of the mesh of rooms V5 and ZB (see Fig. 1).

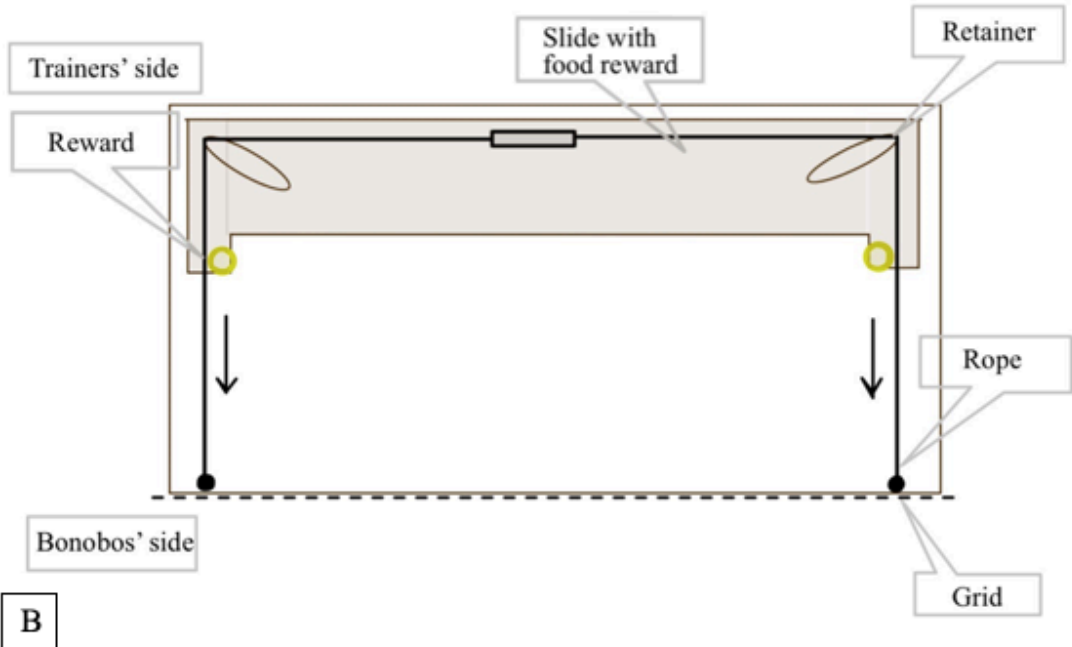
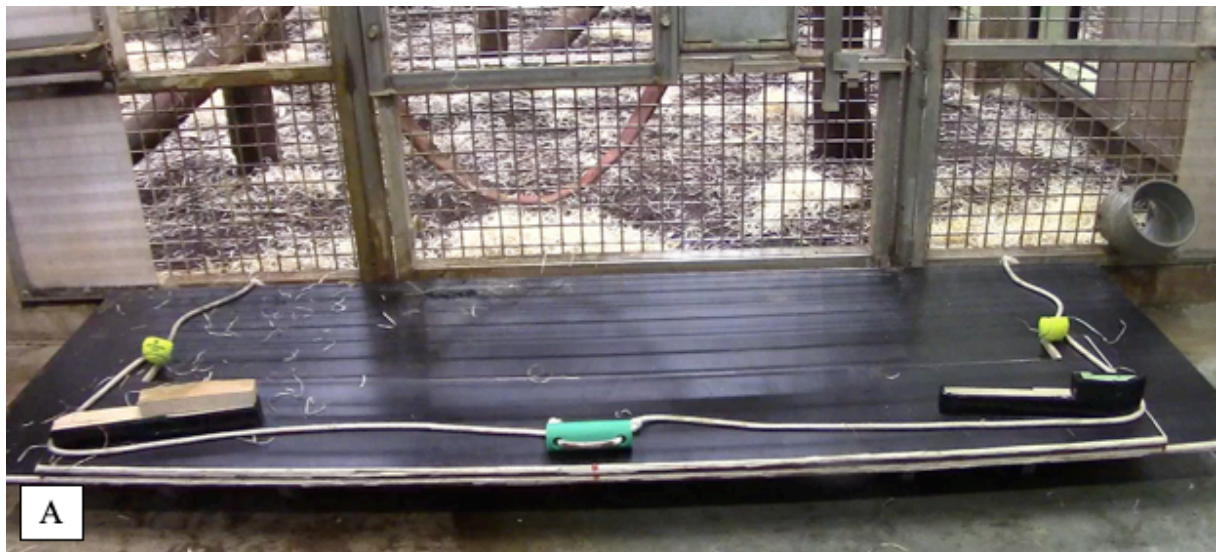


Figure 2 Experimental set-up. A. Photograph showing the set-up from the trainers' side. B. Schematic drawing of the set-up from above.

2.3.1 Procedures

Familiarization Phase: Prior to conducting the cooperation tests, it was crucial to acclimate the bonobos to the cooperation apparatus. The board was initially positioned close to their enclosure, allowing the bonobos easy access to the food without the need for pulling. This step ensured that the bonobos became familiar with the apparatus and understood that it was a source of food. To draw their attention and enhance their interest, food was prominently displayed and

held up before initiating a trial. This familiarization process was designed to reduce any novelty-related anxiety and to facilitate a smoother transition to the actual testing phase.

Testing Phase: The testing phase began by positioning the platform such that the ropes were within reach of the bonobos, with food placed on it to entice participation. Each trial was initiated under these conditions. Upon successful completion of a trial, where the bonobos cooperatively pulled the ropes to bring the platform closer and accessed the food, the experimenter waited for the animals to release the ropes before removing the platform out of their reach. This was done to reset the apparatus with the rope and food properly repositioned for the next trial. If the bonobos failed to solve the task within a predetermined time frame (designated as 1 minute (Martin et al., 2021)), the trial was marked as a failure and the platform was removed. Each testing session consisted of 10 trials conducted simultaneously in two separate rooms, V5 and ZB. Cooperative behaviour was evaluated by observing how the bonobos engaged in pulling the ropes during these sessions. The interactions were categorized into three main types: alone interactions, dyadic interactions, and no interactions. Alone interactions were those where only one individual pulled the rope. Dyadic interactions involved two individuals, and no interactions were trials where no participants engaged with the setup. This categorization allowed for a detailed analysis of the different types of interactions.

