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INDIFFERENT HIPPIES

Prosociality and inequity aversion as proximate mechanisms of cooperation in bonobos

Thesis for the degree of Doctor in Science: **Biology**
To be defended by

Jonas Verspeek / Faculty of Science, Department of Biology, University of Antwerp / Antwerpen, 2022

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Indifferent hippies: prosociality and inequity aversion as proximate mechanisms of cooperation in bonobos

Onverschillige hippies: prosocialiteit en aversie tegen oneerlijkheid als proximate mechanismen van coöperatie bij bonobo's

Thesis submitted for the degree of Doctor in Science: Biology
To be defended by

Jonas Verspeek
University of Antwerp

Antwerpen, 2022
Promotor
Prof. dr. Jeroen Stevens

Chairman
Prof. dr. Peter Aerts

Jury members
Prof. dr. Marcel Eens
Prof. dr. Sarah Brosnan
Prof. dr. Gottfried Hohmann

Table of contents

Acknowledgements

In the following chapters, I will present the results of my PhD study entitled 'Indifferent hippies: prosociality and inequity aversion as proximate mechanisms of cooperation in bonobos'. Most of the data were collected in Zoo Planckendael during the four years of my project (from 2018 – 2021). In chapter 4, I used behavioural data from 5 European Zoos (Apenheul, Twycross Zoo World Primate Centre, Wuppertal Zoo, Frankfurt Zoo and Wilhelma Zoological and Botanical Garden). While the majority of these data were collected as part of the PhD project of Nicky Staes, I collected an additional round of behavioural data on the bonobo group in Wilhelma Zoological and Botanical Garden as part of my master's thesis. This opportunity not only introduced me to the fascinating social lives of bonobos, but it also resulted in my very first peer-reviewed publication (see chapter 4).

In addition to the studies regarding the proximate mechanisms of cooperation in bonobos, I was also involved in many other projects in bonobos and other species. Some of these projects have resulted in publications, about culture (van Leeuwen et al., 2020) and abnormal behaviour (Laméris, Staes, et al., 2021) in bonobos but also about the implementation of relatively novel methodologies like a touch-screen task to study the emotional Stroop effect in bonobos (Laméris et al., 2022) or the use of multi-zoo social network analysis to investigate the influence of individual factors on the bonobos' position in the network (Torfs et al., in prep.). Thanks to the close association with the Antwerp Centre for Research and Conservation research group, I was also involved in some publications about other species, like Lemurs (Laméris, Verspeek, et al., 2021; Salas et al., 2021), chimpanzees (Staes et al., subm.), penguins, gorillas, okapis and many more (Salas et al., in prep.).

However, a PhD is much more than the sum of its publications. I believe that throughout my PhD journey, processes underpinning publication, interactions with other researchers, guidance of students and working in a variety of environments have allowed me to develop as a researcher but also as a person. Just like the cooperative behaviour of bonobos is based on and influenced by all social interactions within their group, many aspects of this PhD project are influenced by the social interactions I had with the people that crossed my path. Therefore, I would like to thank these people.

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Summary

Cooperation is a key component of social life. Although it is common among the animal kingdom, cooperative interactions seem an evolutionary puzzle as they involve behaviours that benefit others, but that also seem to conflict with the theory of natural selection, which emphasizes competition and predicts that individuals should act in their own interest. Studies of cooperation in animals, try to understand in which ways human cooperation is unique, how cooperation in humans has evolved, what factors explain between-individual variation in cooperative behaviour and what selective pressures acted upon the evolution of cooperation in animals. Because cooperative behaviours involve an immediate cost to the actor, natural selection must have produced mechanisms to regulate cooperation to overcome any adverse effects of these costs. The two main proximate mechanisms that regulate cooperation are prosociality and inequity aversion, which are considered to be the promotor and stabiliser of cooperation, respectively. In this thesis, I study a social group of bonobos (Pan paniscus) in Zoo Planckendael, using a combination of behavioural and physiological measures in different experimental paradigms to explain the variability in these proximate mechanisms of cooperation in bonobos. Bonobos have been suggested to be an ideal species to study prosociality and IA. First, because they are one of our closest living relatives and studying prosociality and IA in bonobos would increase our knowledge on how unique the level of prosociality and IA in humans is. Second, because bonobos have been described as 'hippies of the primate world', who are highly tolerant, prosocial, empathic and cooperative, but prosociality and inequity aversion as drivers of cooperation have not been extensively studied in this species.

In order to obtain results that would allow for intra- and inter-species comparisons, I implemented three methodological studies before focusing on prosociality and inequity aversion. First, to decide which food items to use in the experimental paradigms of my PhD, I determined the bonobos' food preference on ten novel food items and all food items of their weekly diet. Using paired-choice tests, I demonstrated that bonobos preferred fruits over vegetables. I also linked the nutritional content of each food item with the bonobos' preference which led to the conclusion that bonobos prefer foods that are high in total energy and carbohydrate content but low in water and micronutrient content. Although my study only included commercially available food items, which complicates comparisons with food preference in the wild, the results do inform us about which food items to select for the experimental paradigms: grapes as a highly preferred food item in the prosociality experiments (chapter 6) and the inequity aversion token exchange task (chapter 7) and parsnip as less preferred food item in the inequity aversion exchange task (chapter 7).

To be able to use salivary cortisol as a physiological measure of arousal in the experimental paradigms of my PhD, a profound validation of the time-lag between the stimulus and the increase and peak in salivary cortisol was needed. Therefore, using a biological validation, I investigated the time-lag between an acute stressor and the urinary and salivary cortisol response in bonobos. Surprisingly, I found that the time-lag between the stressor and the maximal cortisol level was similar in urine and saliva. I did show a faster and steeper increase in salivary cortisol than urinary cortisol after the stressor. In addition, I also demonstrated inter-individual variation in the baseline and stress levels of cortisol. Altogether, these results highlight the importance of appropriate validation studies to confirm the relevant sampling window and to be aware of inter-individual differences in the physiological response

to stimuli. Based on these results, I concluded that saliva should be samples 15 to 40 minutes after the stressful event to detect a change in the salivary cortisol levels.

In the third methodological chapter, I demonstrated the repeatability of the composite measure of relationship quality and investigated whether bonobos, like many species, prefer to bond with similar others. The preference for similarity has been suggested to be an important aspect of cooperation, because more similar individuals are expected to form strong and reliable social interactions in which emotionally mediated reciprocity may lead to high levels of successful cooperation. Besides relatedness and the sex combination of the dyad, I showed that bonobos that are more similar in the personality trait Sociability form relationships of higher qualities. Dyads with high quality relationships were predicted to show higher levels of prosociality and lower levels of inequity aversion.

To study prosociality, I first used a novel provisioning experiment that had previously been used to measure prosociality in chimpanzees. In this experiment, bonobos could push a button to provide juice from a distant fountain to benefit group members (chapter 5). All three experiments were conducted in a group setting but differed in the payoff distribution between the actor and receiver. Second, to allow for inter-species comparisons, I also implemented two validated food provisioning prosociality paradigms, the prosocial choice task (PCT) and the group service paradigm (GSP) (chapter 6).

To study inequity aversion in bonobos, I used the standard token exchange task. To complement the standard behavioural measures with the emotional component of inequity aversion, I also investigated a behavioural, rough self-scratching, and a physiological measure, salivary cortisol, of arousal.

Interestingly, the results of all prosociality experiments showed that the Zoo Planckendael bonobos mainly behaved out of self-interest: in more than half of the juice-provisioning acts, the subject also obtained juice; bonobos did not prefer the prosocial above the selfish option in the PCT and adult bonobos did not provision group members in the GSP. These findings showed that bonobos, like chimpanzees, behaved indifferently to the welfare of others, which contrasts with the popular image of the prosocial and food sharing bonobo, who is often portrayed as a “hippie of the primate world”. I concluded that this popular image is mainly the result of an age bias in previous experimental studies that looked for evidence of prosociality in bonobos in order to confirm the predictions of the self-domestication hypothesis. I also demonstrated that bonobos reacted to receiving less than a partner by refusing trials and moving away from the experimenter while they never refused trials when receiving more than a partner. The level of inequity aversion was influenced by the relationship quality between individuals. I showed that stronger bonded individuals were more tolerant towards inequity. Further, subjects were more aroused when receiving a better reward than a partner, suggesting that bonobos do notice when being favoured but do not respond to it behaviourally.

Altogether, the results of this thesis highlight the importance of validated methodologies and provide supporting evidence for the nuanced view of the prosocial, food-sharing and tolerant hippie ape. I demonstrated that adult bonobos do not behave prosocially in food-related paradigms, which can be explained by the competitive nature around the highly preferred food items, and which corresponds to the food-related behaviour of bonobos in the wild. I also showed that in bonobos, like chimpanzees, the tolerance to inequity is limited to a certain level and linked to specific partners. Although the results contribute to the existing knowledge on the proximate mechanisms of bonobos, I also provide a critical view on the artificial contexts of the implemented experimental paradigms. To fully understand how the proximate mechanisms, prosociality and inequity aversion, interact to result in successful cooperative relationships, more research on diverse social bonobo groups is crucial.

Samenvatting

Samenwerking, verder coöperatie, is een sleutelconcept van het leven in sociale groepen. Echter, coöperatie kan als een evolutionair raadsel beschouwd worden aangezien coöperatieve gedragingen vaak een voordeel voor een ander opleveren. Bijgevolg lijken coöperatieve gedragingen in conflict met de theorie van natuurlijk selectie, die stelt dat organismen in eigen belang handelen en dat individuen dus eerder in competitie zouden treden. Aangezien coöperatie vaak gepaard gaat met een onmiddellijke kost voor de actor, moet natuurlijke selectie verschillende proximate mechanismen in de hand gewerkt hebben die samenwerking reguleren om de negatieve effecten van deze kosten te beperken. Twee van deze proximate mechanismen zijn prosocialiteit en inequity aversion (IA), de afkeer tegen ongelijkheid, respectievelijk de promotor en stabilisator van coöperatie. Het doel van dit doctoraatsonderzoek was om de variatie in deze proximate mechanismen in bonobos (Pan paniscus) te bestuderen. Ik combineerde gedragsobservaties met fysiologische metingen om te onderzoeken hoe de bonobo's in Zoo Planckendael reageren tijdens de verschillende experimenten. Bonobo's worden vaak naar voor geschoven als de ideale soort om prosocialiteit en IA te bestuderen. Eerst en vooral omdat ze één van onze meest nauw verwante soort is. Het bestuderen van prosocialiteit en IA in bonobo's zou daarom kunnen bijdragen aan onze kennis over hoe uniek de mate van prosocialiteit en IA in mensen is. Ten tweede worden bonobo's vaak voorgesteld als zeer vredelievende, tolerante, voedsel delende en prosociale 'hippie mensaap'. Op basis van deze eigenschappen voorspelden onderzoekers dat bonobo's zeer prosociaal en heel tolerant naar oneerlijkheid zouden zijn.

Om prosocialiteit en IA bij bonobo's te kunnen bestuderen, voerde ik eerst drie methodologische onderzoeken uit. Het doel van hoofdstuk 2 was om te onderzoeken welke voedselbeloningen gebruikt konden worden tijdens de experimenten om prosocialiteit en IA te meten (hoofdstuk 6 en 7). Om dat te weten te komen, onderzocht ik de voedselvoorkeur van de bonobo's in Zoo Planckendael voor tien nieuwe voedselitems en alle voedselitems van het wekelijkse dieet. Door gebruik te maken van gepaarde-keuze testen, toonde ik aan dat de bonobo's fruit boven groenten verkozen. Daarnaast correleerde ik ook de nutritionele inhoud van elk voedselitem met de voedselvoorkeur voor dat item. Daaruit bleek dat bonobo's energierijk voedsel verkiezen dat veel koolhydraten, weinig water en weinig micronutriënten bevat. Op basis van deze resultaten koos ik druif als zeer geprefereerde en pastinaak als minder geprefereerd voedsel item welke gebruikt konden worden in de prosocialiteit experimenten (Hoofdstuk 6) en het IA token ruilexperiment (Hoofdstuk 7).

Naast de standaard gedragsobservaties, wilde ik ook de emotionele component van prosocialiteit en IA bestuderen. Daarvoor wilde ik de hoeveelheid cortisol in speeksel als fysiologische maat voor zenuwachtigheid onderzoeken. Vooraleer deze fysiologische maat bij bonobos gebruikt kon worden, moest onderzocht worden wat het ideale interval zou zijn om speeksel te verzamelen opdat een effect op de cortisol respons gevonden zou worden. Daarom heb ik met behulp van een biologische validatie onderzocht hoe de cortisol respons in urine en speeksel van bonobo's verliep na het zien van een acute psychologische stressor. In tegenstelling tot wat de literatuur voorspelt, bereikte de cortisol respons in urine en speeksel de maximale waarde na een zeer gelijkaardig tijdsinterval (160 minuten). De cortisol waarden in speeksel vertoonden wel een snellere en steilere stijging dan de cortisol waarden in urine. Daarnaast vond ik ook interindividuele verschillen in zowel de controle als stress-gerelateerde cortisol waarden. Dit onderzoek toont dus het belang van de geschikte validatiemethode aan om te bepalen wanneer het ideale interval zou zijn om speeksel te verzamelen. Idealiter zou speeksel 15 tot 40 minuten na een stressvolle stimulus verzameld moeten worden om een verandering in de cortisol waarden waar te kunnen nemen.

In het derde methodologische hoofdstuk demonstreerde ik de bruikbaarheid van de samengestelde maat voor relatiekwaliteit en onderzocht ik of bonobo's, net als verschillende andere diersoorten, geneigd zijn om sterkere sociale relaties aan te gaan met gelijkaardige individuen dan met individuen die meer verschillen. De voorkeur voor meer gelijkaardige individuen zou aan de basis liggen van coöperatie aangezien gelijkaardige individuen sterkere en meer betrouwbare sociale relaties zouden aangaan. Binnen dergelijke sociale relaties zou emotioneel gemedieerde reciprociteit tot meer succesvolle coöperatie leiden. De sterkste sociale relaties tussen bonobo's werden gevonden tussen genetisch verwante individuen, maar ook tussen genetisch niet verwante vrouwen. Ook bleek dat individuen met een meer gelijkaardige persoonlijkheid wat betreft de factor Sociabiliteit, sterkere vriendschappen vormden. Verwacht werd dat dyaden met sterkere relaties meer prosociaal zouden zijn en een minder sterke IA respons zouden vertonen.

Om prosocialiteit en IA in bonobo's te onderzoeken, gebruikte ik verschillende experimenten en combineerde ik gedragsobservaties met fysiologische gegevens met als doel om de variatie in deze proximate mechanismen te verklaren. Eerst namen de bonobo's deel aan een fruitsapexperiment dat eerder gebruikt was om prosocialiteit bij chimpansees te bestuderen. In dit experiment konden de bonobo's op een knop drukken om fruitsap aan groepsleden te geven (hoofdstuk 5). Om de mate van prosocialiteit bij bonobo's met eerdere studies en met andere diersoorten te kunnen vergelijken, gebruikte ik ook twee gevalideerde experimenten: de prosocial choice task (PCT) en de group service paradigm (GSP). De drie experimenten die prosocialiteit testten werden in groepssetting toegepast en verschilden in de voordelen voor zowel donor als de partner. Wanneer de resultaten van de drie experimenten gecombineerd worden, kan er geconcludeerd worden dat de Zoo Planckendael bonobo's voornamelijk uit eigen belang handelden: in meer dan de helft van de keren dat fruitsap gedoneerd werd, profiteerde de donor zelf; de bonobo's kozen er niet voor om groepsgenoten te bevoordelen in de PCT en volwassen bonobo's gaven geen enkel voedselitem aan anderen in de GSP. Bijgevolg kunnen we concluderen dat de bonobo's in deze studie, net als chimpansees, zich onverschillig gedroegen ten opzichte van het welzijn van groepsgenoten. Dit is in sterk contrast met het populaire idee van de prosociale en voedsel-delende bonobo. De verklaring voor deze tegengestelde bevindingen is te vinden in het feit dat vorige experimentele studies, die bewijs voor prosocialiteit in bonobos zochten om de zelf-domesticatie hypothese te bevestigen, voornamelijk uitgevoerd werden bij jonge individuen.

In hoofdstuk 7 gebruikte ik het standaard IA token ruilexperiment. Naast de gebruikelijke gedragsmaten voor IA, onderzocht ik ook de emotionele component van IA, namelijk de mate van zenuwachtigheid die mogelijks veroorzaakt werd door oneerlijkheid. Om de mate van zenuwachtigheid te bepalen, gebruikte ik de gedragsmaat ruw zelf-krabben en de fysiologische maat cortisol concentratie in speeksel. Het onderzoek toonde aan dat de bonobo's stopten met ruilen en weggingen van de onderzoeker wanneer ze minder dan de partner kregen, maar geen enkele mogelijkheid om te ruilen afwezen wanneer ze meer dan een partner kregen. Ook bleek dat de mate van IA beïnvloed werd door de relatiekwaliteit tussen de partners, namelijk dat dieren met sterkere sociale banden meer tolerant waren ten opzichte van oneerlijkheid. Daarnaast bleek ook dat dieren zenuwachtiger werden wanneer ze de betere beloning kregen dan hun partner, wat suggereert dat hoewel de bonobo's niet reageerden op het krijgen van een betere beloning dan een partner, ze dit wel merkten.

De resultaten van dit doctoraatsonderzoek tonen het belang aan van gevalideerde methodologieën en suggereren dat het beeld van de prosociale, voedsel-delende en tolerante "hippie mensaap" genuanceerd moet worden. Ik toonde aan dat volwassen bonobo's niet prosociaal zijn in voedsel-gebaseerde experimenten, wat gedeeltelijk verklaard kan worden door de competitieve context die de zichtbare voedselitems creëren. Bovendien komt de afwezigheid van prosociaal voedseldelen overeen met het voedsel-gerelateerd gedag van bonobo's in het wild. Net als in chimpansees, was de tolerantie voor oneerlijkheid in bonobo's niet onbeperkt en afhankelijk van de partner. Hoewel de resultaten van deze doctoraatsthesis bijdragen aan onze kennis over de proximate mechanismen van samenwerking in bonobos, bespreek ik de artificiële experimentele context met een kritische blik. Om een volledig beeld te krijgen van hoe de proximate mechanismen, prosocialiteit en IA, op elkaar inwerken om tot succesvolle coöperatieve interacties te komen in bonobo's, is er bijkomend onderzoek op diverse groepen nodig.

General Introduction

The aim of this PhD was to combine several research methods to investigate the two proximate mechanisms of cooperation, prosociality and inequity aversion, in bonobos. In the first part of this introduction, I discuss the relevance of cooperation research and provide an insight in the challenges and evolutionary origins of cooperative behaviour. In the second part, I present the general framework of this PhD project, including the two proximate mechanisms of cooperation. In the fourth and final part of the introduction, I focus on why bonobos are an interesting study species to investigate the proximate mechanisms of cooperation.

Cooperation

For centuries, cooperation has been an integral part of philosophical and psychological speculations. It was only in the last half-century that researchers have begun to empirically investigate cooperative behaviour. In the 1960s, a few key studies led to a radical change in the way biologists viewed the evolution of cooperation, marking the beginning of the modern study of this research field and the start of modern behavioural ecology and socio-biology. Most biologists at that time believed that interactions evolved for the good of the species. Contrasting this pervasive attitude, Hamilton's seminal papers explained how natural selection was intrinsically selfish (Hamilton, 1964a, 1964b). His inclusive fitness theory argued that cooperative interactions should be more common among related than unrelated individuals because the former share more genes. Hamilton's work has spurred the interest in allomaternal care / cooperative breeding as explaining factor for cooperation (Jeram L. Brown, 1994). However, the inclusive fitness theory did not explain cooperation among unrelated individuals, which has been referred to as "the central theoretical problem of socio-biology" (Wilson, 1975).

The challenge of cooperation

Animals and humans engage in a myriad of cooperative interactions like mobbing of potential predators, cooperative hunting, coalitionary support and reciprocal allogrooming (Clutton-Brock, 2009a). This has led to various definitions of cooperation (e.g. see Connor, 2010). One of these is "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" (Brosnan & de Waal, 2002). Although cooperation is common in nature, such acts of helping and sharing represent an interesting evolutionary puzzle. Many cooperative behaviours involve an immediate cost to the actor, i.e. fitness reduction, while benefitting the receiver of the act. The fitness loss can consist of three different components: First, it arises due to a time delay inherent in the returned benefit from the partner, giving the partner an opportunity to increase the delay and provide less benefits than he receives or to not reciprocate at all; Second, cooperative interactions involve an opportunity for exploitation, also called free riding, which arises when partners do not, or not equally, return benefits; Third, partners may also show other forms of defection like refraining from a high-risk act of mutual support, e.g. a coordinated attack on a predator or rival, or they might systematically claim more than its fair share after cooperative actions (van Schaik, 2016). Because of these costs, cooperative acts have long been called altruistic. However, a persistent tendency to behave truly altruistic should be selected against and cooperation would have been selected against by natural selection. Cooperation is widespread across the animal kingdom, which implies that natural selection must have resulted in a variety of mechanisms to stabilise cooperation to overcome these threats of exploitation. Indeed, the 'altruistic' acts in nature have become stabilised because of some return benefit to the actor (J. R. Stevens & Hauser, 2004; West et al., 2007a, 2007b). In the following parts, I follow Tinbergen's (1963) classification to first describe the ultimate aspects of cooperation: how can cooperation be adaptive and which selection mechanisms were responsible. Next, I will discuss the proximate mechanisms of cooperation and provide the general theoretical framework of this thesis.