Successes and failures were meticulously recorded for each trial. A success was defined as a cooperative interaction that resulted in a positive outcome, whereas failures were recorded when the interaction did not yield a successful result. This binary classification helped in quantifying the effectiveness of the cooperative interactions.

2.4 Data analysis

2.4.1 Determining Relationship Quality (RQ)

In this study, we assessed the relationship quality among all bonobo dyads using a model that has previously been described (Stevens et al., 2015; Verspeek et al., 2019) (see appendix for an explanation about how the model was defined). In short, to determine the relationship quality for each of the dyads of the study population, we extracted dyadic scores for eight behavioural variables, that were collected in naturalistic interactions: aggression frequency, aggression symmetry, counter-intervention, grooming frequency, grooming symmetry, peering frequency, proximity, and support (For definitions see Table 2). Using the *predict ()* function we fitted the existing relationship quality model of Verspeek et al. (2019) onto the newly collected dyadic

behaviours, resulting in one Relationship Value and one Relationship Compatibility score for each of the dyads.

We conducted an exploratory factor analysis (EFA) to reduce the behavioural variables into composite factors that represent underlying patterns in relationship quality. In the EFA, varimax rotation and Kaiser normalization was used to extract the composite measures for each of the eight dyadic variables. After initially following Kaiser’s rule to determine the number of components to retain, we confirmed the number of factors through parallel analysis. Significant factor loadings, defined as those at or exceeding |0.4|, were interpreted as indicative of strong contributions to the identified factors, ensuring that our analysis robustly captures the dimensions of relationship quality.

Table 2 : Behavioural variables entered in the Principal Component Analysis (Stevens et al., 2015)

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

In our study, we utilized two linear mixed-effects models (LMEM) to investigate the effects of age difference and genetic sex combination on the components Value (model1) and Incompatibility (model2) of relationship quality. These models were chosen to account for the non-independence of data within groups, with random effects specified for individual participants to handle the variability associated with repeated measures from the same subjects. We conducted an analysis of variance (ANOVA) with a Chi-square test to assess the significance of each fixed effect in the models. This approach allowed us to determine the

contribution of age difference and genetic sex combination to variations in relationship quality measures. Further, pairwise comparisons were performed to explore differences between the categories of genetic sex combination, providing detailed insights into how these factors specifically influence relationship dynamics.

To ensure the robustness of our analysis, we also checked the normality of the distribution of the Value and Incompatibility scores using the Shapiro-Wilk test and visualized its distribution through histogram analysis. To assess the assumptions of normality and homogeneity of variances, we used diagnostic plots (residuals vs. fitted and QQ plots). Furthermore, we evaluated the uniformity and dispersion of the residuals with the DHARMA package (Hartig, 2024).

To visually represent the relationships among individuals in our study, we generated sociograms based on the outcomes from the Value and Incompatibility components of our analysis. We first categorized the relationship values into different classes to differentiate the strength and nature of the interactions. These classes were then used to vary the thickness of the edges in the sociograms, providing a clear depiction of the relationship intensity between pairs of individuals. The sociograms were designed to be undirected, reflecting the mutual nature of the interactions, with individual names labelled for clarity. We employed an aesthetically pleasing layout to ensure that the sociogram was both informative and easy to interpret. The visualization highlighted variations in relationship quality and allowed for an immediate visual interpretation of the complex social dynamics within the group.

2.4.2 Cooperation experiment

The total number of trials (240) was divided into two main categories: all interactions and interactions with another individual (dyadic interactions). All interactions included both alone and dyadic interactions. For the dyadic interactions' category, only trials involving two individuals were considered, excluding trials with no interaction or with a single individual. This segmentation provided a clearer picture of the cooperative dynamics between individuals. The proportion of successes was calculated for both categories. For all interactions, the proportion of successes was determined by dividing the number of successes by the total number of trials (240). For interactions with another individual, the success proportion was calculated by dividing the number of successes in dyadic interactions by the total number of dyadic trials (85). Individual performance was analysed in detail, taking into account the number of interactions alone, interactions with another individual, successes, and failures for each participant. Success proportions were calculated for each individual, both for all

interactions and for interactions with another individual. Bar graphs were used to represent the number of successes per session, the number of trials and successes per dyad, and the breakdown of interactions and successes by individual. Finally, descriptive statistics were employed to summarize the data, with proportions and percentages calculated to provide a clear understanding of the success rates.

3 Results

3.1 Components of relationship quality

Fitting the existing model (Stevens et al, 2015; Verspeek et al, 2019) on our data, we determined the relationship value and compatibility and generated sociograms based on the outcomes from the Value and Incompatibility components of our analysis (Figure 3). The relationship values and compatibilities for this study population ranged from -1.67 to 3.45 and from 0 to 0.86 , respectively.

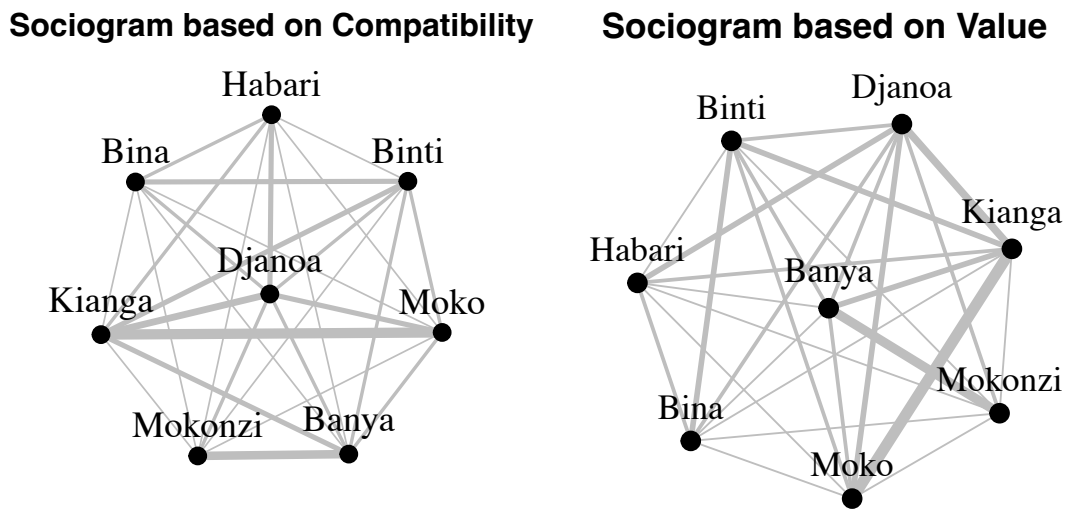


Figure 3 : Sociograms based on the outcomes from the (a) Compatibility and (b) Value components

3.2 Factors influencing relationship quality

The first component of relationship quality, Value, was significantly influenced by genetic sex combination ($\chi^2 = 47.78$, $df = 4$, $p < 0.001$) but there was no significant effect of age difference ($\chi^2 = 0.0029$, $df = 1$, $p = 0.96$).

Female-female dyads demonstrated higher values in comparison to female-male (FM, $n = 27$) dyads ($\beta = 0.63$, $SE = 0.21$, $t = 2.96$, $P = 0.037$). Female-female (FF) dyads also showed lower values compared to mother-daughter (MD, $n = 3$) dyads ($\beta = -1.17$, $SE = 0.40$, $t = -2.94$, $P = 0.037$) and mother-son (MS, $n = 6$) dyads ($\beta = -0.95$, $SE = 0.32$, $t = -2.93$, $P = 0.039$). Additionally, female-male (FM) dyads exhibited significantly lower values compared to both mother-daughter (MD) dyads ($\beta = -1.79$, $SE = 0.40$, $t = -4.45$, $P = 0.0004$) and mother-son (MS) dyads ($\beta = -1.58$, $SE = 0.31$, $t = -5.04$, $P = 0.0001$). Male-male (MM, $n = 6$) dyads displayed significantly lower values compared to MD ($\beta = -2.16$, $SE = 0.51$, $t = -4.25$, $P = 0.0009$) and

MS dyads ($\beta = -1.94$, $SE = 0.41$, $t = -4.76$, $P = 0.0001$). There were no statistically significant differences in value between female-female (FF) and male-male (MM) dyads ($\beta = 0.99$, $SE = 0.38$, $t = 2.58$, $P = 0.10$), nor between mother-daughter (MD) and mother-son (MS) dyads ($\beta = 0.22$, $SE = 0.49$, $t = 0.45$, $P = 0.99$) (Figure 4).

For the second component, relationship compatibility, there were no significant effects of genetic sex combination ($\chi^2 = 5.87$, $df = 4$, $p = 0.21$) or age difference ($\chi^2 = 0.86$, $df = 1$, $p = 0.35$) (all p-values were greater than 0.05) (Table 3).

Table 3 : Effects of genetic sex combination and age difference on the components Value and Compatibility.

Component		Estimate \pm SE	t value	p
Value	Intercept	0.20 \pm 0.23	0.87	0.39
	Age difference	-0005 \pm 0.009	-0.054	0.96
	GSC (FF vs FM)	0.63 \pm 0.21	2.96	0.04
	GSC (FF vs MM)	0.99 \pm 0.38	2.58	0.10
	GSC (FF vs MD)	-1.17 \pm 0.40	-2.94	0.04
	GSC (FF vs MS)	-0.95 \pm 0.32	-2.93	0.04
	GSC (FM vs MM)	0.36 \pm 0.30	1.20	0.75
	GSC (FM vs MD)	-1.79 \pm 0.40	-4.45	<0.001
	GSC (FM vs MS)	-1.58 \pm 0.31	-5.04	<0.001
	GSC (MM vs MD)	-2.16 \pm 0.51	-4.25	<0.001
	GSC (MM vs MS)	-1.94 \pm 0.41	-4.76	<0.001
	GSC (MD vs MS)	0.22 \pm 0.49	0.45	0.99
Compatibility	Intercept	0.066 \pm 0.18	0.36	0.72
	Age difference	-0.008 \pm 0.008	-0.93	0.36
	GSC (FF vs FM)	-0.19 \pm 0.19	-1.03	0.84
	GSC (FF vs MM)	-0.17 \pm 0.32	-0.53	0.98
	GSC (FF vs MD)	0.44 \pm 0.39	1.14	0.79
	GSC (FF vs MS)	0.31 \pm 0.30	1.03	0.84
	GSC (FM vs MM)	0.02 \pm 0.29	0.083	1.00
	GSC (FM vs MD)	0.63 \pm 0.38	1.65	0.47
	GSC (FM vs MS)	0.50 \pm 0.29	1.74	0.42
	GSC (MM vs MD)	0.61 \pm 0.46	1.33	0.67
	GSC (MM vs MS)	0.48 \pm 0.37	1.3	0.69
	GSC (MD vs MS)	-0.13 \pm 0.45	-0.29	1.00