The evolution of cooperation

Hamilton's theory of inclusive fitness suggests that the evolutionary benefit of cooperation between related individuals can be explained by focusing on the effect of a gene on the individual that bears it, but also on others that share genes that are identical by descent, namely kin (Hamilton, 1964b, 1964a).

While many cooperative interactions happen between kin, unrelated actors also cooperate in a wide variety of contexts. Therefore, Trivers (1971) proposed his so-called theory of "reciprocal altruism": genes for altruistic behaviour may be selected if the individuals differentially allocate their altruistic acts to partners that have been altruistic themselves. While many definitions for reciprocal altruism exist, the core idea is that "support is directed at those individuals who are likely to reciprocate it, but under the condition that, after some initial investment phase, further support is contingent on reciprocation in kind" (van Schaik, 2016). The idea of reciprocal altruism has received a strong support from economic games (Colman, 1998; but see Brosnan, Salwiczek, et al., 2010; Bshary & Bronstein, 2004, 2011). These theoretical models involve highly structured decision tasks in which outcomes of players are dependent upon their choices and those of their partners. They are usually used to understand which factors influence decision-making and which choices may evolve towards successful evolutionary strategies (Camerer, 2003). Using economic games, Axelrod and Hamilton (1981) investigated evolutionary stable strategies for situations in which the players are likely to encounter each other in future interactions, i.e. the iterated prisoner's dilemma (Axelrod & Hamilton, 1981). They showed that if the probability of meeting a given partner in the future was higher than a critical threshold, the conditionally cooperative strategy called "Tit for Tat" was the most robust and evolutionary stable solution. Tit for Tat suggests an individual to cooperate initially with a partner and to subsequently copy the partner's last move. Several variants of this strategy have been proposed. They usually involve a conditional strategy that yield the highest fitness return when participants cooperate. Although numerous extensions of this game have been investigated, exclusive reliance on the prisoner's dilemma and its strategies has led to neglect important factors in cooperative interactions in real life (Raihani & Bshary, 2011; van Schaik, 2016). Group living individuals in a naturalistic setting can choose their partners, which is usually based on previous interactions or observations. Also, although individuals can only "defect" or "cooperate" in the game, the most common response to a defecting partner in nature will be to stop interacting with that partner. While the mathematic result is the same, it involves different behavioural mechanisms (van Schaik, 2016). Each of the strategies in the game that produce beneficial fitness outcome, involve strict contingency: a player's next move depends on the other player's previous move. In nature, contingent reciprocity (i.e. calculated reciprocity) is only seldomly, if at all, observed in non-human animals (Clutton-Brock, 2009b; Connor, 2010; M. D. Hauser et al., 2009). Not because it is beyond their cognitive abilities (Cheney et al., 2010; Dufour et al., 2009), but rather that most dyadic cooperation in non-human animals is observed between closely associated individuals or friends, in which cooperative actions are likely exchanged in an approximately symmetrical matter through emotional bookkeeping (Evers et al., 2015; Schino & Aureli, 2010). These individuals develop a 'stake' in each other and in the continuation of cooperation, explaining the absence of strict contingency (Roberts, 2005). Cooperative interactions between closely bonded individuals are also categorised as pseudo-reciprocity: benefits are exchanged reciprocally but there is a lower risk of defection (Raihani & Bshary, 2011).

The proximate mechanisms of cooperation

The various forms of cooperation imply that selection must have produced proximate (psychological) mechanisms to promote and stabilise cooperation (Mcauliffe & Thornton, 2015). Each species should have its own set of regulatory mechanisms that fit the species' cooperative behaviour in the wild. To explain these proximate mechanisms and how they are connected with each other, I use the cooperation model, which is based on previous diagrams by de Waal and Suchak (2010) and Yamamoto and Takimoto (2012) (Figure 1.1).

The two central components are the proximate mechanisms of cooperation: prosociality and inequity aversion. Although several definitions of prosociality exist (e.g. Dovidio, 1984; Jensen, 2016b; Padilla-Walker & Carlo, 2014; Pfattheicher et al., 2022; see also Box 1), I follow the definitions of Amici et al. (2014) and Cronin (2012) that define prosociality as "any behaviour performed by one individual to alleviate the needs of other individuals or to improve their welfare, without the actor necessarily incurring extra costs to provide these benefits". This rather broad definition includes a wide range of behaviours in different context like sharing, helping and even consoling, but it is not overly inclusive. The various forms of cooperation involve reciprocal prosocial acts between partners. Therefore, prosociality has been suggested to be the proximate promoter of cooperation (Fletcher, 2008; Jaeggi, Burkart, & van Schaik, 2010; Silk, 2012).

Reciprocation is often separated in time, increasing the opportunity of exploitation: when prosocial acts by one individual are seldomly reciprocated by another individual, this may lead to unequal payoffs. On the long-term this can lead to possible negative fitness consequences. To avoid exploitation and freeriding by non-reciprocal partners, it was proposed that inequity aversion evolved, acting as a stabiliser of cooperation (Brosnan, 2011; Brosnan & Bshary, 2016; Fehr & Schmidt, 1999). Inequity aversion has been defined as "the affective, cognitive and behavioural response to inequitable outcomes" (Oberliessen et al., 2016).

Prosociality and inequity aversion are suggested to start from psychological traits that prefer similarity with others (Yamamoto & Takimoto, 2012). Many animals recognize and prefer to

Box 1. Prosociality research resembles a field of wild flowers

The field of prosociality has received remarkable interest over the past decades (Pfattheicher et al., 2022; see chapter six of this thesis). However, despite the impressive amount of studies, the term prosociality often takes on different meanings (West et al., 2007b; Pfattheicher et al., 2022; see below). Due to the conceptual and terminological ambiguity, researchers risk using the same term for different concepts and different terms for the same concept (known as jingle and jangle fallacies (Block, 1995)). This complicates (interdisciplinary) comparative work and hinders cumulative science (Pfattheicher et al., 2022). In addition to providing unambiguous definitions and providing operationalizations that match these definitions, researchers should acknowledge the diversity of prosocial behaviour as it exists (Dunfield et al., 2011; Tomasello and Vaish, 2012; Padilla-Walker & Carlo, 2014; Decety et al., 2016; Pfattheicher et al., 2022; see below and chapter six and eight of this thesis). In my thesis, I used the definition of Amici et al. (2014) and Cronin (2012).

interact with genetically related individuals if they have the opportunity to do so (Chapais, 2001; Silk, 2006) (see indirect fitness benefits). Furthermore, unrelated individuals form long-term social bonds, which are characterized by regular exchanges of benefits that are often emotionally mediated (Roberts, 2005; Schino & Aureli, 2010). Such close associations are more likely to occur between individuals that are more similar in traits like age, sex and personality (Carter et al., 2015; de Waal & Luttrell, 1986; McPherson et al., 2001). This is called the principle of homophily: interactions occur at higher rates among similar individuals than among dissimilar individuals (McPherson et al., 2001). Similarity, familiarity, relationship quality and prior positive experiences will increase basic emotional contagion, which eventually can lead to sympathetic concern (see below) (de Waal, 2008). The ability to understand others (including capacities like perspective-taking) is not necessary for prosocial behaviour to develop (Koski & Sterck, 2010). However, empathy, and especially sympathetic concern, can directly function to promote prosocial behaviour directly (Koski & Sterck, 2010; Yamamoto & Takimoto, 2012). In addition to the preference for similarity in cooperative partners, individuals also prefer similar payoff-distributions in cooperative interactions. Therefore, the ability to recognize unequal payoffs and to react to it, allows individuals to avoid unfavourable partners and functions to stabilise cooperation (Brosnan, 2006b, 2011; Fehr & Schmidt, 1999). Similarity and social bonding also promote cooperation through increased social tolerance and prosociality and reduced sensitivity to inequity (de Waal & Suchak, 2010).

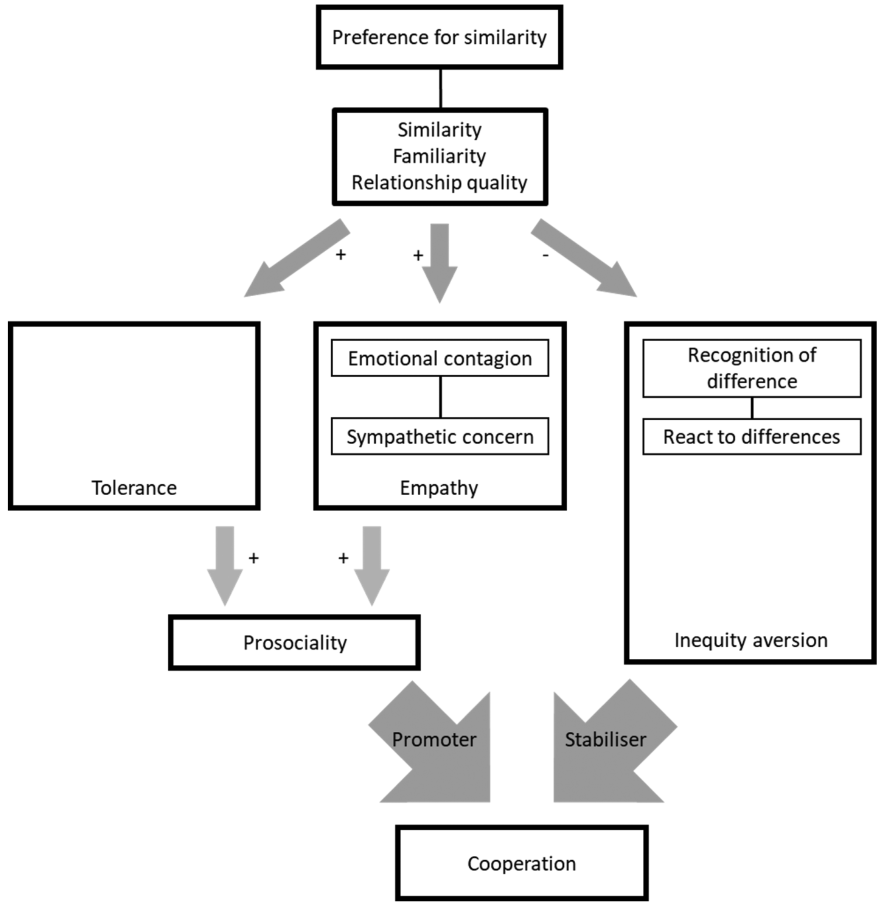

Fig. 1.1 The cooperation model links the proximate mechanisms of cooperation with the preference for similarity and tolerance as other relevant factors (de Waal & Suchak, 2010; Yamamoto & Takimoto, 2012).

Prosociality, the promoter of cooperation

The various forms of cooperation include prosocial behaviours that, depending on the context and the triggers, can be divided in two types: reactive and proactive prosociality. Most prosocial acts are reactive and are triggered by extrinsic stimuli. The reactive prosocial response depends on the presence and strength of the stimulus, an explicit signal of need, which is often modified by kinship and the social bond strength. To result in the greatest potential benefit, reactive prosocial acts should be adjusted to the recipient's need (Hamilton, 1964b; Trivers, 1971). Therefore, actors should be sensitive to signals or signs of need (Jaeggi, Burkart, & van Schaik, 2010). Responding to signals of need, i.e. a stimulus directed at the actor, does not require special abilities because they evolved in a form that most successfully elicits the desired response (Zahavi, 1987). The ability to read and respond to signs of need, i.e. a stimulus not directed to the actor, often depends on theory of mind capacities. Therefore, actors with a well-developed theory of mind may be better at adequately react prosocially in certain contexts.

Different forms of reactive prosociality can be distinguished (Fig. 1.1). In the most basic form, emotional contagion, observers contagiously match the emotional distress of the signaller (Hatfield et al., 1993; Yamamoto & Takimoto, 2012). For example, young primates, including children, will often display noisy temper tantrums. They exploit emotional contagion to induce maternal distress, in an attempt to change the mother's behaviour to their advantage (de Waal, 2008). A more evolved mechanism, sympathetic concern (also called cognitive empathy), combines emotional contagion with appraisal of the other's situation: the emotional state of the observer is not affected by the signaller's emotional state, but the observer does respond with the appropriate prosocial act to the signaller's need (de Waal, 2008). The best-documented example of sympathetic concern is consolation, i.e. "comforting behaviour directed at a distressed party, such as a recent victim of aggression". Next, when animals can understand the needs of others, i.e. perspective-taking, they can perform targeted helping like providing help and care, based on the other's specific need (de Waal, 2008; Yamamoto & Takimoto, 2012). Empathy may also promote prosociality through a feedback mechanism: if animals are affected by the positive emotion of a conspecific that they helped, emotional contagion will work as positive feedback that promotes future prosocial behaviour (Yamamoto & Takimoto, 2012). Thus, empathy, in its different forms, is suggested to be an important motivational mechanism for a wide variety of situations in which prosocial acts are dispensed according to a certain need. However, other forms of prosocial behaviour like food sharing are not necessarily associated with or elicited by empathy (J. R. Stevens & Gilby, 2004).

In the absence of any obvious extrinsic stimuli, prosociality can also be initiated by an intrinsic motivation, which is called proactive prosociality. Proactive prosocial behaviour emerges in the absence of obvious external stimuli. For example, when an animal has caught a prey item, it may suppress its own motivation to feed immediately, but calls in other animals to share the prey. While the highest levels of proactive prosociality would be expected among kin, infants often need to extensively beg for food from their mothers before receiving it, and often still need to take it, indicating that mothers do not spontaneously show proactive food-sharing towards their infants. Proactive food sharing is however common in cooperatively breeding species, such as callitrichids or various canines, in which not only parents, but also alloparents (pro)actively seek opportunities to provide help. In reality, it is impossible to rule out all extrinsic stimuli, suggesting that proactive prosociality can be seen as a high intrinsic motivation or a high sensitivity to the (limited) remaining stimuli (Jaeggi, Burkart, & van Schaik, 2010; Trivers, 2006). Natural selection has changed sensitivity to extrinsic and intrinsic stimuli, depending on the average certainty of return benefits, which has led to species-specific prosocial behaviour (de Waal, 2012; Jaeggi, Burkart, & van Schaik, 2010; Koski & Sterck, 2010).

Hypotheses regarding the evolution of prosociality

Currently, four hypotheses have been proposed to explain the evolutionary origin of the different forms of prosociality (Cronin, 2017; Decety et al., 2016; Krupenye, Tan, et al., 2018): 1) the human uniqueness hypothesis, 2) the cooperative breeding hypothesis, 3) the self-domestication hypothesis and 4) the empathy hypothesis. Although these different hypotheses explain prosociality at different levels, they are not mutually exclusive as prosocial behaviour has been suggested to be multidimensional and flexible (Decety et al., 2016; Tomasello & Vaish, 2012).

The human uniqueness hypothesis predicts that the degree of prosociality in humans requires specific levels of socio-cognitive functioning, such as theory of mind and inhibitory control (Burkart et al., 2009, 2014; Drayton & Santos, 2016). Although many studies have demonstrated prosociality in a variety of species, this hypothesis predicts that humans not only have the cognitive preconditions, but also the motivational component to show unique levels of prosociality (Burkart et al., 2009). Humans behave prosocially in response to signals and signs of need but also show high levels of proactive prosociality, reflecting a high intrinsic motivation (Burkart et al., 2014; Henrich et al., 2005; Jaeggi, Burkart, & Van Schaik, 2010). This high intrinsic motivation has been linked to the psychological adaptations to cooperative breeding (see cooperative breeding hypothesis below). In addition, because they live in large fission-fusion societies with high interdependence among individuals, humans have acquired a strong sensitivity to the presence and size of the audience. Thus, this hypothesis predicts that prosociality has been under stronger positive selection during human evolution (Jaeggi, Burkart, & van Schaik, 2010).

The cooperative breeding hypothesis postulates that (proactive) prosociality is linked to the amount of allomaternal care, i.e. care by non-mothers (Burkart et al., 2009). The psychological adaptations to cooperative breeding, in species like callitrichids and some corvid species (Burkart et al., 2009; Horn et al., 2020), including increased attention to the needs of groupmates and the propensity to share resources, increase the expression of proactive prosocial behaviour (Burkart et al., 2009; Burkart & van Schaik, 2010). In cooperatively breeding species, allomaternal care is often essential to offspring survival (Snowdon & Ziegler, 2007). Therefore, caretakers must proactively seek opportunities to provide food to others (Burkart & van Schaik, 2010). In conclusion, the cooperatively breeding hypothesis suggests higher levels of (proactive) prosociality with increasing levels of allomaternal care.

The self-domestication hypothesis states that selection against reactive aggression produced morphological, physiological, behavioural and psychological side effects that resemble those reported as characteristic for domestic animals, i.e. the domestication syndrome (Hare, 2017; Hare et al., 2005; Hare & Tomasello, 2005). This hypothesis was largely based on the work of Dmitry Belyaev and colleagues who experimentally selected foxes to be interested and friendly towards humans as opposed to aggressive and fearful towards them (Trut, 1980; Trut et al., 2009). In addition to the lower aggressiveness, numerous features of the domestication syndrome were observed to emerge in the selected foxes. Their faces became wider and flatter and their skulls became shorter and more slender (Trut et al., 2009). Behaviourally, selected fox kits became evenly skilled as dog puppies to use basic human communicative gestures and showed more prosocial behaviour towards humans (Hare et al., 2005). Importantly, prosocial behaviour in these studies has been defined as "positive and affiliative behaviour and does not imply whether these behaviours are selfishly or unselfishly motivated" (Hare & Woods, 2017) (see also Box1; p10). Following this hypothesis, 'prosociality' arose as a by-product of selection against reactive aggression and selection for increased tolerance. Thus, higher levels of prosociality are expected in species that are less emotionally reactive and more tolerant (Hare, 2017; Hare et al., 2012)

The empathy hypothesis posits that the proximate mechanism that elicits prosocial behaviour is empathy (de Waal, 2008). While a noncognitive emotional form of empathy is suggested to be pervasive throughout the animal kingdom, in certain species a more complex form arises when combined with additional cognitive functions like for example theory of mind (de Waal, 2008; Koski & Sterck, 2009; Preston & de Waal, 2002). Since basic empathic responses promote prosocial acts (de Waal, 2008; de Waal et al., 2008), the likelihood of expressing prosocial behaviour depends on the ability to match the emotional state of group members (de Waal, 2008; de Waal et al., 2008; de Waal & Suchak, 2010). Species that possess higher levels of empathic abilities are therefore expected to behave more prosocially.

Measuring prosociality in non-human animals

In the last decades, an increasing number of experimental studies has focused on prosociality in various species from birds over dogs to primates (for a brief review, see Chapter 6). Prosociality studies mainly used two types of experimental paradigms (reviewed in Jensen, 2016; Marshall-Pescini et al., 2016; Yamamoto & Takimoto, 2012): targeted helping (also called instrumental helping) and food provisioning paradigms. Targeted helping paradigms exist in many forms, and examine whether animals help others in situations that they cannot resolve on their own (Jensen, 2016b; Yamamoto & Takimoto, 2012). In these contexts, subjects mainly react in response to directed signals of need, eliciting reactive prosociality (Jaeggi, Burkart, & Van Schaik, 2010). Critics of these paradigms have stated that helping paradigms require elaborate cognitive abilities in terms of perspective taking, since subjects have to understand their partner's goal or need (Yamamoto & Takimoto, 2012). This may explain why the strongest targeted helping is found in species with high levels of such cognitive abilities (Barnes et al., 2008; de Waal, 2008; Jaeggi, Burkart, & Van Schaik, 2010; Yamamoto & Takimoto, 2012).

Food provisioning tasks investigate whether subjects provide rewards to conspecifics. Most studies have implemented paradigms that are loosely based on the dictator game in human experimental economics (Engel, 2011): one individual receives a valuable resource, in humans this is typically money, that can be split with another individual (Jensen, 2016b). Although results differ between conditions and cultures, people often give 20% of the endowment to their partner (Camerer, 2003). In animals, the most commonly used food provisioning task is the prosocial choice task (PCT), sometimes also called a mutualistic preference task (reviewed in Jensen 2016; Marshall-Pescini et al. 2016; Tan, Kwetuenda, and Hare 2015). This task was originally developed for chimpanzees (Pan troglodytes) by Jensen et al. (2006) and Silk et al. (2005). Subjects can choose between either a selfish option (1/0), in which only subjects obtain a reward for themselves, and a prosocial option (1/1), in which a food reward is delivered to the subject and the recipient. Since subjects gain identical payoffs for the same effort in either option, they should prefer the prosocial option (1/1) only if they have a prosocial preference. An interesting variant of the PCT is the group service paradigm (GSP) (Burkart et al., 2014; Burkart & van Schaik, 2013; House et al., 2014). In this paradigm, the subject's reward is removed, making this task costly. The two reasons for removing the subject's reward is that 1) the presence of the food at the subject's side may distract; and 2) induce a more competitive context and that the presence of the different food items might make the PCT cognitively too complex as subjects need to process multiple food locations in making a choice (Burkart et al., 2014). Interestingly, the adjusted payoffs turn the standard PCT into an instrumental helping task since only recipients receive a reward at a low cost for the subject, namely the energetic cost to pull the handle (House et al., 2014; Tan et al., 2015).