Significant results are in **bold**. GSC: Genetic Sex Combination

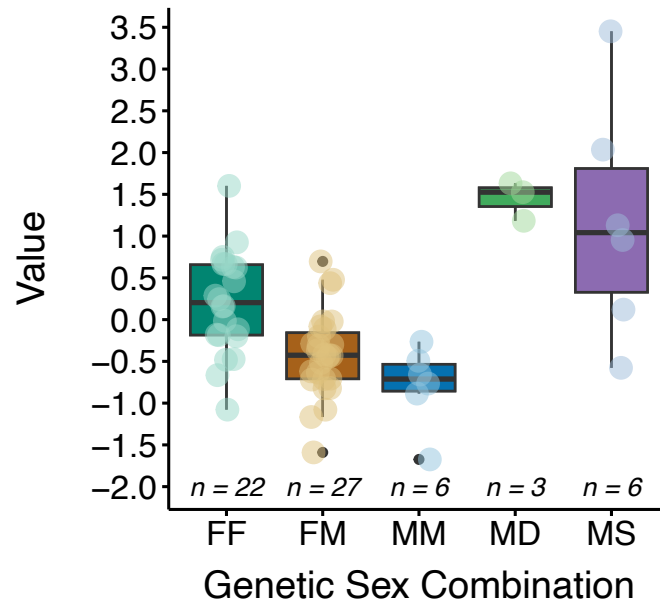


Figure 4 Median relationship value of unrelated male-male (MM), unrelated female-male (FM), unrelated female-female (FF), mother-daughter (MD) and mother-son (MS) dyads.

3.3 Cooperation experiment

A total of 12 sessions were conducted, with 2 simultaneous setups. Each session comprised 10 trials, resulting in a total of 240 trials. Out of these 240 trials, there were 26 successes, yielding a cooperation success rate of 11%. When considering only the trials during which two individuals were present—excluding those where no interaction occurred and those where only a single individual was present—there were 85 trials. In this subset, the success rate was 31%. Figures 5, 6, and 7 present the results by session, by dyad, and by individual respectively. Table 4 provides the detailed data for each individual who interacted with the setup at least once in the presence of another individual.

3.3.1 Number of Successes per Session

The Figure 5 illustrates the distribution of successes across the 12 sessions. The data shows a variation in the number of successes per session, with session 2 having the highest number of successes ($N = 7$), followed by session 9 ($N = 4$), and sessions 7, 10, 11, and 12 each having 3 successes. Sessions 1, 4, 5, and 6 had no successes at all.

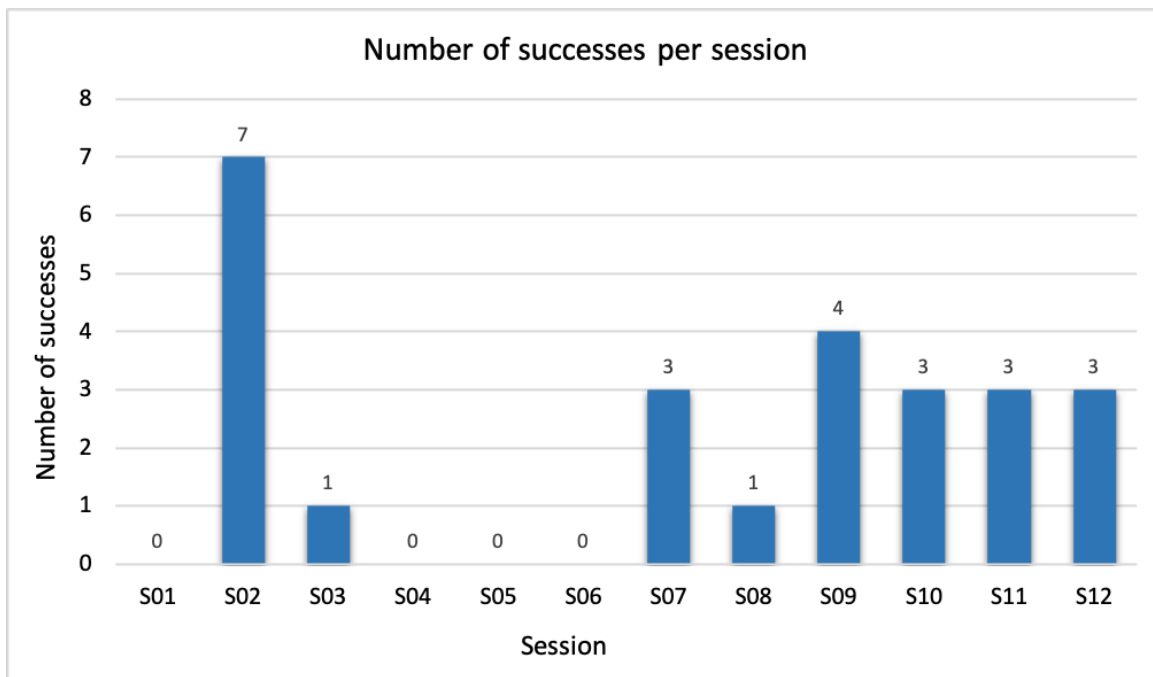


Figure 5 Distribution of successes across the 12 sessions.

3.3.2 Number of Trials and Successes per Dyad

Figure 6 presents the number of total trials and the number of successes for each dyad. The dyad KG-SW participated in the highest number of trials ($N = 24$) and achieved the most successes ($N = 8$). Other notable dyads include NA-SW and NA-WK, with 8 trials, and achieving 3 and 2 successes respectively. Only 10 out of the 59 possible dyads cooperated successfully during the loose-string experiment.