Prosociality in non-human animals

Here, I provide a short overview of the experimental studies that focused on prosocial behaviours in non-human animals. Partly due to the variability in experimental contexts, for almost every positive prosociality result in a species or taxon, also a null result or negative result exists (Cronin, 2017; Marshall-Pescini et al., 2016). A prosocial tendency has been observed in various primate species including New World monkeys (e.g. capuchin monkeys (Sapajus apella) (Lakshminarayanan & Santos, 2008; Takimoto et al., 2010a; Takimoto & Fujita, 2011; but see Amici et al., 2014; Burkart & van Schaik, 2013; Claidière et al., 2015; House et al., 2014); common marmosets (Callitrix jacchus) (Burkart et al., 2007, 2014; Burkart & van Schaik, 2020; J. S. Martin et al., 2021; but see Mustoe et al., 2015); cotton-top tamarins (Saguinus oedipus) (Burkart et al., 2014; Cronin et al., 2010; but see Cronin et al., 2009; J. R. Stevens, 2010)) and Old World monkeys (e.g. rhesus monkeys (Macaca mulatta) (Chang et al., 2011); long-tailed macaques (Macaca fascicularis) (Massen, van den Berg, et al., 2010)). In contrast, great apes, including chimpanzees, bonobos and orangutans, were mostly indifferent to the partner's outcomes in the PCT and GSP (e.g. (Amici et al., 2014; Brosnan et al., 2009; Burkart et al., 2014; Jensen et al., 2006; Silk et al., 2005; Tan et al., 2015)), while they did show targeted helping ((Melis, Warneken, et al., 2011; Warneken & Tomasello, 2006; Yamamoto et al., 2009, 2012). However, other studies found no targeted helping in the same ape species (Krupenye, Tan, et al., 2018; Liebal et al., 2014; Nolte & Call, 2021; Tennie et al., 2016)).

In addition to the numerous prosociality studies in primates, recent work has also focused on non-primate species. Using different experimental paradigms, positive prosociality results have been found in birds (e.g. corvids (Horn et al., 2016, 2020; Schwab et al., 2012) but see (Horn et al., 2021); parrots (Brucks & von Bayern, 2020; Krasheninnikova, Brucks, Blanc, et al., 2019; Laumer et al., 2021) but see (Heaney et al., 2020)), rodents (Hernandez-Lallement et al., 2015; Lalot, Liévin-Bazin, et al., 2021; Márquez et al., 2015; Schweinfurth & Taborsky, 2018), canids (Dale et al., 2016; Dale, Palma-Jacinto, et al., 2019; Quervel-Chaumette et al., 2015), cetaceans (Lalot, Delfour, et al., 2021; Nakahara et al., 2017) and even fish (Satoh et al., 2021).

Inequity aversion, the stabiliser of cooperation

During the evolution of cooperation, actors may have developed the capacity to compare their own efforts and payoffs with those of their partners. Cooperation is only beneficial for both partners if the outcome of the cooperative interaction is equitable in the long-term. Species that regularly cooperate are expected to have a well-developed capacity for effort evaluation and to show a negative response to excessive payoff imbalances (Brosnan & de Waal, 2014). Therefore, inequity aversion allows to detect and respond to unequal payoffs, facilitating the search for partners that equally divide rewards, hence stabilising and increasing the benefit of cooperation over time (Brosnan, 2011; Fehr & Schmidt, 1999). Aversion to inequity is a mechanism that encourages individuals to seek out new beneficial partners. If the new partner is indeed more equitable, the individuals will have an absolute gain, despite the temporary short-term cost. Even reactions that increase short-term inequity may serve to increase long-term equity by encouraging individuals into relationships that are more beneficial (Brosnan, 2011). Importantly, it has been suggested that this would not mean that individuals must ‘understand’ that they receive less than a partner. If individuals can recognize the different payoffs and change their behaviour, natural selection can act on this. It is suggested that inequity aversion has a strong emotional component: individuals may get frustrated in response to an unequal situation, which may be sufficient motivation to change the current situation and leave the cooperative interaction (Brosnan, 2011; Brosnan & Bshary, 2016). Indeed, economic game studies and brain-imaging studies in humans have showed that inequity aversion involves a strong emotional component (Sanfey et al., 2003; K. Watson & Platt, 2006; Yamagishi et al., 2009). Inequity aversion can be categorized in two types: disadvantageous and advantageous inequity aversion. Disadvantageous inequity aversion is a negative response to an unequal outcome in which an individual obtains less than a partner, also called undercompensation. Advantageous inequity aversion is the negative response to receiving more than a partner, called overcompensation (Fehr & Schmidt, 1999). In humans, disadvantageous and advantageous inequity aversion are not treated the same: humans more often react to receiving less than receiving more than a partner (Loewenstein et al., 1989). Since individuals often rely on emotionally mediated reciprocity (Massen et al., 2019), inequity aversion is also expected to be influenced by emotions (Massen et al., 2019; McGetrick & Range, 2018). In humans, negative emotions like anger, disgust and jealousy have been linked to inequity aversion (Cubitt et al., 2011; Matsuzawa & Tanimoto, 2018; McAuliffe et al., 2014). In support of the role of emotions in inequity response, brain imaging studies in humans have shown an increased activation of specific brain areas that are linked to negative emotions when being treated unfairly (X. Cheng et al., 2015; Sanfey et al., 2003). Thus, although the negative reactions to inequity involve different cognitive mechanisms, they might involve both rational and conscious decision-making and an emotional response (Talbot et al., 2016). Therefore, there has been an increasing interest in studying the endocrine and sympathetic nervous system responses that underlie subjects’ aversion to inequity, which may indicate a shift in their arousal levels following inequity (Massen et al., 2019). The strong emotional responses to inequity have been suggested to be a commitment device that causes individuals to respond in predictable ways to situations that might seem ‘irrational’ in the short-term, but leads to a more beneficial situation in the long-term (Brosnan, 2006b; Frank, 2001). Reacting to an unequal payoff may discourage others from behaving inequitably towards them in the future or may encourage other equitably minded individuals to seek them out for future interactions, leading to more beneficial cooperation (Brosnan, 2006a).

The evolutionary steps of inequity aversion

The evolution of inequity aversion has been suggested to have happened through a series of steps, each with a benefit for the actor, ultimately resulting in the complex understanding of inequity and fairness and the ability to respond to it like we see in humans (Brosnan, 2006a, 2009; Brosnan & de Waal, 2004).

The first requirement is the ability to notice when rewards differ between individuals (Brosnan, 2006b, 2009). Actors need to pay attention to each other in a context in which the other individual does not affect them, requiring an advanced cognitive capacity. This ability might have its origin in a different context than inequity, like for example social learning or coalitionary support, where individuals acquire information that does not immediately affects them (Brosnan, 2006b). Thus, actors can compare their payoff to that of others.

The second step is to react negatively to the difference in reward distribution between oneself and another. Therefore, an individual not only needs to notice the outcomes of another (the first step), but also react negatively to the difference (Brosnan, 2009). This ability may provide an important fitness benefit since the negative response to inequity stimulates actors to seek new and more equitable partners (Brosnan & Bshary, 2016). As mentioned, the search for more equitable partners does not need to be intentional since actors that do regularly switch partners will automatically enhance their own evolutionary fitness.

In the third step, actors take deliberate actions to rectify inequity towards the self. It requires an understanding of the consequences that one’s actions have on the outcome of another, and the ability of self-inhibition, namely, to give up the immediate reward (Brosnan, 2009).

In the final step in the evolution of inequity aversion, the response against advantageous inequity, i.e. overcompensation, evolves. In this case individuals get uncomfortable when receiving more than another (Brosnan, 2009; Fehr & Schmidt, 1999). In humans, usually rectify by providing material compensation or use psychological levelling mechanisms like justification or derogation (Brosnan, 2009).

Measuring inequity aversion in non-human animals

It can be challenging to develop experimental paradigms that allow to investigate complex human behaviours, like inequity aversion, in species that do not talk and may differ in several aspects (Talbot et al., 2016). To study inequity aversion in animals, mainly two types of experimental paradigms have been used: token exchange paradigms and platform inequity experiments.

To investigate whether a certain animal species shows a level of inequity aversion, a necessary first step is to study the (behavioural) reactions of individuals of that species to differential reward provisioning (first two levels of the evolution of inequity aversion). The token exchange paradigm is the basic procedure to investigate inequity aversion in animals (see Chapter 7 for a brief review). The first study to implement this paradigm was conducted on capuchin monkeys (Brosnan & de Waal, 2003). The monkeys had to exchange a stone for a reward. Subjects always received a less-preferred reward, while a conspecific either received the same type of reward (equity condition) or a more preferred reward (inequity condition) for an exchange. The responses of subjects were compared between these two conditions as a measure for inequity aversion. Typically subjects reacted by refusing food rewards or refusing to participate in the following trials. Although only behaviours are observed, and no conclusions can be made about the intentions or underlying motivation of animals, this inequity paradigm allows to determine whether certain precursor behaviours, from which a sense of fairness may have evolved in humans, are present in that species (Brosnan, 2006b, 2021; Brosnan & de Waal, 2004).

Other studies have implemented platform inequity experiments, which are largely based on economic games, in which simple decisions (e.g. accept or reject) can be studied to understand more complex behaviour, like inequity (Brosnan, 2013; Konow & Schwettman, 2016; Oberliessen & Kalenscher, 2019). In these tasks, subjects usually sit side-by-side, separated by a partition or face each other with the apparatus placed between them. The subject can pull a bar or drawer to deliver food to itself and/or the partner. Typically, subjects can choose between different payoffs that often include equality (e.g. subject and partner receive a grape) and inequality (e.g. two grapes for the subject and no grape for the partner). Depending on the distribution of food rewards and the possibility of partners to either accept or reject the offer, different results have been found (reviewed in Oberliessen and Kalenscher 2019).

Behavioural studies using these two approaches provide interesting comparative results across animals but often only measure overt behaviours. While human subjects can verbalize how they feel and why they made certain decisions, researchers can only report the behaviour that animal subjects do (Brosnan, 2021; Talbot et al., 2016). In addition to the behavioural measures, studies should therefore aim to explore the emotional component of inequity aversion (Massen et al., 2019). For example, refusals in the token exchange task may reflect the general state of frustration across experimental trials, rather than a trial-by-trial comparison of rewards. Also, it is possible that while noticing inequity, subjects might simply not want to respond (Talbot et al., 2016). Complementing the behavioural measures with measures of the emotional component allows to investigate the multifaceted nature of inequity aversion.

Inequity aversion in non-human animals

Most studies on inequity aversion tasks in non-human animals have focused on primates. Among the New World Monkey species that were tested, callitrichids, owl monkeys (Aotus azarai) and squirrel monkeys (Saimiri sciureus and Saimiri boliviensis) did not respond to disadvantageous inequity (Freeman et al., 2013; Neiworth et al., 2009; Talbot et al., 2011 but see Mustoe et al., 2016), while capuchin monkeys did (Brosnan & de Waal, 2003; Van Wolkenten et al., 2007, but see Silberberg et al., 2009). Among Old World monkeys, rhesus macaques and long-tailed macaques responded negatively to receiving less than a partner (Hopper et al., 2013; Massen et al., 2012). Within the great apes, inequity aversion was not found in Sumatran orangutans (Pongo abelli) (Bräuer et al., 2009; Brosnan and Talbot) and Western lowland gorillas (Gorilla gorilla gorilla) (Sosnowski et al., 2021). In contrast, chimpanzees (Brosnan et al., 2005; Brosnan, Talbot, et al., 2010; Hopper et al., 2014) but see (Bräuer et al., 2009; Engelmann et al., 2017), and possibly bonobos (Pan paniscus) (Bräuer et al., 2009) reacted negatively to disadvantageous inequity. One study also reported advantageous inequity aversion in one of two groups of chimpanzees, using the inequity aversion task (Brosnan, Talbot, et al., 2010).

Studies focusing on non-primates, also have reported mixed results. While dogs and wolves (Canis lupus) reacted to receiving less than a partner in some studies (Brucks, Range, et al., 2017; Essler et al., 2017; Range et al., 2009, 2012), other studies in dogs failed to find such aversive reactions (Brucks et al., 2016; Brucks, Marshall-Pescini, et al., 2017). Several studies in corvids have demonstrated negative responses to disadvantageous inequity (Di Lascio et al., 2013; Wascher & Bugnyar, 2013). While parrots initially showed no negative response (Heaney et al., 2017; Krasheninnikova, Brucks, Buffenoir, et al., 2019), a recent study showed inequity aversion to unequal effort in in Goffin's cockatoos (Cacatua goffiniana) (Laumer et al., 2020). Overall, the findings to date fit the cooperation hypothesis, which states that species that regularly cooperate with kin and non-kin in a variety of contexts, have evolved the tendency to respond to inequity (Brosnan & de Waal, 2014; Fehr & Schmidt, 1999).

Bonobos as study species

Bonobos have long been understudied due to the late recognition of bonobos as a species, the civil war in the Democratic Republic of Congo and the remote area that bonobos live in (Hickey et al., 2012; Stanford, 1998). The first scientific publications about behaviour in bonobos mainly reported about the female-dominated societies and their exuberant sex lives (e.g. de Waal, 1990; Parish, 1996).

As a result, bonobos have long been and are often still considered as the peaceful, prosocial, sexually active, and non-competitive 'hippie ape'. This has not only captured the public imagination, but also largely impacted the behavioural bonobo research in captivity. Although the degree of differences between bonobos and chimpanzees has been debated (e.g. Stanford 1998; Fruth, Hohmann, and McGrew 1999; de Lathouwers and van Elsacker 2006; Doran et al. 2002; Palagi 2006), some researchers hold onto the strong dichotomy between both species and use the peaceful and tolerant bonobo framework to explain their experimental and/or observational findings.

Socio-ecological characteristics

Bonobos are one of our closest living relatives. Together with chimpanzees they form the genus Pan and share 98.7 % of their DNA with humans (Prüfer et al., 2012). Together with humans, gorillas and orangutans, bonobos and chimpanzees belong to the Hominidae family. The split between the Pan and Hominoid line has been estimated around 5 million years ago, while bonobos and chimpanzees only diverged between 0.8 to 2.5 million years ago (Prado-Martinez et al., 2013; Prüfer et al., 2012; Won & Hey, 2005). Although most experimental studies on cooperation focused on chimpanzees, bonobos possess many characteristics that make them a relevant species to study the proximate drivers of cooperation.

Bonobos are endemic to the Demographic Republic of Congo and live south of the Congo river, in the Congo basin (T. Kano, 1992). They live in relatively stable multimale-multifemale communities of about 10 to 63 individuals (Furuichi & Thompson, 2008; T. Kano, 1992; Surbeck, Girard-buttoz, et al., 2017), although larger groups have been reported (see review in J. M. G. Stevens, 2020). Members of these communities live in flexible fission-fusion societies, where smaller subgroups, called parties, split up and merge frequently during the course of the day (Kano, 1992; review in Van Elsacker et al., 1995). Bonobo groups are highly cohesive, which is largely the result of female behaviour. Females prefer to aggregate in large parties in which they frequently interact with one another. Although the aggregation in larger social groups comes with a cost, female bonobos might want to attend larger parties for two social reasons. First, females may want to associate with their adult sons. Bonobos are a male-philopatric species, meaning that males stay in their natal groups while females migrate to other communities when they reach maturity (Furuichi, 1989; T. Kano, 1992). As a result, the strongest bonds, with high rates of affiliative interactions, are found between mothers and their sons (Furuichi & Ihobe, 1994; T. Kano, 1992; J. M. G. Stevens et al., 2006, 2015). Mothers also support their sons in agonistic conflicts, which allows the sons to obtain a higher dominance rank and facilitates their access to mating partners (Furuichi, 1997; Furuichi & Ihobe, 1994; T. Kano, 1992; Surbeck et al., 2011, 2019). Second, females also associate with other females to cooperatively dominate males, which allows them to have priority of access during feeding and to avoid harassment by unrelated males (Furuichi, 1997; Moscovice et al., 2019; Nurmi et al., 2018; Parish, 1994; Vervaecke, de Vries, et al., 2000b). Both reasons to aggregate with group members correspond with the hypothesis that individuals prefer to associate with the potentially best cooperation partners (Gilby & Wrangham, 2008; Surbeck, Girard-Buttoz, et al., 2017).

When female bonobos reach sexual maturity, they leave their natal group and migrate to a neighbouring group. In this new group, young immigrant females engage in frequent social interactions with other young individuals and with older and higher ranking senior females that already established in the group, i.e. specific senior females (Furuichi, 1989; Idani, 1991). The immigrant females usually initiate the social interactions, which helps them to improve their social status and to integrate well in the group (Idani, 1991; Toda & Furuichi, 2020, 2022). Although they are unrelated, females engage in strong associations, which allows them to improve their status in the male-philopatric society (Parish, 1994; J. M. G. Stevens et al., 2006, 2008; Surbeck & Hohmann, 2013). Often, alliances against males are caused by low-intensity displays and pestering of males (T. Kano, 1992; Parish, 1996; Tokuyama & Furuichi, 2016). Such male harassment is usually directed towards females and infants and serves to test dominance relationships. Often, such intimidations are retaliated against by a coalition of females (Hohmann & Fruth, 2003b; T. Kano, 1992; Parish, 1996; Vervaecke, de Vries, et al., 2000b).

Bonobo communities occupy territories that can overlap considerably (Badrlan & Badrian, 1984; Idani, 1990a; T. Kano, 1992), resulting in regular inter-group encounters (L. Cheng et al., 2021; Idani, 1990a; T. Kano, 1992; Lucchesi, Cheng, Janmaat, et al., 2021). These inter-group encounters in bonobos are also thought to be highly tolerant and peaceful. In reality, they involve both affiliative and aggressive interactions because of the different sex-specific strategies in response to the different forms of competition (L. Cheng et al., 2021, 2022; Hohmann & Fruth, 2002; T. Kano, 1992; Sakamaki et al., 2018; Tokuyama et al., 2019). Inter-group interactions encompass different cost and benefits for the two sexes: females from different groups should compete for food resources, while males should compete for females (Kitchen & Beehner, 2007). The cost-benefit balance for each individual during inter-group interactions determines how tolerant or hostile the inter-group associations may be (Grueter et al., 2012). Most intergroup encounters are observed when food is abundant and when a higher number of adult females with maximum swellings are present (Hohmann & Fruth, 2002; Lucchesi, Cheng, Janmaat, et al., 2021; Sakamaki et al., 2018). In this case, inter-group female competition over food resources is usually low, while the opportunity to copulate with extra-group males is high. To avoid harassment by males, females form tolerant and cooperative relationships within and across groups, suggesting that they simply select partners irrespective of their group when the coalition yields direct benefits (Tokuyama et al., 2019). Males seem to gain less from inter-group associations than females, and may therefore show more aggression than females during inter-group encounters (L. Cheng et al., 2021; Fruth & Hohmann, 2018; Tokuyama et al., 2019). While males can copulate with out-group females to increase their fitness, they are unable to prevent their in-group females from copulating with out-group males (Tokuyama et al., 2019). This could explain

why males remain at a distance and interact less often than females during inter-group encounters (Furuichi, 2011; Idani, 1990a). Within-group dominance of older females over males probably may enable them to decide when to terminate an inter-group association (Furuichi, 2011; Tokuyama et al., 2019; Tokuyama & Furuichi, 2017). Male-male dyads do not form strong bonds or share food but do occasionally form coalitions against other males (Furuichi & Ihobe, 1994; T. Kano, 1992; J. M. G. Stevens et al., 2006; Surbeck, Boesch, et al., 2017; Surbeck & Hohmann, 2015). Aggressions between bonobo males are lower in frequency and intensity than between chimpanzee males (Surbeck, Boesch, et al., 2017), are more frequent in the presence of more within-group oestrous females (Hohmann & Fruth, 2003b). Thus, an increasing body of evidence suggests that bonobos' relationship within and between communities are more complex than initially thought.

Bonobos as a model species to study prosociality and inequity aversion

To investigate to what extent human prosociality is unique (i.e. human uniqueness hypothesis), it is important to study both of humans closest living relatives, chimpanzees and bonobos (Prüfer et al., 2012). While chimpanzees have been studied extensively in several prosociality paradigms, knowledge on our other closest living relative is also needed to fully understand to what extent human prosociality can be considered unique.

Also, based on their socio-ecology, bonobos are an ideal study species to investigate the proximate mechanisms of cooperation. While the cooperative breeding hypothesis predicts low levels of (proactive) prosociality in the independently breeding bonobo (Burkart et al., 2014), the self-domestication hypothesis predicts high levels of prosocial behaviour (Hare, 2017; Hare et al., 2012). As a result of their seemingly affiliative and tolerant behaviour in the wild, they have been proposed as a likely candidate for self-domestication and therefore an ideal species to study prosociality (Hare, 2017; Hare et al., 2012; Hare & Wrangham, 2017). Because of their reduced sexual dimorphism, smaller heads, lighter bodies and more juvenilized characteristics than chimpanzees, bonobos were hypothesized to be a good model for self-domestication (Wrangham & Pilbeam, 2000). To find evidence for this hypothesis, researchers specifically looked for evidence of prosociality in bonobos. They predicted that bonobos should show greater prosociality than chimpanzees and more flexible social skills relating to cooperation and communication (reviewed in (Hare & Woods, 2017; Tan & Hare, 2017). Bonobos consistently co-fed on monopolizable food, while chimpanzees did not, which allowed bonobos to cooperate in an experimental task more flexible than chimpanzees (Hare et al., 2007). Bonobos repeatedly shared food in their possession in the absence of clear sign of signals of need, i.e. proactive prosociality, or the opportunity to reciprocate within the experiment (Hare & Kwetuenda, 2010; Krupenye, Tan, et al., 2018). They opened a door to share food and preferred to do so with strangers over group-mates (Tan & Hare, 2013), and proactively provisioned food to members of other groups (Tan et al., 2017). It was hypothesized that strong female alliances and sexual selection against male aggression removed the threat of lethal inter-group aggression in bonobos, returning the costly interaction into a highly beneficial one, leading to higher levels of tolerance, prosociality and xenophilia (Hare et al., 2012; Tan et al., 2017). Thus, the bonobo self-domestication puts a strong emphasis on tolerance as the most important proximate mechanism of cooperation (see cooperation model). However, all of these studies were done in a sanctuary outside of Kinshasa, Lola Ya Bonobo.

In this sanctuary, bonobos arrive as wild-caught infant or juvenile orphans, typically victims of pet trades and bush-meat. During their first few years, individuals rehabilitate with a nursery 'cohort group', where each bonobo is assigned to a substitute human mother. After this nursing phase, individuals are integrated in larger, mixed social groups. To equilibrate group dynamics, individuals are regularly transferred between groups (Clay, 2011). Thus, the findings that showed high levels of tolerance and proactive prosociality, that supported the bonobo self-domestication hypothesis, were mainly based on subadult subjects. Therefore, additional research is needed to obtain a more representative view on bonobo prosociality. Also, in contrast to the highly prosocial sharing of the orphaned subadult bonobos, other studies that replicated some of the experimental designs in more diverse bonobo groups (i.e. consisting of individuals of a wider age range and different backgrounds), failed to find the previously reported high levels of social tolerance, cofeeding and prosociality in bonobos (Bullinger et al., 2013; Cronin et al., 2015; Jaeggi, Stevens, et al., 2010). One study that replicated the door-opening paradigm in a more diverse bonobo group, showed that bonobos preferred to feed alone but let conspecifics in as soon as food was no longer involved (Bullinger et al., 2013). Food sharing experiments in Planckendael showed that bonobos were less tolerant and less likely to share food and co-feed than chimpanzees (Cronin et al., 2015; Jaeggi, Stevens, et al., 2010). Additional instrumental helping studies in bonobos also showed mixed results. While only one subject transferred one stick in a first study (Liebal et al., 2014), a more recent study, that re-tested half of the same subjects in another paradigm, reported high rates of tool transfers (Nolte & Call, 2021). Two other instrumental helping studies showed that "juvenile and young adult bonobos" helped conspecifics to obtain food (Tan et al., 2017) but did not transfer tools to conspecifics (Krupenye & Hare, 2018). The limited food provisioning studies on bonobos showed that they voluntarily handed food items to other (Krupenye, Tan, et al., 2018) but failed to behave prosocially in a horizontal variant and token variant of the PCT (Amici et al., 2014; Tan et al., 2015). Although incongruent findings can be attributable to intergroup differences in prosociality (e.g van Leeuwen et al. 2021), these recent studies provide a more nuanced view on prosociality in bonobos.

Bonobos have also been shown to possess a certain level of Theory of Mind (Krupenye et al., 2016; Krupenye, MacLean, et al., 2018) and to show post-conflict third-party affiliation, i.e. consolation (Clay & de Waal, 2013a; Palagi et al., 2004b; Palagi & Norscia, 2013). Following the empathy hypothesis, their empathic abilities should allow bonobos to show high levels of (empathy-based) prosociality (de Waal, 2008; de Waal et al., 2008; de Waal & Suchak, 2010).

In contrast with the number of prosociality studies, only very limited research has been done on inequity aversion in bonobos. One study (Kaiser et al., 2012) implemented an experimental game in bonobos and chimpanzees, in which proposers could choose between a pair of choices that were either fair (50/50) split between proposer and responder or unfair (e.g 80/20). Responders could accept the offer by pulling a rope or could reject by not pulling it. The study reported that proposers acted purely selfish and that responders showed very limited rejection rates. They concluded that both apes maximize their payoffs and are insensitive to inequity (Kaiser et al., 2012). However, during the familiarisation phase of the study, subjects only experienced very limited trials and subjects did not have to reach a certain criterium for success before they could participate in the actual experiment. Thus, these negative findings could as well reflect the lack of understanding of the responders. One study that implemented the token exchange inequity aversion task in chimpanzees, orangutans and bonobos reported that bonobos were the only ape species with a tendency to show disadvantageous inequity aversion (Bräuer et al., 2009). This is in strong contrast to self-domestication hypothesis, which would predict high levels of tolerance and food sharing and potentially even advantageous inequity aversion.

Study outline

The overall aim of my PhD was to complement the existing knowledge about both proximate mechanisms of cooperation in bonobos. Specifically, by implementing multiple experimental paradigms, I aimed to explain the variability in prosociality and inequity aversion using the socio-ecological approach. This thesis is composed of two sections.

Section one: methodological approaches

The first section (chapter 2, 3 and 4) aims to investigate methodological aspects, which were essential to conduct the experimental research in the next section. To determine which food items to use in the experimental paradigms of my PhD, I first wanted to determine the bonobos' food preference on ten novel food items. Therefore, in chapter two I use paired-choice food tests to determine food preference of the Planckendael bonobos for ten novel food items and 23 familiar food items. To investigate the influence of specific nutrients on their preference, I also correlate the nutritional composition of the food items with the bonobos' preference and compare my findings with the food preference patterns of other great apes. The results of this first chapter can help future studies, including mine, in deciding which food items to use in their experimental studies.

While inequity aversion and prosociality have been suggested to have a strong emotional component (Massen et al., 2019; Soares et al., 2010), they have been evaluated only by behavioural responses. For the first time, I aimed to include physiological measures to look at the underlying emotions of the proximate mechanisms of cooperation. Individuals are expected to be more aroused in situations with unequal payoffs, which can be measured by the level of salivary cortisol (T. M. O'Connor et al., 2000). However, prior to using such a physiological measure, the sampling window to detect an effect after a specific event must be determined. Therefore, in chapter three I implement a biological validation for urinary and salivary cortisol in bonobos. I determine the time-lag between a psychological stressor and the increase and peak in urinary and salivary cortisol levels and investigate inter-individual variation in the baseline and stress levels of cortisol. With this study I aim to confirm relevant sampling windows for cortisol sampling in experimental studies.

Most successful cooperative interactions are likely to be based on emotional bookkeeping between closely associated individuals (Evers et al., 2015; Schino & Aureli, 2010), suggesting that the quality of the relationship may influence the level of inequity aversion and prosociality among cooperative partners. To measure the quality of relationships, I wanted to use the composite measure of relationship quality, which has been suggested to be more comprehensive and conceptually more coherent than the simple measures like proximity or amount of grooming (Fraser et al., 2008; J. M. G. Stevens et al., 2015). Thus, in chapter four I investigate the repeatability and applicability of the composite measure of relationship quality to measure social bond strength in bonobos (J.

M. G. Stevens et al., 2015). Since prosociality and inequity aversion are suggested to start from psychological traits that prefer similarity with others (Yamamoto & Takimoto, 2012) and because close associations are more likely to occur between individuals that are more similar (Carter et al., 2015; de Waal & Luttrell, 1986; McPherson et al., 2001), I also investigate whether the relationship quality between bonobos is influenced by similarity in genes, sex and personality.

Section two: the proximate mechanisms of cooperation in bonobos

In the second section, I implement multiple paradigms to study prosociality and inequity aversion in bonobos. Chapter five describes the implementation of a novel provisioning experiment in a group setting, which has previously been used to measure prosociality in chimpanzees (van Leeuwen et al., 2021). In this experiment, bonobos can provide juice from a distant fountain, benefitting a group member. The set-up allows for free choice of participation and therefore allows to investigate individual and social factors that influence prosociality in bonobos.

In chapter six I implement two validated food provisioning prosociality paradigms in a group context: the prosocial choice task and the group service paradigm (Burkart & van Schaik, 2013; Silk et al., 2005). The results of this chapter allow to compare the prosocial choices of bonobos in a different context as the payoff for the actor in these tasks differs.

In chapter seven, I implement the token exchange inequity aversion paradigm in bonobos. Using a comparable method as the only previous inequity study in bonobos (Bräuer et al., 2009), I provide additional information on the capacity of bonobos to notice and react to unequal payoffs. I investigate a behavioural and physiological response to inequity and investigate whether the relationship quality between partners influences their tolerance for inequity.

Chapter eight, the final chapter, provides a general discussion, linking the results of the previous chapters to each other, to the general framework of cooperation and the socio-ecology of bonobos. In the final part, I also highlight some limitations of this study and future perspectives.

Food preference and nutrient composition in captive bonobos (Pan paniscus)

Jonas Verspeek
Jeroen M. G. Stevens

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Abstract

Food preference has been studied in a range of Hominoidea in the wild and captivity allowing for interspecific comparisons. Chimpanzees (Pan troglodytes) and gorillas (Gorilla gorilla gorilla) preferred low-fibre, high-sugar foods, suggesting that frugivory and their dietary overlap are results of their shared preference for the same nutrients. Comparable tests of the nutritional preference of bonobos do not exist. In this study we examined food preferences of five captive bonobos for 23 familiar and ten novel food items. We performed paired-choice food tests resulting in a clear rank order in food preference with minor individual differences. Fruits were more preferred than vegetables. We correlated nutritional composition of the food items with the bonobos' preference. We found that preferences for familiar food items were positively correlated with total energy and carbohydrate content and negatively correlated with water and micronutrient (sodium, calcium, phosphorus, iron, zinc, manganese, selenium) content. Food preference for the novel food items also significantly correlated positively with total energy and carbohydrate content. Our study supports the idea that food preference among bonobos follows the pattern of the other great apes and that the shared frugivorous diets may be the result of a common preference for the same nutrients. In the wild, these preferences may be less clear due to the interference of preferred nutrients with secondary compounds. Combining food preference data and nutritional information can help in providing a healthy diet with a balanced nutrient composition in captivity. Individual food preferences can help in optimizing food choice for positive reinforcement training and food-related tasks in future research.

Introduction

The majority of primate species include a large variety of foods in their diet (Hughes, 1993; Richard, 1985). Feeding on these food items does not happen randomly. Optimal foraging theory predicts that animals show marked preferences and select their food based on the availability, the time needed to find and consume the items, as well as on the nutrient composition (Barton & Whiten, 1994; Felton et al., 2009; T. Kano, 1992; Pyke, 1984; Raubenheimer et al., 2015; Schoener, 1971; Stephens & Krebs, 1986). Animals maximize their net intake of energy or other necessary nutrients which resulted in adaptive food selection patterns that are present today (Chivers, 1998; Milton, 1979; Stephens & Krebs, 1986)[1].

At first, food preference studies focused on secondary compounds like phenolics, alkaloids or tannins, which are toxic or inhibit digestion of proteins and polysaccharides, to explain food choice since foods high in these compounds are avoided by primates (Ganzhorn, 1989; Glander, 1982; Milton, 1979). Determining nutrients that correlate positively with food preference is complicated by the complex nutritional content of the food items and the trade-off that primates have to make between the need to meet their nutritional requirements on one hand and the avoidance of secondary compounds on the other (Milton, 1981). To overcome this problem food preference studies in captive primates often include commercially available food items with well-known nutritional content and low quantities of secondary compounds (B. Holland et al., 1991; Jildmalm et al., 2008).

An accurate method to study food preference, which has been widely used in different species, is the paired choice test (Clay & Zuberbühler, 2009; Laska et al., 2000, 2003; Remis, 2002; Slocombe & Zuberbühler, 2006). In this test, two food items are presented simultaneously to the subject which has to select one of the two. After all possible combinations are presented, food items are ranked based on the percentage of times the subject selected each item. This method allows differentiation in preferred and less-preferred food items and can control for potential confounding effects such as size of food items, stage of maturity, novelty of food and social context (Jildmalm et al., 2008). Paired choice tests have been implemented in a range of primate species, making interspecies comparisons possible. In spider monkeys (Ateles geoffroyi) (Laska et al., 2000), squirrel monkeys (Saimiri sciureus) (Laska, 2001), capuchin monkeys (Sapajus apella) (Visalberghi et al., 2003), gorillas and chimpanzees (Remis, 2002) food preference correlated with the total energy content of the food items. Macaques (Macaca nemestrina) (Laska, 2001) and gibbons (Hylobates lar) (Jildmalm et al., 2008), on the other hand, preferred foods with high levels of carbohydrates instead of the total energy content. This suggests that some primate species seem to be more opportunistic with regard to their preferred source of metabolic energy (Jildmalm et al., 2008).

Like chimpanzees, bonobos are mainly frugivorous (Badrian et al., 1981; Badrian & Malenky, 1984; Hohmann et al., 2010; Loudon et al., 2019; Potts et al., 2011; Serckx et al., 2015; Uwimbabazi et al., 2019; White, 1992). Beside fruits, terrestrial herbaceous vegetation (THV) is the most important dietary component for wild bonobos (Badrian & Malenky, 1984; Bermejo & Sabater, 1994), accounting

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[1] See Chapter 8: General Discussion of this thesis

for the largest proportion of protein intake (Malenky & Stiles, 1991). The THV proportion in the bonobo diet can be considered intermediate in comparison with the diets of chimpanzees and gorillas (Conklin-Brittain et al., 2001). Bonobos eat both THV and fruit (respectively accounting for 25 % and 55 % of the diet), mountain gorillas consume primarily THV (91 % of the diet), while chimpanzees consume more fruit and less THV (respectively accounting for 64% and 7% of the diet) (Badrian & Malenky, 1984; Malenky & Wrangham, 1994; Wrangham, 1986). Comparative nutritional analyses of plant foods consumed by chimpanzees and bonobos showed that food items of chimpanzees contain more high energy sources like lipids, while bonobos select food items which are low in tannin contents and high in non-structural carbohydrates including starch (Hohmann et al., 2006, 2010). However, when combining observations from different chimpanzee populations, chimpanzees and bonobos consumed similar levels of starch and carbohydrate (Hohmann et al., 2010).

Previous studies on food preference in bonobos, only compared a limited number of food items as part of a larger study (Clay & Zuberbühler, 2009; Shorland et al., 2019). However, studying food preference over an extensive amount of food items may be more useful as it can help in designing appropriate diets in captivity (National Research Council (2003)) and in optimizing reward choice for positive reinforcement training. Moreover, future food-related experiments should include novel food items with known food preference to avoid interference with the daily diet.

The aim of this study was to assess food preference in captive bonobos in paired choice tests on ten novel food items, i.e. food items that were not part of the weekly diet, that could be used in future socio-cognitive tasks like for example inequity aversion (Brosnan & de Waal, 2003). To have a better understanding of bonobo food preference in general, we also presented the different food items of their diet, hereafter called familiar food items, to them and correlated food preference with the nutritional content of the food. Following the optimal foraging theory (Stephens & Krebs, 1986), we predicted that bonobo food preference correlates with the total energy content of the food items. The high sugar content of fruits and the frugivorous diets of wild bonobos (Badrian et al., 1981; Badrian & Malenky, 1984; Serckx et al., 2015; White, 1992), and their predilection for fruits in captivity (Clay & Zuberbühler, 2009) suggest that non-structural carbohydrate content of food items may also be an influencing factor of bonobo food preference. We further predicted that bonobo food preference correlates with protein concentration since protein-rich THV accounts for the second largest dietary compound of wild bonobos (Badrian & Malenky, 1984; Bermejo & Sabater, 1994; Malenky & Stiles, 1991). Further, we expected that food preference is independent of micronutrient concentration since diets of wild bonobos are sufficient for meeting micronutrient requirements (Council, 2003; Hohmann et al., 2019; T. Kano, 1992). Finally, we predicted that food preference does not correlate with water content, since wild bonobos drink water from running and standing water sources (Hohmann & Fruth, 2003a; T. Kano, 1992) and there has not been selection for obtaining water from plant foods. We also determined whether food preference on the novel food items correlates with similar nutrients as the familiar food items.

Methods

We collected food preference data on ten novel items and the diet of five adult bonobos (two females, three males, between 11 and 39 years old) of Zoo Planckendael in Belgium, in 2018 (Table 2.1). This bonobo group was housed in an enclosure consisting of nine interconnected rooms of various sizes (between 15 and 65 m^2) that can be separated by sliding doors to allow temporary separation for testing. All subjects, except for mothers with their dependent infants, were trained to enter individually in each of the different enclosures. Since 2009, the diet of the bonobos in zoo Planckendael consisted of 23 commercial fruits and vegetables, complemented with primate pellets and seasonal browse (Table 2.2). The bonobos were typically fed four times per day. Water was available ad libitum at all times.

Table 2.1 Study subjects at Zoo Planckendael

Individual	Sex	Study age^a	Weight (k)	Descendance
Hortense	Female	39	38,50	Wild born, parent-reared, group housed
Vifijo	Male	23	38,70	Captive born, parent-reared, group housed
Djanoa	Female	22	34,68	Captive born, parent-reared, group housed
Zamba	Male	19	38,55	Captive born, parent-reared, group housed
Habari	Male	11	33,70	Captive born, parent-reared, group housed

^{a} Study age: individual's age when the study took place.

[2] See also table 9.1 Overview of the study subjects p 144

Table 2.2 Foods used in this study

Common name	Scientific name
Familiar food items	
Apple*	Pyrus malus
Banana*	Musa paradisicum
Broccoli	Brassica oleracea botrytis italica
Carrot	Daucas carota
Cauliflower	Brassica oleracea botrytis
Celery	Apium graveolens
Chicory	Cichorium intybus
Chinese Cabbage	Brassica rapa pekinensis
Cucumber	Cucumis sativas
Endive	Cichorium endivia
Green bean	Phaseolus vulgaris
Kiwi*	Actinidia deliciosa
Leeks	Allium ampeloprasum porrum
Lettuce	Lactuca sativa
Orange*	Citrus aurantium
Pear*	Pyrus communis
Pepper	Capsicum annuum felipe
Potato	Solanum tubersum
Red Cabbage	Brassica oleracea capitata f. rubra
Savoy	Brassica oleracea sabauda
Tomato	Lycopersican esculentum
White Cabbage	Brassica oleracea capitata
White Radish	Raphanus sativus Longipinnatus
Novel Food items	
Blue Grape*	Vitis vinifera
Dried Apricot*	Prunus armeniaca
Dried prune*	Prunus domestica
European Radish	Raphanus sativus
Green grape*	Vitis vinifera
Melon*	Cucumis melo
Parsnip	Vitis vinifera
Pumpkin	Cucurbita moschata
Sweet potato	Ipomoea batatas
Zucchini	Cucurbita pepo pepo

*Fruits

Food item selection

We conducted food preference tests on the ten novel items and all familiar vegetables and fruits (Table 2.2). We adjusted the food portion of the diet to include foods to be used in the trials to avoid over-feeding. For the ten novel food items (Table 2.2) all individuals got to taste each item 3 times before starting the trials. The rationale for choosing these novel food items was that (1) none of them was part of the diet in captivity, (2) the novel items differed in nutrient composition and therefore taste and (3) these items are available in produce markets in Belgium all year round. These food items will be used in future socio-cognitive tasks. All food items were always selected with the same degree of ripeness to minimize possible intraspecific variation in nutrient composition. We used nutritional information on the food items from literature (B. Holland et al., 1991) and report them on a percent dry weight basis.

Procedures

We assessed food preference of the ten novel and the familiar food items using paired-choice food trials (Benz & Leger, 1992). We conducted these trials one hour after the first meal and before the second meal to avoid interference with the diet. We tested each bonobo individually to avoid competition that might affect food choices. We presented all possible binary combinations of the ten novel food items (Table 2.2) to each individual. Only one testing session was conducted per individual per day consisting of 20 trials. For the 23 familiar food items (Table 2.2) testing sessions consisted of 25 ± 10 trials on average. We presented each combination 5 times to avoid coincidental artefacts. Due to practicalities (move of the bonobos to another building and arrival of new individuals) paired tests between the novel and familiar food items could not be conducted. Therefore, each subject received 1490 food trials in total. All food items were cut in cubes with a side length of approximately 1 cm to avoid a size effect on the bonobos' choice behaviour. First, we showed a photo of each food item to the individual, on the side where food would be presented, which might help their choice when the distinction between the cubes of the actual food items was unclear (Huskisson et al., 2020; Tabellario et al., 2020). Next, food cubes of the corresponding items were shown and then put on a 30 x 60 cm wooden shelf which was pushed towards the subject. We placed food items > 20 cm apart allowing the subjects to only take one item. After a selection was made, we retracted the wooden shelf and removed the non-chosen food item before the next trial. If no selection was made within 20 seconds, the trial was discarded. We alternated the position of the food items on the slide to counterbalance possible position preferences or problems associated with individuals hand preference. We reduced cueing effects (Beran, 2012) by the experimenter by avoiding to look at the food items after putting them on the shelf.