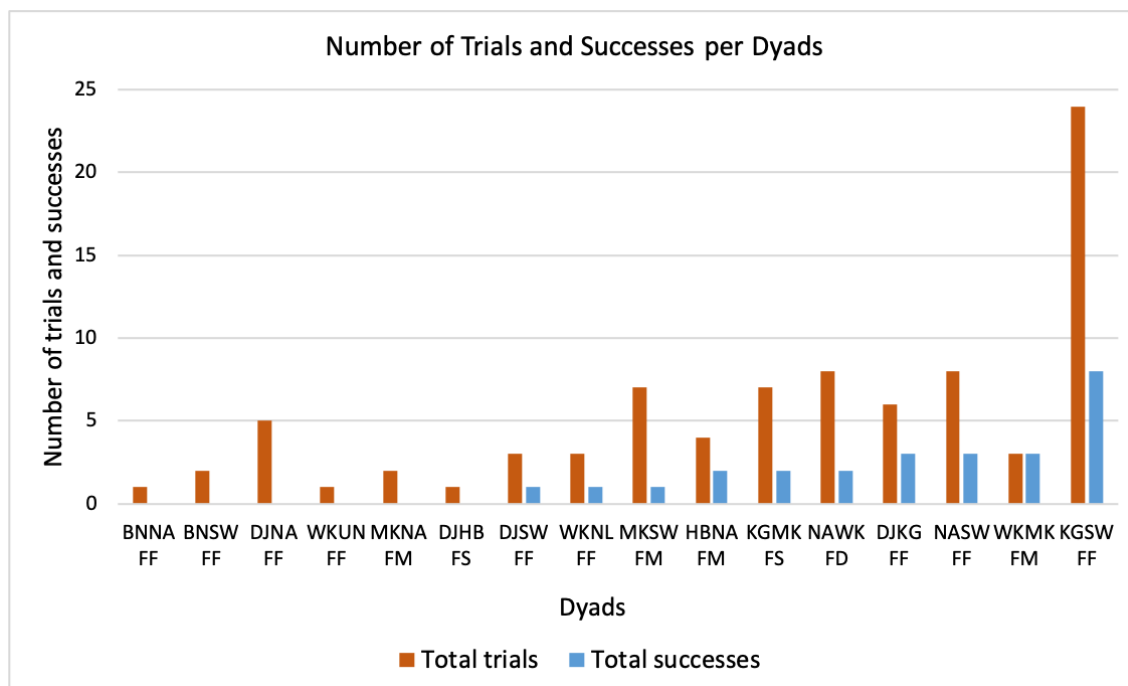


Figure 6 Number of total trials and the number of successes for each dyad

3.3.3 Breakdown of Interactions and Successes by Individual

Figure 7 provides a comprehensive view of the number of participations in the experiment (alone and with another individual), failures, and successes for each individual. Swahili (SW) participated the most (N = 89) and had most successful cooperative interactions (N = 13). Kianga (KG) also had a high number of interactions (N = 51) and successes (N = 13). Other individuals with notable performance are NA, MK, and WK, with numbers of both interactions and successes. The analyses of individual performance revealed varying levels of success and interaction among the participants. The table 4 below summarizes the data for each individual, including the number of interactions, successes, and failures, as well as the proportion of successes for all interactions and specifically for interactions with another individual. Among the 12 individuals who interacted with our setup, there were 3 juveniles (2-6 years), 4 adolescents (7-14 years), and 5 adults, with only 3 being males and 9 being females, indicating a higher proportion of females.

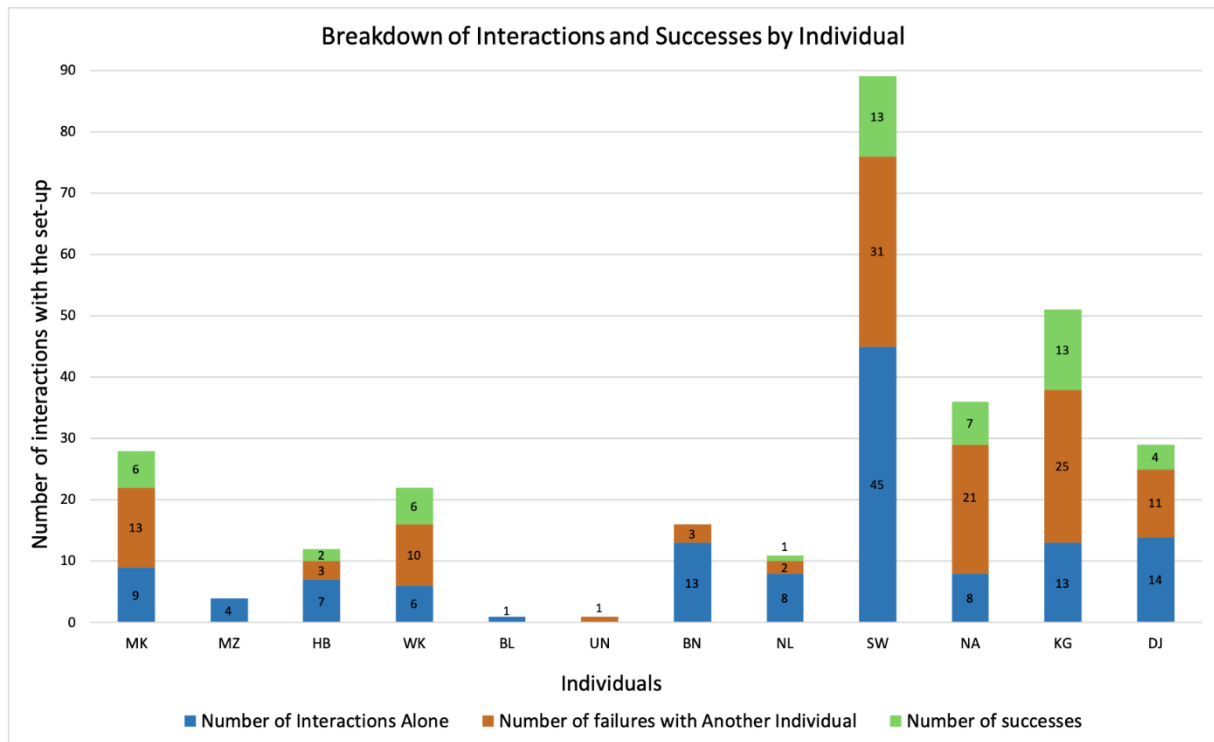


Figure 7 Number of participations in the experiment (alone and with another individual), failures, and successes for each individual.