Analysis of Food Preference

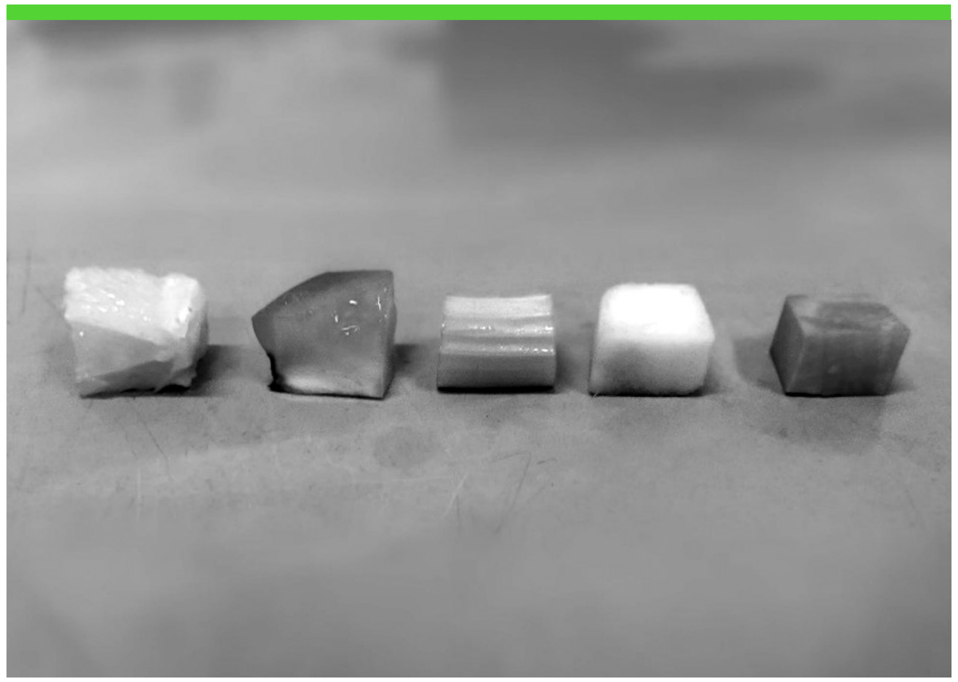
We video recorded all 7450 trials (1490 trials per bonobo) which were afterwards scored by one observer to avoid inter-rater differences. We calculated individual and group food preference scores from proportions of selections via a standard method (Benz & Leger, 1992). Following Remis (2002) we constructed contingency tables with foods selected being arrayed across the top, and items not selected arrayed at the side of a 10 x 10 matrix for the novel items and a 23 × 23 matrix for the dietary food items. Values in each cell represent the proportions of trials each food in a pair was chosen (column) or not (rows). We entered values of 0.5 on the diagonal of the matrix to drop these non-trials when converting to z-scores. We then converted the whole matrix into z-scores. Next, we summed and averaged these scores for each food item which resulted in positive and negative food preference scores. We added the absolute value of the lowest preference score to the preference score of each food item to obtain food preference hierarchies with arbitrary zero points and meaningful interval scale distances.

Statistical analysis

To explore whether food preference differed between food items, we ran two linear mixed models with food preference score for the novel and the familiar items as dependent variables (z-transformed), food item as fixed factor and individual as random factor to account for repeated measures of each individual (lme4 package 1.1-13 (Bates et al., 2015)). Next, we compared the full model with the null model. When a significant effect was found, we performed post-hoc pairwise comparisons, using Tukey test for multiple comparisons of means. We used independent-sample t-tests to test for differences in food preference between fruit and vegetables. We used Spearman's rank correlation to study the relationship between food preference and the nutrient composition of each food item. Diagnostic plots (residual vs. fitted, QQ plots) were used to confirm the assumptions of normality and homogeneity of variances. All statistical analyses were conducted using R (version 3.5.1; (Team, 2017).

Ethical note

All research complied with the ASAB guidelines (ASAB, 2020). This study was approved by the Scientific Advisory Board of the Royal Zoological Society of Antwerp and The University of Antwerp (Belgium) and endorsed by the European Breeding Program for bonobos.



Results

All individual bonobos participated in the tests and showed clear food preferences. Of all trials, 98 % were successfully completed (n = 7450).

Familiar food items

Food preference for the familiar foods differed significantly (χ^2 (22) = 342.1616, P <0.0001; Fig. 2.1). Fruit items (median = 1.85) had significantly higher individual mean preference scores than vegetables (median=0.76) (Wilcoxon signed-rank test: Z = -7.54, p < 0.0001, r = -0.70). Banana was clearly the most preferred food item and was significantly preferred over all vegetables (Tukey, P <0.01; Fig. 3.1), carrots excluded (Tukey, P = 0.30). Lettuce was the least preferred type of food by all individuals but one, which preferred lettuce over endive. For kiwi, potato, green pepper, green beans and savoy, individual food preferences showed more variance than for the other familiar food items (whiskers in Fig. 2.1).

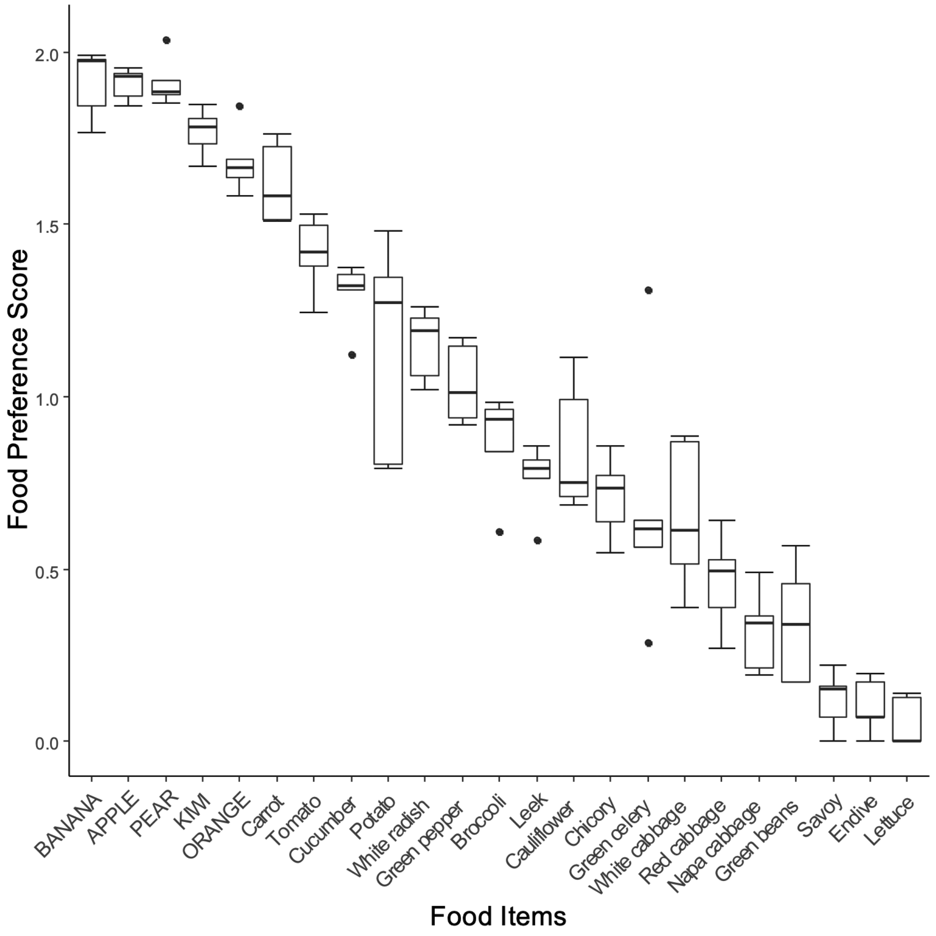


Fig. 2.1 Median food preference scores of five bonobos for all familiar food items. The box plots represent medians (dark horizontal lines), inter-quartile range (boxes), minima and maxima (whiskers) and outliers (dots). Fruits are labelled in capitals.

The Spearman rank-order correlations between food preference and the nutritional content of the 23 familiar food items showed that food preference correlated positively with the total energy content (r = 0.68, P < 0.001) and the amount of carbohydrates (r = 0.66, P < 0.001) (Table 2.3). The type of carbohydrate did not matter since the amount of glucose (r = 0.51, P = 0.02), fructose (r = 0.52, P = 0.01) and sucrose (r = 0.54, P = 0.01) all significantly correlated with food preference. For familiar food items, preference also significantly, but negatively, correlated with water content (r = -0.59, p <0.01), the amount of folate (r = -0.76, P < 0.0001), riboflavin (r = -0.51, P = 0.01) and several minerals (sodium, calcium, phosphorus, iron, zinc, manganese and selenium) (r > 0.40, P < 0.05 for these minerals). Other nutrients did not significantly influence food preference on familiar food items. However, we found a negative trend (rho = -0.41, P = 0.05) for the correlation between food preference and the amount of proteins in the food items. Table 2.4 shows the Spearman rank-order correlations between the different nutrients of the diet.

Table 2.3 Spearman rank-order correlation between average food preference score and the nutrient content for the food items of the diet and novel food items.

	Familiar food items (N=23)		Novel Food items (N =10)	
	Rho	**P**	**Rho**	**P**
Macronutrients				
Energy	0.680	0.001 *	0.670	0.033 *
Water	-0.590	0.006 *	-0.590	0.074
Protein	-0.410	0.026 *	-0.120	0.736
Lipids	0.040	0.900	-0.230	0.526
Carbohydrates	0.660	0.001 *	0.730	0.016 *
Dietary fibre	0.030	0.850	0.110	0.764
Sugar Fibre Ratio	-0.020	0.859	-0.800	0.200
Starch	0.160	0.540	-0.250	0.481
NSPa	-0.340	0.090	-0.110	0.764
Carbohydrates				
Glucose	0.510	0.010 *	0.580	0.077
Fructose	0.520	0.008 *	0.620	0.054
Sucrose	0.540	0.012 *	-0.040	0.906
Vitamins				
Vitamin B6	0.210	0.332	-0.220	0.541
Vitamin C	-0.050	0.870	-0.450	0.189
Vitamin E	0.000	0.942	0.210	0.555
Vitamin K1	-0.170	0.307	-0.530	0.117
Folate	-0.760	<0.001 *	-0.690	0.026 *
Pantothenate	-0.030	0.582	0.070	0.855
Biotin	0.320	0.297	0.380	0.274
Thiamine	-0.230	0.145	-0.070	0.841
Riboflavin	-0.510	0.006 *	0.080	0.824
Tryptophan	-0.220	0.230	-0.050	0.893
Niacin	-0.180	0.368	-0.130	0.712
Carotene	-0.240	0.236	-0.050	0.881
Minerals				
Sodium	-0.440	0.036 *	-0.150	0.684
Potassium	-0.310	0.103	-0.070	0.855
Calcium	-0.680	0.000 *	-0.270	0.446
Magnesium	-0.040	0.803	-0.010	0.987
Phosphorus	-0.540	0.005 *	-0.130	0.726
Iron	-0.610	0.002 *	-0.210	0.554
Copper	0.210	0.329	0.680	0.030 *
Zinc	-0.450	0.019 *	-0.270	0.459
Chloride	0.080	0.964	0.120	0.738
Manganese	-0.420	0.037*	-0.180	0.621
Selenium	-0.540	0.004 *	-0.260	0.461
Iodine	0.280	0.271	0.160	0.651

[a] Non-starch polysaccharide

Table 2.4 Spearman rank-order correlation between the nutrients that correlated with food preference of the familiar food items.

	Energy	Water	Protein	Carbohydrate	Glucose	Fructose	Sucrose	Folate	Riboflavin	Sodium	Calcium	Phosphorus	Zinc	Iron	Manganese	Selenium
Energy	-	-0.95	0.21	0.94	0.63	0.63	0.58	-0.44	-0.12	-0.44	-0.35	-0.07	-0.01	-0.29	-0.17	-0.2
Water	***	-		-0.93	-0.64	-0.62	-0.63	0.4	0.15	0.38	0.24	0.02	0.01	0.2	0.08	0.09
Protein			-	0.07	-0.1	-0.07	-0.19	0.6	0.73	0.08	0.33	0.8	0.74	0.57	0.42	0.48
Carbohydrates	***	***		-	0.72	0.68	0.62	-0.49	-0.26	-0.47	-0.35	-0.18	-0.08	-0.43	-0.2	-0.24
Glucose	**	***		***	-	0.94	0.68	-0.3	-0.32	-0.31	-0.12	-0.3	-0.28	-0.34	-0.27	-0.17
Fructose	**	**		***	***	-	0.58	-0.27	-0.21	-0.47	-0.21	-0.31	-0.29	-0.35	-0.23	-0.18
Sucrose	**	**		**	***	**	-	-0.41	-0.2	-0.1	-0.12	-0.32	-0.44	-0.32	-0.3	-0.01
Folate	*	.		*			.	-	0.67	0.38	0.63	0.61	0.57	0.65	0.43	0.56
Riboflavin			***					***	-	0.16	0.26	0.65	0.61	0.52	0.39	0.51
Sodium	*	.		*		*		.		-	0.56	0.15	0.14	0.28	-0.1	0.37
Calcium				.				**		**	-	0.51	0.32	0.62	0.32	0.63
Phosphorus			***					**	***		*	-	0.73	0.84	0.64	0.59
Zinc			***				*	**	**			***	-	0.6	0.48	0.33
Iron			**	*				***	*		**	***	*	-	0.64	0.63
Manganese			*					*	.			***	*	**	-	0.35
Selenium			*					**	*	.	**	**		**		-

Significance: *** < 0.001, ** < 0.01, * < 0.05,. < 0.1

Novel food items

Food preference differed significantly between the novel food items (χ^2 (9) = 86.45, P <0.0001). Bonobos preferred novel fruit items (mean = 1.30) over novel vegetables (mean = 0.49) (t test: t = -5.57, df = 43.43, P <0.0001). Food preferences on plum, apricot, and melon showed more individual differences when comparing with the other novel food items (Fig. 2.2).

Food preference on the novel food items showed a significant positive correlation with total energy content (r = 0.67, P = 0.03), the amount of carbohydrates (r = 0.73, P = 0.02) and the amount of copper (r = 0.68, P = 0.03) (See Table 2.3). We found a negative correlation between food preference and the amount of folate (r = -0.69, P = 0.03). Spearman rank-order correlations between the different nutrients of the novel food items can be found in table 2.5.

	Energy	Carbohydrate	Folate	Riboflavin	Copper
Energy	-	0.98	-0.41	0.34	0.92
Carbohydrate	***	-	-0.5	0.27	0.93
Folate			-	-0.36	-0.31
Riboflavin				-	0.28
Copper	***	***			-

Significance: *** < 0.001, ** < 0.01, * < 0.05,. < 0.1

Table 2.5 Spearman rank-order correlation between the nutrients that correlated with food preference of the novel food items.

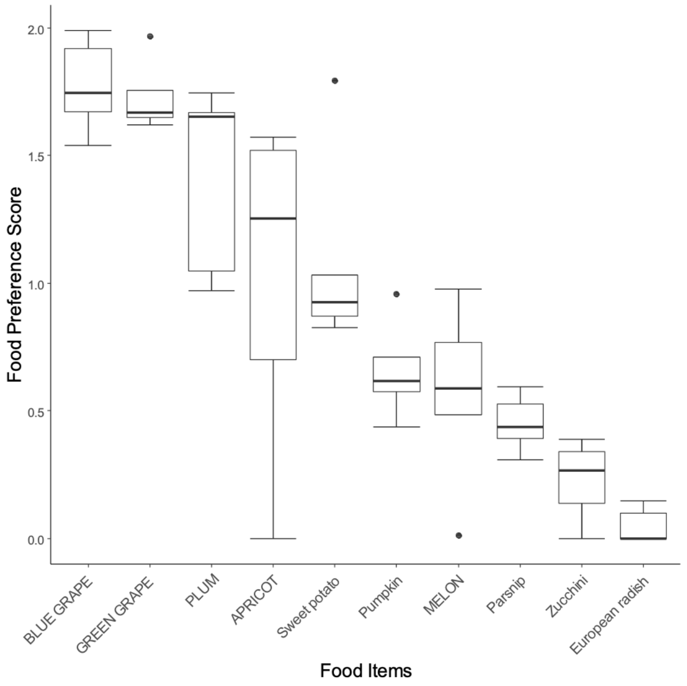


Fig. 2.2 Food preference scores of five bonobos for the ten novel food items. The box plots represent medians (dark horizontal lines), inter-quartile range (boxes), minima and maxima (whiskers) and outliers (dots). Fruits are labelled in capitals.

Discussion

Our results show that, as can be expected, captive bonobos have clear food preferences in paired-choice food experiments using cultivated foods. Fruits were more favoured than vegetables, and food items were more preferred when high in energy and carbohydrates, and low in folate levels. Bonobos also showed lower food preference for food items with high water, sodium, calcium, phosphorus, iron, zinc, manganese and selenium content.

Food preference of the familiar food items correlated positively with total energy content, which was predicted given the optimal foraging theory (Stephens & Krebs, 1986). Carbohydrate content also correlated with food preference, which is similar to findings in spider monkeys (Laska et al., 2000), squirrel monkeys (Laska, 2001), capuchin monkeys (Visalberghi et al., 2003), gorillas (Ganas et al., 2008; Remis, 2002; Remis et al., 2001; Remis & Kerr, 2002), chimpanzees (Hladik & Simmen, 1996; Remis, 2002; Reynolds et al., 1998) and wild bonobos (Hohmann et al., 2006, 2010). Carbohydrates are rapidly hydrolysed in the large intestine contributing to maximize the net intake of energy (Sterling et al., 2013). Protein content correlated negatively with food preference. Food preference did not correlate with the amount of lipid and starch in the food items. This could be due to the fact that we only included commercially available fruits and vegetables, which contain lower levels of lipids and starch in comparison with food items of wild bonobos and other primates (Hohmann et al., 2010; B. Holland et al., 1991; Schwitzer et al., 2008). In the wild, the high consumption rate of THV by bonobos supplements their frugivorous diet with proteins, lipids and starch resulting in energy rich diets (Hohmann et al., 2006, 2010). Bonobos therefore seem to be opportunistic feeders with regard to energy gain. Water content correlated negatively with food preference on the familiar food items. We predicted that food preference would not be correlated with water content, given that wild and captive bonobos obtain water from different sources (Hohmann & Fruth, 2003a; T. Kano, 1992), allowing them to select foods independently of their water content. However, foods containing high amounts of water are low in energy and carbohydrate content (e.g. cucumber (B. Holland et al., 1991)), which may explain the negative correlation.

We did not expect the negative correlations between the different micronutrients and food preference[3]. The amount of folate and riboflavin, two vitamins with a crucial role in maintaining new cells and preventing DNA from changing (Watanabe & Miyake, 2017), correlated negatively with food preference. Further, food preference on the familiar food items correlated negatively with the contents of sodium, calcium, phosphorus, iron, zinc, manganese and selenium. These correlations might be by-products of the bonobo preference for energy-rich food items, since the total energy content correlated negatively with folate and sodium content and folate content was positively correlated with riboflavin, calcium, phosphorus, iron, manganese, and selenium contents. Studies on spider monkeys (Laska et al., 2000), squirrel monkeys (Laska, 2001), macaques (Laska, 2001) and gibbons (Jildmalm et al., 2008) also suggested that preferences for certain minerals might mainly be by-products of preferences for other nutrients, resulting in variable results across studies. Our study included many leafy vegetables with a lower total energy and higher mineral content (B. Holland et al., 1991), increasing the range of mineral contents across the food items, which might explain why we find more correlations between food preference and various micronutrients.

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[3] See Chapter 8: General Discussion of this thesis

Similar to our findings on the familiar food items, food preference on the novel food items also correlated positively with energy and carbohydrate content, meaning that novel food selection is mainly based on carbohydrate content given its strong correlation with energy content in the novel foods (Table 2.3). While, no clear-cut patterns of seasonality are present in the production of bonobo plant foods in the wild, patterns of fruit production did vary greatly between and even within species (Badrian & Malenky, 1984). In seasonal habitats, preferred and fallback foods often rotate. Primates, including bonobos, may have to survive on fallback foods for a certain period of the year. Therefore, prioritizing carbohydrate-rich foods, when available, results in a fast intake of energy (Marshall & Wrangham, 2007; Sterling et al., 2013) hence replenishing their energy reserves. Further, food preference on the novel, but not the familiar, foods correlated positively with copper content, which can be attributed to the higher copper concentrations of the preferred novel fruits. The amount of copper in the novel food items was almost perfectly positively correlated with the total energy content, again suggesting a by-product of the bonobo preference for energy-rich food.

While food preference on most of the food items was consistent across individuals, some individual differences were found. For the familiar food items, we found more variable preferences for kiwi, potato, green pepper, green beans, and savoy. For the novel food items, grapes were highly preferred by all individuals but one, which preferred dried plum and sweet potato over grape. Another individual never chose apricots resulting in a preference score of 0, and larger interindividual variation. And finally, one individual preferred parsnip and European radish over melon. These individual differences can help in optimizing food choice for positive reinforcement training and for future food-related tasks by accounting for individual preference and motivation.

Our study contributes to the knowledge on food preferences among the great apes. While several dietary differences have been found, other studies showed very similar food and nutritional preferences between chimpanzees and gorillas (Conklin-Brittain et al., 2001; Fitz-Gerald et al., 1970; Lodwick & Salmi, 2019; Remis, 2002; Tutin et al., 1991; Yamagiwa & Basabose, 2006) and chimpanzees and bonobos (Hohmann et al., 2010). The shared frugivorous diets of bonobos and chimpanzees (Conklin-Brittain et al., 2001) might be the result of a common preference for the same nutrients (Hohmann et al., 2010; Remis, 2002; Ungar, 1995). Differences in nutritional compositions and seasonality of plants have resulted in diets that allow each species to meet their nutritional needs with minimal intake of detrimental nutrients. By providing cultivated food items, containing negligible concentrations of detrimental nutrients, differences in nutritional preference decrease. Food selection based on the total energy content of food items might be a shared trait between gorillas, chimpanzees (Remis, 2002) and based on our results also for bonobos, while for gibbons carbohydrate content is more important (Jildmalm et al., 2008). Comparable research on orangutans is needed to fully compare nutritional preference among all hominoids.

We do however need to make an important note concerning diets in captivity. Commercially available fruits have been bred for increased sweetness and palatability containing high levels of sugar and energy but low contents of fibre, vitamins and minerals (B. Holland et al., 1991; Milton, 1999; Rafert & Ono Vineberg, 1997). Food intake patterns of captive primates therefore often deviate from the wild: foraging times are much shorter and captive diets are too concentrated in carbohydrates (Schwitzer & Kaumanns, 2003). These deviations from the species-specific adaptive patterns of feeding may lead to health problems (Plowman, 2013) and even changes in behaviour (Britt et al., 2015; Cabana et al., 2018; Cassella et al., 2012). While we show that bonobos prefer energy-rich food items, zoos should optimize their captive diets by providing a balanced variety of food items containing low amounts of carbohydrates to avoid health issues and behavioural abnormalities and ensure their well-being in captivity. Like in other primates, the nutrient composition of fruits in the wild bonobo diet differs substantially from the cultivated fleshy fruits (B. Holland et al., 1991; Rafert & Ono Vineberg, 1997; Schwitzer et al., 2008). Captive diets should therefore provide more vegetables, browse, and monkey pellets with high protein and lipid concentrations to substitute the sugar-rich food items.

Due to practicalities, we did not carry out paired-choice food trials between the dietary items and the novel food items. A follow-up study on the comparison between them would be interesting to assess where the novel items fit into the preference ranking of the familiar food items. Future food preference studies could also include food items with different, possibly adjusted, amounts of secondary compounds (Glander, 1982) to assess how they influence food preference. In the wild, chimpanzees ate food items where tannins and phenols were associated with lipids, while in bonobo foods lipid concentrations were independent of these nutrients. Moreover, tannin and phenol levels were significantly higher in the chimpanzee habitat, while foods eaten by both species contained very similar amounts of these antifeedants (Hohmann et al., 2006). This suggests that food plant selection in bonobos may happen more independently of antifeedant content and therefore be more opportunistic than in chimpanzees. To fully rule out potential experimenter bias, a next step would be to repeat these food preference test with an opaque screen between subject and experimenter and real-time video observations with minimal subject-researcher interactions and compare the results of both methods.

In summary, our results show that captive bonobos have clear food preferences in a paired-choice food test using commercially available foods. Correlational analyses demonstrated that bonobos maximize their net energy intake by preferring food items with high levels of carbohydrates.

Time-lag of urinary and salivary cortisol response after a psychological stressor in bonobos (Pan paniscus)

Jonas Verspeek
Verena Behringer
Daan W. Laméris
Róisín Murtagh
Marina Salas
Nicky Staes
Tobias Deschner
Jeroen M. G. Stevens

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Abstract

Cortisol is often measured as a marker for stress. Therefore, a profound validation of the time-lag between the stressor and the increase and peak in cortisol levels is needed. No study measured both the urinary and salivary cortisol time-lag after a psychological stressor. In this study, we used a frequent sampling study design to (1) describe the urinary and salivary cortisol pattern during a control day; and (2) characterize the induced excretion pattern of urinary and salivary cortisol after a psychological stressor in six zoo-housed bonobos. Liquid chromatography-tandem mass spectrometry was used to analyse 71 urine and 162 saliva samples collected on a control and a test day. We found that the time-lag between the stressor and the maximal cortisol concentration was similar in urine and saliva (160 min after the stressor). However, salivary cortisol after the stressor did show a faster and steeper increase than urinary cortisol. We also show inter-individual variation in the baseline and stress levels of cortisol, which should be considered in future cortisol studies. Our research highlights the importance of validation studies to confirm relevant sampling windows for cortisol sampling in order to obtain biologically meaningful results.

Introduction

Animals have developed behavioural and physiological adaptations to cope with stressors. One physiological response to a stressor is the activation of the hypothalamus-pituitary-adrenal (HPA) axis, which is a cascade of events, mediated by an integrated network of neuroanatomical structures and peripheral organs leading to physiological changes that help to restore homeostasis. This cascade is initiated after a stressor is perceived as such by the brain of an animal (Herman et al., 2016; Reeder & Kramer, 2005; Sapolsky et al., 2000). At first, activation of the paraventricular nucleus (PVN) of the hypothalamus results in the release of catecholamines (epinephrine and norepinephrine) from the peripheral nerves and the adrenal medulla of the sympathetic nervous system (SNS). Simultaneously, the neurons of the activated PVN in the hypothalamus secrete corticotropin-releasing hormone (CRH), which is transported through the hypophyseal portal system where it stimulates the anterior pituitary gland to release adrenocorticotropic hormone (ACTH) into the blood stream. In the course of minutes, ACTH stimulates the adrenal glands to release glucocorticoids (GCs). Following excretion, GCs are transported in the circulation, either free or bound to proteins such as corticosteroid-binding globulin (CBG). The unbound GCs are small and lipid-soluble and can easily diffuse through lipid-rich cell membranes via passive intracellular diffusion. Once they arrive at the secretory endpiece of the salivary glands, these unbound GC's pass through the cells into saliva (Kirschbaum & Hellhammer, 1989, 2000). The bound GC molecules are too large to leave the capillaries, and thus remain in circulation. The GCs in circulation are transported to target tissues, where they bind to receptors in the brain, liver, kidneys and other tissues. This results in an array of effects, including the release of additional energy for necessary physiological functions to respond to the stressor. After exerting their function in these target tissues, GCs are metabolized in the liver and kidney into compounds that are eliminated in urine and faeces. Once the organism has responded to the stressor, high GC and ACTH levels activate a negative feedback loop, which inhibits the HPA axis and SNS cascade (Reeder & Kramer, 2005; Sapolsky et al., 2000). While this general stress-response is conservative across all vertebrate taxa, variations in the response exist due to many extrinsic (e.g. time of day, disease, social status) and intrinsic factors (e.g. species, body condition, reproductive status) (review in (Mormède et al., 2007; Sheriff et al., 2011)). In measuring the individuals GC response, both the magnitude and duration are biologically relevant, since hormone-receptor interactions happen during the entire time of the response and not just at the maximum of the GC release (Dallman & Bhatnagar, 2011).

Cortisol is the main GC in many mammals and is therefore often used as a physiological marker of the stress response (T. M. O'Connor et al., 2000). During days with minor HPA-axis challenges, secretion of cortisol from the HPA-axis follows a characteristic circadian pattern. In diurnal animals, cortisol and GC metabolite levels in plasma, urine and saliva are highest in the morning and decrease throughout the day (Fries et al., 2009; Kalsbeek et al., 2012; Reeder & Kramer, 2005; Touma & Palme, 2005).

Stress-induced activity of the HPA axis can be measured in a variety of sample types and matrices, each having advantages and disadvantages (see reviews Behringer & Deschner, 2017; Mormède et al., 2007; Palme, 2019; Sheriff et al., 2011). In brief, cortisol levels in blood represent a short-term stress response (Kirschbaum & Hellhammer, 1989), which allows for measuring the effect of a specific event on the activation of the HPA-axis. However, the handling and restraining of animals during blood collection can already be stressful and lead to an increase in cortisol levels (Balcombe et al., 2004; Reeder & Kramer, 2005; L. M. Romero & Reed, 2005; Sheriff et al., 2011). Therefore, repeated blood cortisol sampling within a short time frame is inadvisable. To avoid this confounding effect, the interest in non-invasive monitoring of cortisol levels in hair, faeces, urine, and saliva has substantially increased (Behringer & Deschner, 2017). Cortisol and GC metabolite levels in hair and faeces reflect blood concentrations over months and days, respectively, and are useful to monitor cumulative and chronic aspects of stress responses (Palme, 2019; Sheriff et al., 2011; Touma & Palme, 2005; Wielebnowski & Watters, 2007). However, to infer the effect of particular events on the activation of the HPA-axis, more short-term changes in cortisol levels need to be measured. Besides correlating averaged hormone concentrations with for example rates of a behaviour across a time span (Crockford et al., 2008; Engh et al., 2006; Rincon et al., 2020; Sannen et al., 2004), one can also implement event-sampling. In event-sampling, hormone samples are collected within a certain time-frame following a single event and are expected to reflect the impact of this specific event (Crockford et al., 2013; Grebner et al., 2004; Lensen et al., 2019; Wittig et al., 2015, 2016). Studies that use event sampling or short-term changes in cortisol levels, require a matrix reflecting those changes in time. Therefore, interest in urinary and salivary cortisol as non-invasive markers for stress has increased (Anestis, 2009; Heintz et al., 2011; Jurke et al., 2000; Lutz et al., 2000). Urinary cortisol has been stated to reflect the longer lasting effect of a certain stressful event, since it represents the pooled cortisol values over minutes to hours, depending on the species (Anestis, 2010; Behringer & Deschner, 2017; Heistermann, 2010), while salivary cortisol concentrations reliably represent circulating cortisol levels with a short time-lag of several minutes (Gröschl, 2009; Heistermann, 2010; Kirschbaum & Hellhammer, 2000; Laudenslager et al., 2006a). To be able to measure the reactivity to a certain event, the sampling moment should be chosen based on the expected timing of the cortisol peak in both matrices. However, no study so far measured a provoked cortisol response after a psychological stressor using both urine and saliva sampling at comparable intervals. Frequent sampling of urine and saliva after such a stressor could provide a profound characterization of the time-lag of both cortisol responses, allowing for a comparison between them.

Cortisol levels can be measured using liquid chromatography-tandem mass spectrometry (LC-MS/MS), which is a technique that has been adapted recently to measure steroids in matrices other than blood. It combines the separation capabilities of high-performance liquid chromatography (HPLC) with those of a conjoined mass spectrometer (Murtagh et al., 2013). Before using a method for biomarker analyses, a species-specific validation is needed since clear differences in metabolism and excretion of GC's exist (Behringer & Deschner, 2017; Buchanan & Goldsmith, 2004; Touma & Palme, 2005). The use of LC-MS/MS has been validated to analyse steroid hormones in saliva in humans (Mezzullo et al., 2016; Montskó et al., 2014) and chimpanzees (Kutsukake et al., 2009) and in urine in bonobos (B. Hauser et al., 2008), but not in saliva in bonobos.

Often physiological validation experiments, like an ACTH challenge, are used to induce artificial changes in circulating GC's using a pharmacological stimulation of the HPA axis (Goymann, 2005; Palme, 2005, 2019; Touma & Palme, 2005). The injected ACTH directly stimulates the adrenals, circumventing the activation of all earlier steps of the HPA cascade (Lovallo, William R. Buchanan, 2000; Palme, 2019). After administration, GC levels increase and reach maximum values after a species- and matrix-specific time-lag. However, to ensure that the expected GC rise is strong enough to be detected by the method, often huge ACTH doses are used (Mormède et al., 2007; Palme, 2019). Such high ACTH stimulation will probably never occur naturally. This may be problematic, since peak characteristics like delay time, maximum and duration are shown to be dose dependent (Fulkerson & Jamieson, 1982; Lay et al., 1996; Schurmeyer et al., 1984). An alternative to detect the biologically relevant adrenal activity is to implement a biological validation. In this procedure, GC levels are monitored in a situation with an expected GC level change, for example the GC response before and after a stressful event. Such procedures offer a more valuable opportunity to validate assays since they provide biologically relevant information (e.g. response time, peak duration) about the actual stress response after a psychological stressor, which can be used in future studies. Because of their invasive character, physiological validation studies were often based on one or a few individuals (Bahr et al., 2000; Möhle et al., 2002; Wasser et al., 2010). However, inter-individual variation in the HPA-axis activity is well documented (Mormède et al., 2007). Ideally, validation studies should include more subjects to detect this variation hence avoiding generalizations based on only one individual response.

The objective of this study was to provide detailed information on the excretion pattern of cortisol in bonobos. Using frequent sampling of urine and saliva in multiple well-trained bonobos we aim to (1) describe the decreasing urinary and salivary cortisol pattern during a day without a stress response challenge to serve as a baseline (control); (2) characterize the induced urinary and salivary cortisol change after an acute, psychological stressor (test) to determine the time-lag of cortisol secretion increase and peak in urine and saliva. Finally, we aim to describe the difference between individual variation in the cortisol pattern during the control and test day in both matrices. Our study of the urinary and salivary stress response in bonobos can inform future research, in which event-sampling is used, to choose an adequate time window and matrix for sample collection.

Methods

Subjects and housing

We studied a group of bonobos at Zoo Planckendael (Belgium) (Table 3.1[4]). During the study period, bonobos were housed in an enclosure consisting of nine interconnected rooms of various sizes (between 15 and 65 m²) which can be separated by sliding doors to allow temporary separation. Using positive reinforcement training, all bonobos were trained to regularly enter each of the rooms in family groups and individually. When being separated, individuals could always hear, smell and see other bonobos. Mothers were never separated from their dependent offspring. The shifting and individual separation is part of the normal morning routine of the bonobos, and therefore, are not considered as a stressor that could affect cortisol levels. The bonobos were fed four times a day and water were available ad libitum.

[4] See also table 9.1 Overview of the study subjects p 144

Table 3.1 Subject information

Sex	Individual	Age (years)[a]	Amount of samples (successfully extracted/collected)			
			Control		Test	
			Urine	Saliva	Urine	Saliva
Female	Hortense	40	7/9	11/15	9/9	13/14
	Djanoa	23	7/9	12/15	7/7	7/8
	Nayoki	6	1/1	7/14	1/1	10/10
	Sakana°	1	-	-	-	-
Male	Vifijo	24	9/9	15/15	9/9	14/15
	Zamba	20	-	7/11	-	13/15
	Habari	12	9/9	15/15	8/8	12/15
	Kikongo°	4	-	-	-	-

[a] Age: individual's age when the study took place
° Did not provide any samples in this study.

Sample collection

Before the onset of this study, five subjects had been trained to deliver urine samples into cups and trays. Six bonobos had also been trained to participate in saliva sample collection using Salivettes (Ref 51.1534, Sarstedt, Nümbrecht, Germany) (Table 1). Samples were collected during two days. On the control day, all independent subjects were housed individually from 9:50 until 12:00 pm. For management reasons, at 12:00 pm the family groups were reunited. Urine samples were taken once every hour between 9:50 and 18:00 h. Saliva samples were taken at short intervals (every 15 to 20 minutes) between 9:50 and 12:00 pm. From 12:00 to 18:00 h, we prolonged the sampling interval for saliva samples to once every hour, simultaneously with the urine sample collection. Exactly one week after the control day, we collected samples on the test day to determine the effect of the stressor on urinary and salivary cortisol levels. The procedures of housing and sampling were identical to those described for the control day. The only difference on this second day was the arrival of the zoo veterinarian in the building at 10:18 h, which is perceived by all individuals as a stressor. In the past, all bonobos had experienced being sedated with a blowpipe by the veterinarian for medical controls or for transfer between enclosures. Previous experience had shown they responded to the presence of the veterinarian by showing behavioural indicators of being stressed, such as increased locomotion, uttering alarm calls or aggressive vocalizations, increased anxiety behaviours (auto-scratching), and the secretion of diarrhoea. Therefore, the presence of the veterinarian with a blowpipe is perceived as a threat by all bonobos, and is assumed to be an appropriate stressor in their zoo environment (Rimbach et al., 2013). After the veterinarian had entered the building, he carried his blowpipe in his hand, stopped in front of each enclosure, and called each bonobo by its individual name. All bonobos responded in the usual way by moving around, seeking comfort from group members (if housed in subgroups) and uttering alarm calls. After two minutes the veterinarian had visited every bonobo in the mentioned procedure and left the building. The control day was implemented to control for possible diurnal effects and to show that the result in the test day was caused by the stressor rather than the sampling regime.

Urine samples (N = 71, mean ± SD = 7.1 ± 3.1 samples/individual/treatment, range = 1 – 9 samples/individual) were directly taken from the cups and trays using a syringe. Next, urine samples were stored in Cryo-vials (Ref. E292.1, Roth, Karlsruhe, Germany) at -20°C until analysis. Saliva samples (N = 162, mean ± SD = 13.5 ± 2.3 samples/individual/treatment, range = 8 – 15 samples/individual) were taken by sweeping the Salivette through the mouth of each subject which took approximately 30 seconds. After collection, saliva samples were immediately placed in Salivette tubes (Ref 51.1534, Sarstedt), and also stored at -20°C until analysis. To minimize differences in sampling time between individuals, saliva was collected by four and urine by five keepers and researchers, who were all familiar to the bonobos. Throughout the control day and the test day, every bonobo was always sampled by the same experimenter to avoid possible bias.

Sample preparation

Urine sample preparation and measurement

The extraction was done following the extraction protocol of Hauser et al. (2008) with adaptions explained in Wessling et al. (2018). An internal standard mix, containing 250 ng/ml d3-testosterone, d4-estrone, d9-progesterone and d4-cortisol, was added to each sample as a quality control. Samples were re-measured if the internal standard recovery deviated by more than 80% of the internal standard. Urinary hormone levels need to be adjusted for variable water content among spot urine samples, which depends on the hydration status of an individual and the time since last urination. Therefore, to compensate for variation in urine concentration, we measured the specific gravity (SG) using a digital handheld refractometer (TEC, Ober-Ramstadt, Germany) and calculated urinary cortisol corrected for SG (Miller et al., 2004). The SG population average was 1.006. We successfully extracted 67 urine samples. Urinary cortisol levels were measured using LC-MS/MS following Wessling et al. (2018) and quantified with MassLynx (version 4.1; QuanLynx-Software).

Saliva sample preparation and measurement

The frozen Salivettes were thawed in the salivette tubes (ref 51.1534, Sarstedt). 100 µl of clear supernatant were transferred into a SafeSeal tube (Multi SafeSeal tubes, 7080.1, Roth) before adding 5 µl of internal standard working solution consisting of internal standard mix (containing 250 ng/ml d3-testosterone, d4-estrone, d9-progesterone and d4-cortisol, e. g. 98%, Prod. No. D-5280, CDN Isotopes) and 100 µl of methanol/ZnSO4 (50 mg/ml). The sample was vortexed then centrifuged at 12,000rpm for 5mins. Prior to solid phase extraction (SPE) the supernatant was diluted with 1 ml water. HR-X cartridges (HR-X, 1ml/30mg, ref 730934 Chromabond) were conditioned with 1 ml methanol followed by 1 ml water. After transferring the supernatant to a cartridge, it was washed with 1 ml water. Steroids were eluted with 1 ml methanol followed by 1 ml ethyl acetate. They were dried down under a stream of compressed air at 45 °C and reconstituted in 100 µl of 30% acetonitrile for LC-MS/MS analysis. To measure salivary cortisol, the same LC-MS/MS procedure was used as described for urinary cortisol (Wessling et al., 2018). We successfully extracted 136 saliva samples. Samples were re-measured if the internal standard recovery deviated by more than 80% of the internal standard.

Method evaluation

For the chemical validation of the LC-MS/MS assay, we used human saliva samples since the available amount of bonobo samples was not enough to perform the necessary validations. To assess the accuracy of the cortisol measurement by the LC-MS/MS assay, two pools of human saliva samples were created: one for men (N = 5) and one for women (N = 5). Each pool was spiked with two different concentrations of internal standard solution (low and high). A 200 µl aliquot of each of the pools, spiked pools, and internal standard solutions were extracted five times and measured by LC-MS to determine extraction efficiency. Average recovery of the saliva samples spiked with the high concentration of the internal standard solution was 100.50% (SD = 6.68) for the males and 98.20% (SD = 4.64) for the females. With the low concentration, average recovery was 101.02% (SD = 3.98) for the males and 105.34% (SD = 5.35) for the females (See Table 3.2). The difference between repeated extracts of each sample group was lower than 7% (See Table 3.3). Internal standard deviation was acceptable (<-60%) for all extracts (See Table 3.4).