Table 4 : Data for each individual, including the number of interactions, successes, and failures, as well as the proportion of successes for all interactions and specifically for interactions with another individual.

Subject	Total ^o	Alone [']	With Partner ^{''}	Failures with Partner	Successes	Proportion Success/Total	Proportion Success with Partner
Bina	16	13	3	3	0	0%	0%
Mokonzi	4	4	0	0	0	0%	0%
Nila	11	8	3	2	1	9%	33%
Habari	12	7	5	3	2	17%	40%
Djanoa	29	14	15	11	4	14%	27%
Moko	28	9	19	13	6	21%	32%
Wakati	22	6	16	10	6	27%	38%
Nayembi	36	8	28	21	7	19%	25%
Kianga	51	13	38	25	13	25%	34%
Swahili	89	45	44	31	13	15%	30%
Balina	1	1	0	0	0	0%	0%
Unabii	1	0	1	1	0	0%	0%

^o Total number that each subject participated

['] Total number that subjects interacted with the set-up alone

^{''} Total number that subjects interacted with the set-up with a partner

4 Discussion

4.1 Relationship quality

The first component of relationship quality, Value, was significantly influenced by genetic sex combinations but not by age differences. As previously described in the literature, female-female dyads had higher values compared to female-male dyads, and lower values compared to both mother-daughter and mother-son dyads. Female-male and male-male dyads had lower values compared to both mother-daughter and mother-son dyads. For the second component, Compatibility, no significant effects were observed based on genetic sex combination or age difference.

These results align with findings from other studies (Stevens et al., 2015; Verspeek et al., 2019).. Indeed, Stevens et al. (2015) also found no effect of age difference on relationship Value and Compatibility. In several studies, mother-child dyads in bonobos have been shown to have strong bonds. This is particularly evident in mother-son relationships, where bonds are exceptionally strong (Furuichi and Ihobe, 1994). This has been observed in captivity, especially in grooming interactions (Stevens et al., 2006). Mothers reduce the proportion of mating by the highest-ranking male and increase the success rate of mating for their sons. Sons and mothers form strong associations, with mothers providing agonistic support to their sons when they are in conflict with other males. Maternal support continues into adulthood in bonobos, as males are philopatric and adult females have high dominance status. It is possible that mothers benefit indirectly from their sons' support for fitness, as evidenced by the lack of female support for unrelated males (Surbeck et al., 2011).

Similarly to other studies, unrelated females maintained higher relationship values compared to those observed between unrelated males and females (Furuichi and Ihobe, 1994). Bonobo females are capable of establishing and maintaining strong affiliative bonds with each other, even when they are not related (Parish, 1996).

The lack of influence of age difference or genetic sex combination on compatibility among bonobos may be explained by their high tolerance levels. Studies have shown that bonobos exhibit lower intensity of both intergroup and intragroup aggression compared to other primates

(Hare, 2017; Hare et al., 2007). Bonobos also use behaviours such as sex and play to reduce social tension during conflicts (Hare et al., 2007; Jaeggi et al., 2010).

Furthermore, rather than being influenced by age or genetic sex combination, compatibility among bonobos may also be influenced by individual personality traits, past experiences, and the quality of social interactions. These individual variations might play a more significant role in shaping social dynamics and reducing intragroup conflict.

4.2 Cooperation

The overall cooperation success rate in the study was 11%, with only a few dyads achieving success. Specifically, out of 59 possible dyads, only 10 showed any successful cooperation. The success rate increased to 31% when only considering only the trials where two individuals cooperated. The level of cooperation varied significantly among individuals, with some, like Swahili and Kianga, showing higher interaction and success rates, while others had little to no success.

The findings of this study are not in line with the self-domestication hypothesis, as bonobos are expected to show high levels of cooperation thanks to their supposedly high levels of tolerance and prosocial tendencies (Hare et al., 2012b). They are in line with the cooperative breeding hypothesis, as cooperative breeding has been linked to higher levels of prosocial behaviour and does likely more successful cooperation (Bergmüller et al., 2007; Jennions, 1994). Since bonobos are non-cooperative breeders, they do not experience the same selective pressures to develop strong prosocial tendencies. This results in a prioritization of individual benefits over collaborative efforts, leading to lower rates of successful cooperation among bonobos. Our observations support this hypothesis, as bonobos showed limited cooperative behaviour, likely due to their reproductive strategy that does not favour extensive cooperation (Bergmüller et al., 2007; Jennions, 1994). Based on the empathy hypothesis however, bonobos are expected to have the capacity to understand the needs and feelings of others, suggesting that they might understand the need to coordinate actions in order to successfully cooperate.

It is important to understand that while theories such as the self-domestication, cooperative breeding and empathy hypothesis describe what species are capable of in terms of prosociality and cooperation, capability does not necessarily translate into action. In other words, simply

because bonobos are capable of cooperating does not imply that they have the motivation to do so. In order to ascertain whether these cooperative behaviours are genuinely displayed, motivation is crucial. When it comes to bonobos, their limited cooperative behaviour may stem from both a lack of motivation to engage in such behaviours and their non-cooperative breeding strategy. To better understand this, researchers have used additional methods to measure the motivation of bonobos in cooperative contexts. For instance, in the study by Melis et al. (Melis et al., 2006), a motivational trial was conducted where unsuccessful dyads in the cooperative task were given the opportunity to retrieve food more easily and succeed at least once to keep them motivated. Using similar motivation trials might ensure that bonobos are attentive and more motivated in order to increase cooperative success.