Table 3.2 Extraction efficiencies of the spiked pool samples of men and women (n = 5)

Sex	Spike conc.	Extraction efficiency (%)	Standard deviation
Men	Low	101.02	3.98
	High	100.45	6.68
Women	Low	105.34	5.35
	High	98.20	4.64

Table 3.3 Coefficient of variation of the extracts (n=5)

	Spike conc.	Cortisol
Internal std	Low	1
Internal std	High	6
Male pool	Not spiked	6
Female pool	Not spiked	2
Male pool	Low	1
Male pool	High	3
Female pool	Low	4
Female pool	High	1

Table 3.4 Internal standard deviation of the extracts (n = 5)

	Spike	Cortisol-d4
Male	None	-43.7
Male	None	-52.4
Male	None	-52.7
Male	None	-54.1
Male	None	-47.1
Female	None	-49
Female	None	-52.3
Female	None	-45.3
Female	None	-52.8
Female	None	-50.1
Male	Low	-52.3
Male	Low	-47.9
Male	Low	-47.5
Male	Low	-51.3
Male	Low	-48.5
Male	High	-51.6
Male	High	-51.4
Male	High	-44.3
Male	High	-48.1
Male	High	-44.6
Female	Low	-49.6
Female	Low	-51.2
Female	Low	-52.3
Female	Low	-51.2
Female	Low	-42.2
Female	High	-44.5
Female	High	-44.3
Female	High	-51.1
Female	High	-53.3
Female	High	-43.6

Statistical analyses

To explore differences in cortisol concentrations between the control and the test day after the arrival of the zoo vet, we used linear mixed models (LMM) using the "lmer" function from the "lme4" package (Bates et al., 2015). On the test day, the amount of samples that were collected prior to the arrival of the stressor (one urine and two saliva samples) didn't allow for statistical testing. Therefore, only cortisol concentrations after the arrival of the stressor were compared. To examine the influence of the within-subject predictor variables (a) sampling time, (b) the quadratic term of sampling time and (c) treatment (control or test) on urinary and salivary cortisol concentrations, we ran two LMMs: one for the urine samples (urinary stress response model) and one for the saliva samples (salivary stress response model). In addition to the main effects, we included all two-way interactions between the main effects as fixed effects. We also included subject-ID as random intercept and sampling time and treatment as random slopes. For all models, we used diagnostic plots (residuals vs fitted and qqplot) to examine assumptions of normality and homogeneity of variances, and we tested uniformity and dispersion of the residuals using the "DHARMa" package (Hartig, 2020). To meet assumptions of homoscedasticity and normality of residuals, we log-transformed the cortisol data. Model stability was assessed by excluding random effects and comparing the estimates derived with those derived for the full data set, indicating no influential random effects. Significance of the fixed effect was determined by comparing the full model with the respective null model, excluding the fixed effect but retaining the random effects, using a likelihood ratio test ("anova" function in R (Field et al., 2012)). All statistical analyses were done using R 3.3.2 (R Core Team, 2016) and plots were generated using the statistical package "ggplot" (Wickham, 2016).

Ethical statement

Animals were never harmed in any way throughout the duration of this study and participation in sample collection was voluntary. Urine and saliva were collected using standard non-invasive methods. The care and housing of all bonobos was adherent to the guidelines of the EAZA Ex-situ Program (EEP). All research complied with the ASAB guidelines(ASAB, 2020) and was carried out in accordance with the national regulations. This study, including all experimental protocols, was approved by the Scientific Advisory Board of the Royal Zoological Society of Antwerp and Zoo Planckendael (EC-3/SGZ (10-12-19)) and The University of Antwerp (Belgium). Informed consent was obtained from all human participants included in this study.

Results

Urinary stress response model

We compared urinary cortisol levels on the control day (mean 4.52 ng/ml corr. SG; range: 0.66 - 16.42 ng/ml corr. SG) and test day (mean 6.36 ng/ml corr. SG; range: 0.84 – 35.63 ng/ml corr. SG). During the control day, the average urinary cortisol levels showed the expected diurnal decline. However, a peak occurred around 12:00 h (Fig. 3.1, solid line). On the test day, when subjects were exposed to the acute stressor, the characteristic diurnal pattern was disrupted, and the urinary cortisol pattern differed from the control day pattern. In contrast to the declining cortisol levels on the control day, after the stressor, mean urinary cortisol levels steadily increased within 40 min and reached a maximum level that doubled the control levels after 160 min (13:00 h: 12.26 ± 5.41 pg/µl). Afterwards, urinary cortisol levels declined and reached control levels 340 min (16:00 h) after the arrival of the stressor (Fig. 3.1, dashed line). Statistical analysis showed that urinary cortisol levels throughout the day showed a different pattern between the control and test day (interaction term of sampling time and treatment: $\chi^2 = 6.00$, df = 1, P = 0.01) (Table 3.5).

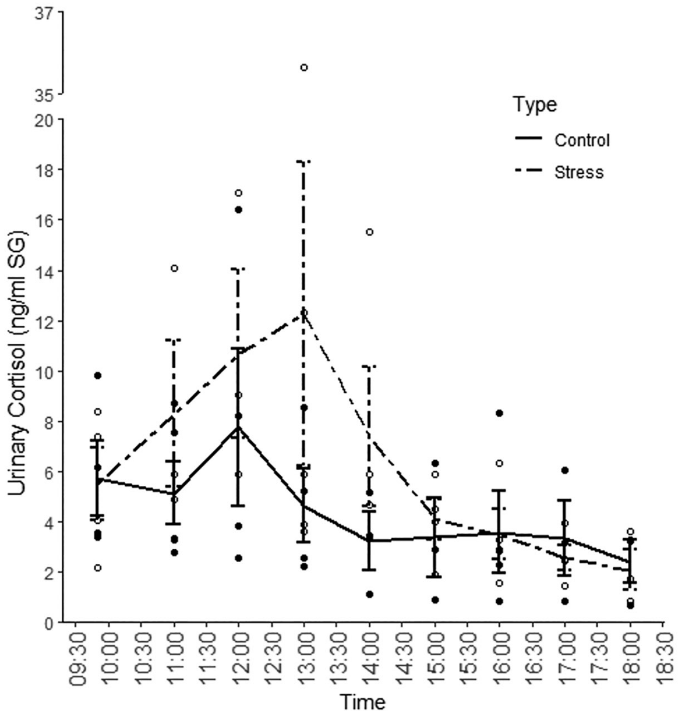

Fig. 3.1 Mean (±SEM) urinary (N=108) cortisol levels in bonobos during the control day (solid line) and stress day (dashed line). The local veterinarian (the stressor) entered the building at 10:18 h. The analyses were conducted on log transformed cortisol data, but actual values are displayed here to provide better visual and interpretable representation of the cortisol response.

Table 3.5 Results of the Linear Mixed Model comparing the urinary cortisol levels between the control and test day

	Estimate	Std. Error	t value	P
Urinary stress response model				
Intercept	2.01	0.23	8.91	
Treatment°	1.02	0.38	2.70	0.13
Sampling time	-0.17	0.05	-3.58	**<0.001**
Sampling time²	-0.02	0.01	-1.36	0.18
Sampling time x treatment	-0.11	0.05	-2.45	**0.014**
Sampling time² x treatment	0.004	0.02	0.16	0.88

°Reference category for treatment was set to control
Boldface indicates significance with P<0.05

Salivary stress response model

We also compared salivary cortisol levels between the control (mean 1.34 pg/µl; range: 0.55 - 3.80 pg/µl) and test day (mean 2.04 pg/µl (range: 0.53 - 8.44 pg/µl). As in the urine samples, salivary cortisol showed the expected declining pattern during the control day. After the exposure to the acute stressor, salivary cortisol levels showed a fast increase within 25 min after the stressor and reached maximum levels after 160 min (13:00 h: 3.56 ± 1.09 pg/µl) which is comparable to urinary cortisol levels. Within 30 minutes, salivary cortisol levels reached levels more than twice as high as the control levels and remained elevated above control levels for more than 240 min (Fig. 3.2). Statistical analysis showed that the salivary cortisol pattern throughout the day differed between the control and test day (sampling time x treatment: $\chi^2 = 38.699$, df = 1, P < 0.001) and that the increase and decrease of salivary cortisol levels throughout both days differed (interaction term of sampling time² x treatment: $\chi^2 = 41.423$, df = 1, P < 0.001) (Table 3.6).

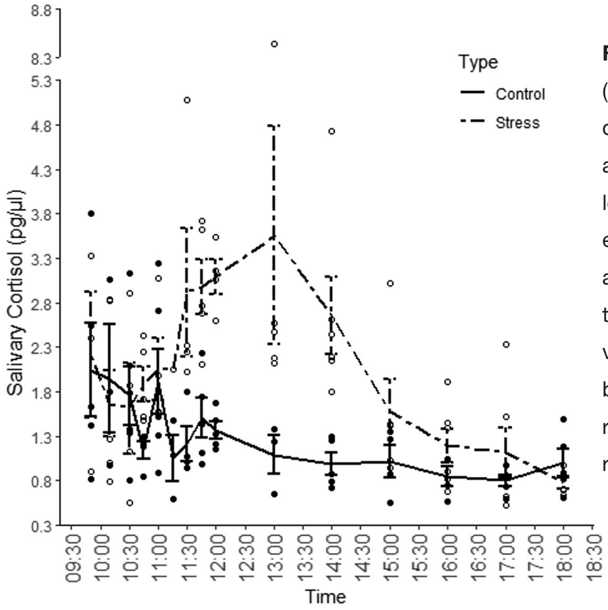

Fig. 3.2 Mean (±SEM) salivary (N=136) cortisol levels in bonobos during the control day (solid line) and stress day (dashed line). The local veterinarian (the stressor) entered the building at 10:18 h. The analyses were conducted on log transformed cortisol data, but actual values are displayed here to provide better visual and interpretable representation of the cortisol response.

Table 3.6 Results of the Linear Mixed Model comparing the salivary cortisol levels between the control and test day

	Estimate	Std. Error	t value	P
Salivary stress response model				
Intercept	0.59	0.26	2.23	
Treatment°	-1.42	0.35	-4.08	**< 0.001**
Sampling time	-0.04	0.06	-0.68	**< 0.001**
Sampling time^2	-0.0008	0.003	-0.26	**< 0.001**
Sampling time x treatment	0.52	0.08	6.22	**< 0.001**
Sampling time^2 x treatment	-0.03	0.005	-6.44	**< 0.001**

°Reference category for treatment was set to control
Boldface indicates significance with P<0.05

Individual urinary and salivary cortisol patterns

We also present the inter-individual variation in urinary and salivary cortisol levels (Table 3.7, Fig. 3.3a & 3.3b). Individuals with the lowest urinary cortisol control levels also had the lowest salivary cortisol control levels. With the exception of one individual (Hortense), a similar pattern can be seen in the cortisol levels during the test day: individuals with a strong cortisol response in urine, also showed a strong cortisol response in saliva; and the individual with the lowest urinary cortisol peak also showed the lowest salivary cortisol peak (Fig. 3.3c & 3.3d). In the subject with the aberrant cortisol pattern (Hortense), higher urinary cortisol levels were found during the control than the test day and no urinary stress response was found during the test day.

Table 3.7 Mean (± SEM) urinary and salivary cortisol concentrations per individual.

	Urinary cortisol (ng/ml corr. SG)		Salivary cortisol (pg/µl)	
Individual	Control	Test	Control	Test
Hortense	8.73 ± 1.41	4.97 ± 0.45	1.79 ± 0.31	2.81 ± 0.24
Vifijo	1.89 ± 0.41	3.60 ± 0.85	0.84 ± 0.05	1.66 ± 0.22
Djanoa	2.94 ± 0.14	9.78 ± 4.31	1.29 ± 0.16	2.50 ± 1.05
Zamba	/	/	1.76 ± 0.18	2.04 ± 0.21
Habari	5.25 ± 0.64	8.37 ± 1.83	1.42 ± 0.15	1.66 ±0.26
Nayoki	3.27	3.6	1.16 ± 0.07	1.73 ± 0.22

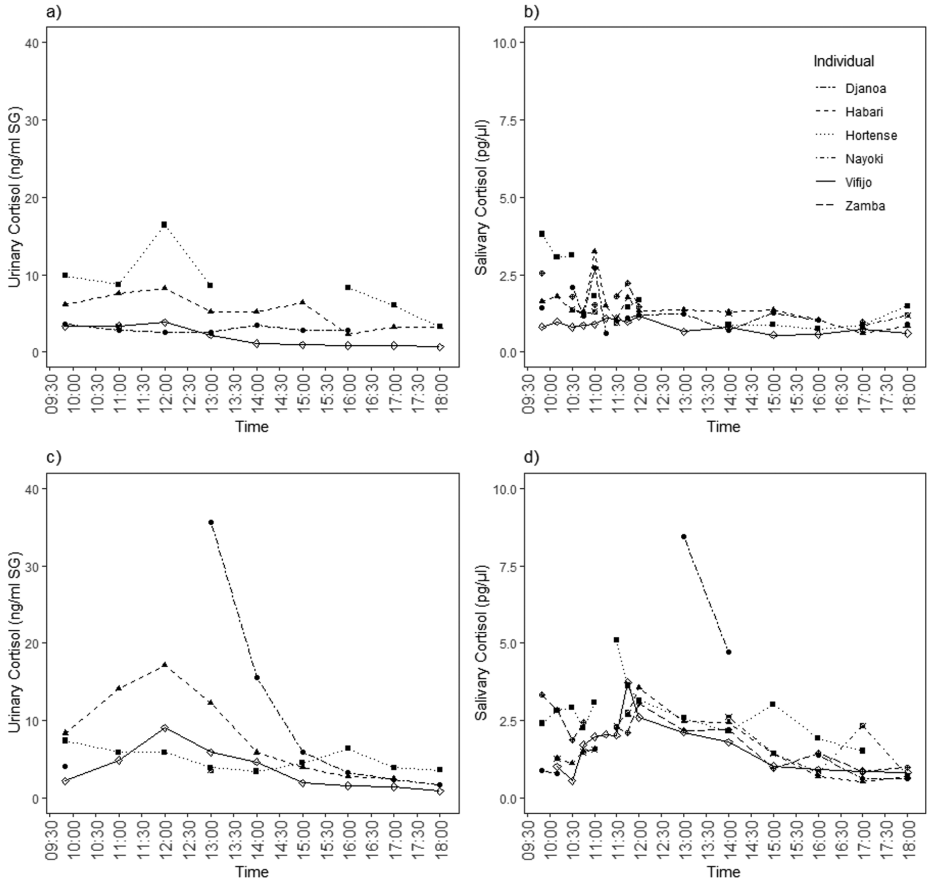

Fig. 3.3 Individual cortisol levels in a) urine during the control day; b) saliva during the control day; c) urine during the test day; and d) saliva during the test day. In the test day, the stressor entered the building at 10:18. The analyses were conducted on log transformed cortisol data, but actual values are displayed here to provide better visual and interpretable representation of the cortisol response.

Discussion

This study provides detailed information on the excretion pattern of urinary and salivary cortisol in bonobos. First, we found the expected decreasing pattern of urinary and salivary cortisol throughout the control day and, secondly, we characterized the increase in urinary and salivary cortisol response after an acute stressor.

As an anticipatory response to awakening, the highest cortisol production occurs in the second half of the night with peak cortisol values in the early morning (Born et al., 1999; Coe & Levine, 1995; Czekala et al., 1994; Fries et al., 2009; Muller & Lipson, 2003). Thereafter, cortisol values decline throughout the day (Kalsbeek et al., 2012; Reeder & Kramer, 2005; Touma & Palme, 2005). Our results also showed the characteristic decreasing pattern of urinary and salivary cortisol, which is in line with previous studies in bonobos that used LC-MS/MS to measure urinary cortisol

(Surbeck et al., 2012) and enzyme immunoassays (EIA) to measure salivary cortisol (Behringer et al., 2009b, 2013; Hohmann et al., 2009). In the present study, sampling was not possible before 9:20 h, so we were not able to include the early morning cortisol levels, which might have shown an even stronger effect of the awakening response. The cortisol levels measured in our study are comparable to urinary and salivary cortisol levels in humans (Y. C. Barrett et al., 2005; Mezzullo et al., 2016) and chimpanzees (Kutsukake et al., 2009; Preis et al., 2019) measured with LC-MS/MS but lower than salivary cortisol levels in bonobos measured with EIA (Behringer et al., 2009b) and RIA (Wobber et al., 2010). This is not surprising given that these assays not only measure the native hormone but also their metabolites due to cross reactivities of their antibodies (Behringer & Deschner, 2017; El-farhan et al., 2017). As extraction efficiency in our study was within the previously reported acceptable range of 80-120% (Mezzullo et al., 2017), our results demonstrate that LC-MS/MS can reliably detect known physiological patterns in bonobo saliva.

While urinary and salivary cortisol levels decreased throughout the day, we also found some slight deviations from this overall pattern: a small cortisol increase was found in both urine (12:00 pm) and saliva (11:45 h). These deviations might be due to excitement in anticipation of husbandry routines like feeding. Previous studies showed that in addition to the photoperiod, several other stimuli like feeding or social cues can alter the decreasing cortisol pattern in mammals (Hohmann et al., 2009; Kalsbeek et al., 2012; Lovallo, William R. Buchanan, 2000; Mrosovsky, 1996). Animals have evolved predictive homeostatic mechanisms and utilize specialized functions of the circadian timing system that enable them to, for example, predict the availability of food whenever it is consistently available at a specific time each day (Boulos et al., 1980; Kirschbaum & Hellhammer, 2000; Moore-Ede, 1986; Richter, 1922; Von Dawans et al., 2012). The short cortisol peak around 12:00 pm in both urine and saliva might therefore be the anticipatory response of the HPA-axis to the daily feeding moment between 11:00 and 11:30. More research is needed to verify whether this anticipatory effect is present so that future studies can take this into account when planning sampling intervals.

We also measured urinary and salivary cortisol levels after an acute stressor, the zoo veterinarian in this case. Since previous encounters between the veterinarian and these bonobos resulted in increased behavioural indicators of stress (e.g. locomotion, alarm calls, scratching), we expected to find a clear cortisol response after the stressor in both urine and saliva. Exposure to the stressor resulted in a significant increase in urinary and salivary cortisol. Moreover, we found that the urinary cortisol pattern throughout the day differed between the control and the test day. While control cortisol levels showed an overall decrease (see above), a cortisol peak was found during the test day. Surprisingly, the maximal urinary cortisol levels were reached within 160 min after the stressor, which is considerably shorter than 5.5 h (330 min) reported for peak excretion of cortisol in primates (Bahr et al., 2000). This difference might be explained by the different settings. The Bahr et al. (Bahr et al., 2000) study administrated radio-labelled cortisol, while we used a psychological stimulus to initiate a stress response. Moreover, the Bahr et al. (2000) study collected urine samples opportunistically of one individual of three primate species. In our study, samples were collected frequently at regular intervals in multiple well-trained subjects of the same species. And finally, primates in the Bahr et al. (2000) study were housed in metabolic cages during the collection time, whereas bonobos in our study were able to show locomotor activities. Differences in the cortisol response between our data and the previous study (Bahr et al., 2000) are expected since cortisol accumulates in urine over time and the cortisol levels in excreted urine are therefore dependent on the frequency of urination. In this previous study, the first chimpanzee sample was collected two hours after injection (Bahr et al., 2000) so no conclusions could be made about the earlier cortisol excretion pattern. Moreover, the first urine sample already contained the second largest radio-labelled cortisol concentration, which might be the result of the accumulation of urinary cortisol over time. In case opportunistic and irregular sampling is used, cortisol levels in urine accumulate over an unknown time frame. We avoided this by implementing regular and shorter sampling intervals so that cortisol levels in urine always accumulate over the same time. This results in more standardized urinary cortisol levels per interval and a urinary cortisol response that represents the actual plasma levels over time. Using more frequent sampling, the time window of the maximal urinary cortisol value after a stressor in great apes was shortened from 24 h (Layne et al., 1964) to 4.5 h (Bahr et al., 2000) and to 160 mins in our study.

For salivary cortisol, we also found that exposure to a stressor significantly increased cortisol levels. Salivary cortisol rose rapidly (between 10 to 40 minutes after the stressor) and reached levels to more than double the control levels. This is in line with a previous study on common marmosets, where translocation to a novel environment resulted in cortisol levels that doubled the levels obtained prior to the translocation (Cross & Rogers, 2004). Previously in bonobos, salivary cortisol has also been found to reach levels nearly twice as high as normal after a parturition event (Behringer et al., 2009b), after the transfer to a new building and after the integration of a new female in the group (Behringer et al., 2012). Surprisingly, the post-stress cortisol peak in our study only reached its maximal level after 160 minutes, and only returned to baseline levels 5 hours later. In humans, salivary cortisol rose 1-3 minutes after a cortisol injection (Kirschbaum & Hellhammer, 1989; Peters, 1982) and reached its maximum levels after 35 to 40 minutes (Gozansky et al., 2005; Kirschbaum & Hellhammer, 2000). Also in one chimpanzee, the maximal salivary cortisol level after an ACTH challenge was reached after 45 min (Heintz et al., 2011). We had expected a delay of salivary cortisol rise when comparing with such physiological validation studies since the injection of ACTH immediately stimulates the adrenals, circumventing earlier steps in the HPA cascade (Palme, 2019). A psychological stressor activates the HPA axis from the start, likely resulting in a longer time-lag of the cortisol peak. A pertinent question in the psychoneuroendocrinology of cortisol is to what extent the time courses of the cortisol responses to pharmacological stimuli differ from physical and psychological stressors (Dayas et al., 2001; Jacobson, 2005; Kirschbaum & Hellhammer, 1989; Oswald et al., 2004), and how different types of stimuli may recruit various aspects of the HPA cascade to different degrees (Herman et al., 2016). The longer time-lag after a psychological stressor in our study in comparison with the time-lag after the pharmacological stimulation in the previous study on one chimpanzee (Heintz et al., 2011) indicates that the time frame of the cortisol response differs between physiological and psychological stimuli. Not only the timing, but also the amplitude of the salivary stress response differs significantly between our study and the previous chimpanzee study (Heintz et al., 2011). In the chimpanzee, salivary cortisol levels after the ACTH stimulation reached peak levels that were at least three, but for most individuals more than five times higher than the maximal levels we measured in bonobos. In response to a stressor, the extent of ACTH release is limited by a rapid feedback mechanism (Herman et al., 2016). In physiological validation studies however, the sudden rise of plasma ACTH levels might not only stimulate faster cortisol secretion, but also immediately activate a strong negative feedback loop, possibly resulting in a high but shortened cortisol peak. In our study, the ACTH levels might have possibly increased more gradually after the activation of the HPA-axis in response to the psychological stressor, and this might have resulted in a delayed feedback and therefore a longer cortisol response compared to physiological validation studies. However, to really compare the two settings and to exclude species-specific differences, future study designs should compare both methods in different species using regular sampling on multiple subjects.