4.2.1 Understanding the task and behavioural response

In order to provide additional insight into the cooperative behaviours of bonobos, it is necessary to measure both their motivation and their understanding of the tasks that they are expected to complete. Although motivation emphasizes their willingness to participate, understanding their cognitive grasp of cooperative tasks provides important insights into their ability and propensity for cooperative behaviours. The bonobos were introduced to the set-up by approaching it from the grid and we quickly observed that the individuals naturally pulled on the rope. From the very first trials, the bonobos demonstrated the ability to complete the task, indicating that they understood the physical properties of the set-up. This means that the low success rate in our study is probably due to a lack of motivation rather than a lack of understanding of the task.

4.2.2 Factors Influencing Interaction with the Setup

To further understand the nuances of bonobos' cooperative behaviours, it is essential to examine the various factors that influence their interactions with the set-up and contribute to their success or failure in these tasks.

4.2.2.1 Behavioural inhibition and attention to partners

In our study, we observed that bonobos struggled to wait for the other individual to be ready to pull the rope, leading them to pull too early and resulting in a failure of the cooperative task. This inability to inhibit their behaviour might indicate a difficulty in exercising inhibitory control in this specific context. According to Diamond (Diamond, 2013), behavioural inhibition can be described as the ability of individuals to restrain their impulses and delay an action to achieve desired outcomes. This ability is crucial for many forms of cooperation and decision-making. Inhibitory behaviour can be measured using tasks like the detour reaching task that

was used in a study by Ashton et al (2018). In that study, bonobos were presented with a transparent cylinder containing food. They had to refrain from pecking directly at the cylinder and instead detour to the open ends to access the food, demonstrating their ability to inhibit their initial impulses (Ashton et al., 2018). It is interesting to note that in different studies, bonobos have demonstrated the ability to inhibit their behaviour. When given the choice between a smaller, instant reward and a larger reward that needed to be waited for, both chimpanzees and bonobos showed a preference for the larger, delayed rewards and exhibited greater patience compared to other nonhuman animals studied thus far (Rosati et al., 2007). In another study, bonobos were given a delayed-gratification task where food would gradually accumulate until the subject chose to consume the reward. In order to assess the bonobos willingness to wait, researchers used both a reliable and an unreliable experimenter in order to alter the subjects' expectations of receiving the food. Bonobos were less likely to wait with the unreliable experimenter. These findings indicate that individuals' expectations regarding the probability of obtaining future rewards influence their ability to balance present and future needs (Stevens et al., 2011). This apparent contradiction between the findings of my study and the previous reports could be explained by the fact that bonobos, although capable of inhibiting their behaviours, may choose not to exercise this ability in certain contexts. In our study, it is possible that the bonobos were not sufficiently motivated to cooperate. One significant distinction is that in the previously mentioned inhibitory experiments, subjects were tested alone and were provided with food only for themselves (Rosati et al., 2007; Stevens et al., 2011). Our study, on the other hand, requires cooperation in order for both participants to get rewarded. The bonobos' behaviour may be affected by this cooperative aspect in a different way than when they are behaving independently. When cooperation is involved, the dynamics change as individuals need to take into account their partner's actions as well as their own. It is also important to ensure that individuals are attentive to their partner's actions. Methods such as those used in the previously mentioned kea study, where researchers implemented a training methodology to enhance attention to partners' actions, have demonstrated significant improvements in cooperative task performance (Schwing et al., 2020). It could be interesting to incorporate the coding of attention to the partner in future studies, as has been previously done by de Waal et al. (De Waal et al., 2008) and Quervel-Chaumette et al.(2015).

4.2.2.2 Social structure and dominance hierarchy

Allowing free choice of participation and partners is relevant as it leads to more ecologically accurate interactions (House et al., 2014). However, because of intra-group competition, group experiments often suffer from reduced participation from certain individuals (Cronin et al., 2017; Verspeek et al., 2022a). Social intolerance can lead to a breakdown in cooperation because dominants may struggle to share rewards with subordinates and subordinates may avoid dominants. Although helpful in some situations, these competing social emotions might impede cooperative tasks that require flexible problem-solving (Hare et al., 2007).

Dominance hierarchies pressured individuals to adopt different strategies based on their rank. When interacting with dominant individuals, subordinate members often need to demonstrate a high degree of inhibitory control and patience as attempting to eat in front of a dominant could have expensive consequences (Amici et al., 2008; Aureli et al., 2008; Stevens et al., 2011; Stevens and Stephens, 2008).

Our results indicate a higher frequency of interaction among females with the setup, with 9 females compared to 3 males among the 12 individuals observed. This observation can be linked to the unique social structure of bonobo societies, where females hold significant influence mainly through association and coalition-building. This structure is characterized by co-dominance among associated females rather than strict female dominance (Beaune, 2012). These coalitions allow females to often have priority access to preferred food sources (Hohmann and Fruth, 1993; White and Wood, 2007). To maintain their high social status and assert their influence within the group, they sometimes exhibit aggression towards males (Beaune, 2012). In order to obtain a deeper insight into these dynamics, it would be useful to examine the dominance structure in our group, paying particular attention to whether the females who interacted more often with the setup are in a dominant position. Understanding the social status and relationships among these females could provide valuable context for their cooperative behaviour observed in this study.

Relatedness is another element that might have an impact on how bonobos interact with the setup. Bonobo mothers invest heavily in their offspring, particularly their sons, by supporting them in social interactions and mating opportunities. (Hohmann et al., 1999; Surbeck et al., 2011). When compared to other mammals of comparable body size, primates — including bonobos — show a longer period of juvenility between weaning and maturity (Kappeler and

Pereira, 2003; Toda et al., 2021). During this extended period, mothers have a critical role in the emotional and social development of their offspring (Harlow et al., 1965). In bonobos, mothers provide all of the parental care which lasts until the offspring are about four or five years old (De Lathouwers and Van Elsacker, 2006). These aspects can explain the frequent presence and interaction of young individuals with the cooperative setup, as they remain close to their mothers.

4.2.2.3 Age effect

In our study, among the 12 individuals who interacted with the setup, there were 3 juveniles and 4 adolescents, indicating a potential age effect. . It has been suggested before that the higher levels of prosocial behaviour in bonobos could be related to the testing of a biased sample of study subjects, including only young orphans (Verspeek et al., 2022). Research on prosociality in bonobos frequently included subadults and juveniles as well as studies describing prosocial tool and food transfers mainly included juvenile, adolescent, and young adult bonobos (Hare et al., 2007; Hare and Kwetuenda, 2010; Krupenye et al., 2018; Nolte and Call, 2021; Tan et al., 2017; Tan and Hare, 2013). This age effect aligns with findings that younger bonobos may exhibit higher other-regarding levels and greater tolerance (Clay and De Waal, 2013; Cronin et al., 2015).

4.2.3 Limits of the study

One significant issue we encountered was cheating behaviours among the bonobos. A few individuals figured out how to cheat so they could get the reward on their own. For example, Swahili discovered that she could move the setup closer and retrieve the reward herself by pulling the rope sharply and forcefully. This behaviour was documented in many interactions with the setup, revealing her high level of interest and regular involvement with the task.

Even if Swahili was able to retrieve the reward, these situations were not considered successful trials for the purpose of our study. As a result, anytime this behaviour was noticed, we removed the setup. To address this problem, we modified the setup's characteristics to prevent such cheating. Younger individuals also managed to get through the bars and use their arms to reach for the reward. Even though these behaviours were uncommon, it nevertheless posed a problem for preserving the integrity of the experimental setup.

An additional limitation of this study was that we only kept track of participants' success or failure in the cooperative task. This method misses essential information that would have helped us comprehend their behaviour better. Other behaviours indicating the subjects' interest in the

experiment should be recorded as well. Keeping track of individuals that were near the setup, when they approach it, and when they leave, for instance, might provide information about how engaged they are with the task. This might also be used to evaluate every individual's level of interest in the setting and connect behaviours to the group structure. Further, observing and coding aggressive and affiliative behaviours during the experiment could lead to a better understanding of the social dynamics of the group. These findings could help in our comprehension of how the bonobos' social interactions are impacted by cooperation—or lack thereof. Studying behaviours outside of the test sessions might also be helpful in figuring out whether the experiment affects relationships between individuals. This could indicate whether cooperative tasks have any long-term effects on the group's social relationships or hierarchical structures.

Furthermore, in our study, we only used grapes as the reward as this was a highly preferred food by the bonobos (Verspeek and Stevens, 2020). Because different kinds of rewards may have varied effects on the motivation and willingness of the bonobos to wait, it is likely that using a range of rewards could produce diverse outcomes.

Moreover, our study's setup and environment may possibly play a role. Even when the benefits are shared, there could be a sense of competition or urgency. This could lead to more impulsive behaviour because bonobos may choose instant action over delayed gratification in a social situation.

In our study, we did not conduct enough trials to definitively confirm or refute the occurrence of cooperation among bonobos or identify the factors influencing this cooperation. More trials over an extended period are necessary to analyse these behaviours more precisely.

By addressing these extra aspects, we can acquire a more complete knowledge of the bonobos' behaviours and the social context in which they engage, thereby increasing the reliability and depth of our findings. Future research should consider several improvements to better understand and assess the efficacy of cooperative tasks in bonobos.

5 Conclusion

In conclusion, this study explored the nuanced concept of cooperation, particularly focusing on bonobos, one of our closest living relatives. The study aimed to investigate the cooperative behaviours of bonobos in a group context using a modified loose-string paradigm, complemented by examining the relationship quality among bonobo dyads. Through a comprehensive review of the literature and empirical data collection, several key insights were gleaned.

The relationship quality among bonobo dyads was significantly influenced by genetic sex combinations but not by age differences. Female-female dyads and mother-offspring dyads exhibited higher relationship values, indicating strong affiliative bonds, particularly between mothers and their offspring. These findings are consistent with previous research highlighting the strong bonds within female bonobo groups and the critical role of maternal support in social dynamics.

The overall success rate of cooperation in the study was relatively low, with only 11% of trials being successful. However, this rate increased to 31% when considering only dyadic interactions. The varied levels of cooperation among individuals suggest that factors such as motivation, understanding of the task, and social dynamics play crucial roles in successful cooperation.

The ability to inhibit impulsive behaviours and pay attention to partners was found to be critical for successful cooperation. Despite bonobos' known ability to delay gratification, their performance in cooperative tasks was limited, potentially due to a lack of motivation or the social context of the task. The female-centered social structure of bonobos influenced interactions with the setup, with females participating more frequently. Understanding the social status and dominance hierarchies within the group could provide further insights into these dynamics. Younger bonobos, particularly juveniles and adolescents, interacted more frequently with the setup, indicating a potential age effect. This aligns with previous studies suggesting higher levels of prosocial behaviour and tolerance among younger individuals.

The study's findings contribute to our understanding of bonobo cooperation and the various factors that influence it. However, the limitations, such as cheating behaviours and the need for

more extensive trials, highlight the necessity for further research. Future studies should conduct more trials over extended periods to provide a robust analysis of cooperative behaviours. Incorporating methods to measure and enhance the motivation of bonobos in cooperative tasks, exploring the role of individual personality traits, past experiences, and social dynamics in shaping cooperative interactions, and investigating the dominance structures within bonobo groups to better understand the social dynamics influencing cooperation are crucial steps forward. By addressing these aspects, future research can gain a more comprehensive understanding of the mechanisms driving cooperation in bonobos, enriching our knowledge of social evolution and behaviour in primates.

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