In comparison with humans, where salivary cortisol levels after a social stress test reached baseline levels after 70 mins (Nierop et al., 2006), it is surprising that salivary cortisol levels in our study remained elevated for five hours after the maximal value. However, a previous study reported that salivary cortisol levels after the birth of a bonobo infant remained elevated for more than seven and a half hours (Behringer et al., 2009b). The arrival of the veterinarian in this study might have had a strong effect on the HPA axis activation resulting in a broader salivary cortisol response. Given that the magnitude and duration of the cortisol response reflect the strength of the stressor (Sheriff et al., 2011), we suggest that the veterinarian indeed is a potent stressor that causes a measurable salivary cortisol peak in bonobos.

Surprisingly, the timing of the urinary and salivary cortisol peak after the stressor was found to be very similar. The maximal average cortisol level in both matrices was reached after 160 min and a similar decline in cortisol levels was found. This is surprising since a longer time-lag in urinary cortisol is expected (Heistermann, 2010). However, our data show a faster and steeper increase in salivary than urinary cortisol levels. This is in accordance with previous literature stating that cortisol in saliva rises faster than in urine (Heistermann, 2010). While the longer rise in salivary cortisol might be the result of the strong effect of the stressor, the urinary stress response does not show such a long peak. Further research comparing the cortisol response to a psychological stressor in both matrices is needed in order to help explain this unexpected result. In addition to the strong effect of the stressor, the anticipatory effect to the feeding moment around 12:00 might have influenced the urinary and salivary cortisol response. To avoid such confounding effects, future studies should not only take the diurnal cortisol pattern but also the effect of husbandry routines into account. We suggest future research to monitor the responses to routine handlings by including control measurements, as we have done in this study. Ideally, experiments involving cortisol measures should be conducted outside of these responses and in the afternoon when cortisol levels and intra-individual variability are lower (Czekala et al., 1994)

We also compared the individual cortisol levels during the control and test day. The inter-individual differences we found might partly be due to the large age variation of the subjects. While cortisol concentrations did not differ between male and female bonobos (Brand et al., 2016; Tkaczynski et al., 2020), cortisol levels gradually increased during the ontogeny of wild bonobos (Tkaczynski et al., 2020). The higher control values of the oldest female could therefore be the result of an age effect. We also found that individual differences in the cortisol levels were consistent across both matrices. Bonobos with low urinary cortisol levels during the control day, had low salivary cortisol levels during the control day and individuals with a lower urinary cortisol peak in the test day also showed a lower salivary cortisol peak during the test day. However, no clear pattern was found across treatment days. While some individuals with low cortisol levels on the control day also showed a lower cortisol peak after the stressor, another individual with low cortisol levels during the control day showed the highest cortisol stress response in both urine and saliva. The inter-individual variability was larger in the urinary than the salivary cortisol levels, which could be due to metabolic differences between individuals since urinary cortisol is metabolized before excretion (Kirschbaum & Hellhammer, 1989; Sapolsky et al., 2000). While overall we found a decreasing pattern of urinary and salivary cortisol levels throughout the control day, we showed individual differences in the amount of cortisol but also in the fluctuations of the cortisol patterns. For the stress response, we found that the time frame of the peak was very similar but that the magnitude showed inter-individual differences. These differences are not necessarily surprising given that individual variation in the HPA axis activity is well documented (review in (Mormède et al., 2007; Sheriff et al., 2011)). Moreover, these individual differences are consistent across both matrices: individuals with a strong urinary cortisol response also show a strong salivary cortisol response. Our findings complement previous results on the existence of individual stress reactivity, which has been linked to differences in behaviour, neurobiology and immune response (Kanitz et al., 2019; Koolhaas et al., 2010). A study on the link between the individual stress responses and personality in a large group of bonobos could be a fascinating topic for future research.

The fact that in one of the subjects a salivary but not an urinary stress response was found, is surprising given that both matrices reliably reflect plasma cortisol levels (Behringer & Deschner, 2017). Also, in this subject, the highest average cortisol levels during the control day were measured. The absence of a urinary cortisol peak in combination with the higher control levels might be indicative of underlying issues with the homeostatic regulation of this individual. These individual variations in the cortisol pattern during the control and the stress day show the importance of including more than one subject in validation studies and of using individuals as their own control using a repeated measures design (Fulkerson & Jamieson, 1982; Honess & Marin, 2006).

Saliva sampling has been shown useful to monitor animal welfare (e.g. Behringer et al., 2014; Kuhar et al., 2005) but also in relation to cognitive tasks (e.g. Elder & Menzel, 2001). Our data support previous research that showed that in bonobos salivary cortisol can be used to monitor short-term effects of stressful events (Wobber et al., 2010). In addition, we show that urinary cortisol can also be used to monitor the effect of an acute stressor. However, in order to find a physiological effect of a certain event, the appropriate time window after the event for sample collection should be chosen based on species-specific excretion patterns in a biologically relevant setting. We therefore suggest that instead of only taking physiological validation results into account, future endocrinological research should also consider biological validation studies when deciding on sampling intervals. Alternatively, studies could conduct a pilot study in which they collect consecutive samples to determine the ideal time window for sample collection after a specific event. Another approach, is to take the urination interval into account in which cortisol levels are compared between samples before and after an event (Wittig et al., 2015). However, in this case, cortisol values are accumulated over a longer period so solutions need to be developed to take this problem into account.

In conclusion, this study provides detailed information on the urinary and salivary cortisol response after a psychological stressor in bonobos. We show that saliva and urine can be used to monitor the cortisol response after an event but also that the time frame of sampling is crucial in order to obtain biologically relevant information. When designing research plans, we suggest future endocrinological studies to consider information from a relevant biological context to decide on the ideal time frame of sampling.

Bonobo personality predicts friendship

Jonas Verspeek
Nicky Staes
Edwin J. C. van Leeuwen
Marcel Eens
Jeroen M. G. Stevens

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Abstract

In bonobos, strong bonds have been documented between unrelated females and between mothers and their adult sons, which can have important fitness benefits. Often age, sex or kinship similarity have been used to explain social bond strength variation. Recent studies in other species also stress the importance of personality, but this relationship remains to be investigated in bonobos. We used behavioural observations on 39 adult and adolescent bonobos housed in 5 European zoos to study the role of personality similarity in dyadic relationship quality. Dimension reduction analyses on individual and dyadic behavioural scores revealed multidimensional personality (Sociability, Openness, Boldness, Activity) and relationship quality components (value, incompatibility). We show that, aside from relatedness and sex combination of the dyad, relationship quality is also associated with personality similarity of both partners. While similarity in Sociability resulted in higher relationship values, higher relationship incompatibility was found between bonobos with similar Activity scores. The results of this study expand our understanding of the mechanisms underlying social bond formation in anthropoid apes. In addition, we suggest that future studies in closely related species like chimpanzees should implement identical methods for assessing bond strength to shed further light on the evolution of this phenomenon.

Introduction

Populations of group-living species comprise individuals who differ in the level of interaction they have with others (Réale et al., 2010; Wolf & Weissing, 2010). These interactions occur non-randomly and often result in lasting and stable social bonds, also called friendships (Silk, 2002a), that can improve individual fitness (Hinde, 1976). For example, offspring survival is higher in social female yellow baboons (Silk et al., 2003b) and in feral horses with more and stronger female-male bonds (Cameron et al., 2009). Similarly, in marmosets, breeding pairs and breeder-helper dyads with stronger bonds contributed more in offspring care (Finkenwirth & Burkart, 2018). In bottlenose dolphins, strong bonds between males increased mating chance (Connor & Krützen, 2015), while male-female bonding increased the lifespan of juvenile males (Stanton & Mann, 2012). Spotted hyenas (Drea & Carter, 2009), chimpanzees (Melis et al., 2006) and also humans (Majolo et al., 2006) engage in more cooperative interactions with friends. Often age, sex, kinship or rank similarity are used to explain variation in the strength of social bonds (MacCormick et al., 2012; Silk et al., 2003a, 2006; Sosa, 2016). However, the influence of these factors is very inconsistent across studies and often species-specific. For example, in chimpanzees strong social bonds are typically formed between related dyads and individuals of similar age, but are also found between unrelated non-age-mates (Langergraber et al., 2009; R. Martin & Christophe, 2003; Mitani, 2009). Social living animals tend to associate with similar individuals (Bouskila et al., 2015; Carter et al., 2015; de Waal & Luttrell, 1986; Massen & Koski, 2014), a phenomenon called homophily (McPherson et al., 2001). In humans homophily has been found across many phenotypic dimensions like sex, age and class (McPherson et al., 2001; Moody, 2004; Shrum et al., 1988) but also personality (Izard, 1960; Nelson et al., 2011; Selfhout et al., 2010). Recently, homophily in personality has been studied as an important factor contributing to the existing variability in social relationships across a range of phylogenetically distant taxa. For example, similarity in exploratory behaviour influenced assortment in female zebra finches (Schuett et al., 2011) and male great tits (Aplin et al., 2013), similarity in Boldness predicted bonding in baboons (Carter et al., 2015) and Sociability scores predicted relationship quality in chimpanzees (Massen & Koski, 2014) and capuchin monkeys (Morton et al., 2015).

While several studies have used relatively simple measures to assess relationship quality, including only one or just a few behaviours like agonistic support (Cooper et al., 2005), proximity (Aplin et al., 2013; Massen & Koski, 2014) or time spent in proximity and grooming (Carter et al., 2015; Seyfarth et al., 2014; Städele et al., 2019), a more inclusive way of determining relationship quality is to use composite measures. Cords and Aureli (2000) introduced a composite model to measure relationship quality consisting of following three components: value, compatibility and security. The *value*[5] of a relationship comprises the benefits that result from that relationship like food sharing or agonistic support. The *compatibility*[6] between two partners is a measure of the level of tolerance between individuals, and reflects the general nature of social interactions in a dyad. This means that in dyads with frequent aggressive interactions and counter-interventions, the nature of the relationship is defined

[5] Defined as “What the subject gains from her or his relationship with a partner, which depends on what the partner has to offer, how willing she or he is to offer it, and how accessible a partner she or he is” (Cords & Aureli, 2000, p178).

[6] Defined as “The general tenor of social interactions in a dyad, which may result from both the temperament of the partners and their shared history of social exchanges” (Cords & Aureli, 2000,178).

as less tolerant. The predictability and consistency of the behaviour of both partners over time describes the *security*[7] of a relationship (Aplin et al., 2013; Fraser et al., 2008; Massen, Sterck, et al., 2010). This three-component model has already been implemented in different study species. Relationship value contained behaviours relating to mainly social affiliation, tolerance and support in chimpanzees (Fraser et al., 2008; Koski et al., 2012), ravens (Fraser & Bugnyar, 2010), Japanese macaques (Majolo et al., 2010), capuchin monkeys (Morton et al., 2015), bonobos (J. M. G. Stevens et al., 2015) and dolphins (Moreno et al., 2017). Relationship compatibility contained aggressive behaviours in all but two studies (Majolo et al., 2010; Moreno et al., 2017) and for the third component of relationship quality, security, mixed results have been found across studies (Cords & Aureli, 2000; Massen, Sterck, et al., 2010; McFarland & Majolo, 2011; Morton et al., 2015; Seyfarth et al., 2014; Städele et al., 2019). Behaviours loading on this component greatly differed, making this component the least consistent across studies.

Homophily in personality seems to be widespread among different taxa, albeit in different personality traits with varying results. Studying closely related species may help in explaining these differences and in understanding how homophily in personality evolved. While homophily in personality has been studied in both humans (Nelson et al., 2011; Selfhout et al., 2010) and chimpanzees (Massen & Koski, 2014), no studies have been done in our other close relative, the bonobo. Bonobo societies are characterized by complex social relationships, where the strongest bonds are found between females (Furuichi, 1989; Parish, 1994; White, 1988) and between females and their adult sons (Fruth et al., 1999; Furuichi, 1989; Hohmann et al., 1999; J. M. G. Stevens et al., 2006). A previous study on bonobos (J. M. G. Stevens et al., 2015) found that relationship value was highest between unrelated female-female dyads and related male-female dyads. Relationship compatibility was highest between female-female dyads and between bonobos with large rank distances. However, not all variability in relationship quality could be explained by sex, rank, age and relatedness (J. M. G. Stevens et al., 2015). In this study, we aim to investigate the potential influence of personality on dyadic relationship quality. Bonobos within the same social group exhibit remarkable individual differences in personality (Garai et al., 2016; Weiss et al., 2015), and bonobos may partly choose who they want to associate with based on similarity or differences in personality. We previously identified personality in bonobos using behavioural observations, and found four personality traits: Sociability, Boldness, Openness and Activity (Staes et al., 2016). Here, we aim to find how similarity in each of the four personality traits impacts dyadic relationship quality in bonobos. Based on previous findings in chimpanzees and capuchin monkeys (Morton et al., 2015) we expect to find a link between similarity in Sociability and relationship value. Our study will be the first to use the composite measure for different aspects of relationship quality to report on the potential role of personality similarity on relationship compatibility.

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[7] Defined as "The perceived probability that the relationship with the partner will change, which relates to the consistency of the partner's behavioural responses" (Cords & Aureli, 2000, p178).

Methods

Behavioural data were collected for captive bonobos housed in six zoological parks: Planckendael (PL) in Mechelen, Belgium; Apenheul (AP) in Apeldoorn, the Netherlands; Twycross Zoo World Primate Centre (TW), Twycross, United Kingdom; Wuppertal Zoo (WU), Wuppertal, Germany; Frankfurt Zoo (FR), Frankfurt, Germany; and Wilhelma Zoological and Botanical Garden (WI) in Stuttgart, Germany. The subjects included 23 female and 16 male bonobos whose ages ranged from 7 to 63 years. All subjects were housed in groups that included juveniles and/or infants, which were excluded from the behavioural data collection. Behavioural data for relationship quality and personality analysis were collected during the same observational periods. Details on group composition and data collection can be found in table 4.1[8].

Table 4.1 Details on group composition, time of behavioural data collection and observers

	Zoo	Adults and subadults	Juveniles	Period	Observers
Round 1	PL	3M / 2F	1M / 1F	Nov. 2011 - Jan. 2012	AP
	AP	2M / 4F	2M / 2F	Mar. - Apr. 2012	AS, NS
	WI	3M / 9F	2M / 2F	May – Jul. 2013.	MB
	FR	3M / 6F	3M / 2F	Apr. - May 2012	SR, NS
	WU	3M / 3F	3M	May. - Jun. 2012	SR, NS
	TW	3M / 6F	1M / 2F	Sep. – Nov. 2012	NS
Round 2	PL	4M / 3F	1F	Nov. 2012 - Jan. 2013	WR
	AP	2M / 4F	1M / 2F	Feb. - May 2013	LJ
	WI*	3M / 9F	2M / 1F	Jul. - Aug. 2014	JV
	FR	3M / 7F	3M / 3F	Feb. - Apr. 2014	MW
	WU	3M / 2F	2M	Jan. - Mar. 2013	WR
	TW*	3M / 6F	2M / 2F	Aug. – Oct. 2013	MB

PL = Planckendael, AP=Apenheul, WI=Wilhelma Zoological and Botanical Garden, FR=Frankfurt Zoo, WU=Wuppertal Zoo, TW=Twycross Zoo World Primate Center. * In Twycross and Wilhelma collection of natural observations but no experimental data was done in round 2

Measures and analysis

We collected a total of 1442.39 hours of focal observations (mean 16.37 hours per individual), 43506 group scans (mean 545 per individual) and 430.96h of all occurrence observations during feedings (mean 28.73 hours per group). Inter-observer reliabilities reached a mean of r = 0.87 across all observers, meaning that all observations were highly reliable. Live scoring of behavioural data was done using The Observer (Noldus version XT 10, the Netherlands).

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[8] See also table 9.2 Overview of the study subjects p 145 & p 146

Personality profiles

Individual personality profiles were available and based on the personality model described in a previous paper (Staes et al., 2016). The behavioural variables used to construct this model were derived from both naturalistic and experimental settings (See tables 4.2 & 4.3) (Staes et al., 2016, 2017).

Table 4.2 Behavioural variables used to determine personality model based on codings (see Staes et al., 2016)

Behavioural variable	Calculated as
Activity	Focal observation time minus time spent resting, sleeping, sitting or autogrooming, divided by total focal observation time
Submission	Frequency per hour of flee, flinch and crouch behaviours during focal observations of all subjects in the group
Aggression given with	Frequency per hour of aggressive intentions, long charges, short charges, direct displays, mutual displays and parallel displays victim showing grin, flee or counter aggression during focal observations of all subjects in the group
Aggression received charges,	Frequency per hour of received aggressive intentions, long short charges, direct displays, mutual displays and parallel displays during focal observations of all subjects in the group
Number of neighbours scans	Average number of group members in subject's proximity in recorded as 'sit with' (S)
Approach others	Frequency per hour of focal subject approaching and staying in 2 m proximity of others
Being approached	Frequency per hour of focal subject being approached
Grooming density given	Number of individuals the subject gives grooming to divided by total available grooming partners
Grooming density received	Number of individuals the subject receives grooming from divided by total available grooming partners
Grooming diversity index	Shannon-Wiener diversity index corrected for group size effect (see text for formula)
Grooming given	Time spent grooming divided by focal observation time
Grooming received	Time spent being groomed divided by focal observation time
Play	Total duration of calm play and rough play divided by focal observation time
Scratching	Total duration of rough and gentle auto-scratching behaviors divided by focal observation time
Auto-grooming	Total duration of auto-grooming divided by focal observation time
Socio-sexual behaviours	Frequency/h of point affinitive behaviour by focal subject (affiliative touch, embrace, sex inspect, sex present, copulation, non-copulatory mount, oral genital massage, genital massage)

Table 4.3 Behavioural variables, their definitions and the experiments they were sampled in using the experimental setup (see Staes et al., 2016)

Behavioural variable	Calculated as	Type of experiment
Manipulate Puzzle	Duration of working the puzzle while touching it divided by total duration of the experiment	Hanging barrel Crate with mesh Reel and feed Turning tube
Tool use	Duration of tool use divided by total duration of the experiment	Crate with mesh
Latency to approach	Duration of interval between entering of the group in the enclosure and first approach towards experiment object	All experiments
Number of approaches	Absolute count of approaches made during the total duration of the experiment	Hanging barrel Crate with mesh Reel and feed Turning tube Leopard
Proximity	Summed durations of time spent within 2m of the object divided by total duration of the experiment	Hanging barrel Crate with mesh Reel and feed Twisting tube Leopard
Taste novel food	One zero sampling of whether they try the novel food during the total duration of the experiment	Durian Blue pasta
Poke leopard	Absolute count of times the subject tries to poke at the fake predator with a tool during the total duration of the experiment	Leopard
Knock barrier	Absolute count of times the subject makes forceful contact with barrier during the total duration of the experiment	Leopard. snake

In short, we included a total of 17 behavioural variables (10 from the naturalistic context and 7 from the experimental contexts). Raw variables were standardized into z-scores for each group before combining data from different zoos. As the definition of personality requires stability of traits between individuals across time, data were collected in two consecutive years for each group allowing us to test for temporal consistency. Intraclass correlations were used to determine temporal stability and only variables that were stable were used to determine personality structure. Dimension reduction analysis on these variables revealed four factors: Sociability, Boldness, Openness and Activity (Staes et al., 2016). Details of each item's loading onto each dimension are shown in table 4.4 (See also table 4.5). Items that showed cross-loadings $>|0.4|$ on multiple components, were considered part of the dimension on which they had the highest loading.

Table 4.4 The behavioural contents of the coded personality dimensions (Staes et al., 2016)

Factor	Adjectives loading on to factor
Sociability	+ Grooming frequencies + Grooming density + Neighbours + Grooming diversity – Latency to approach puzzles/durian – autogroom
Openness	+ Approaches to puzzles/others + Play + Proximity to puzzles + Taste pasta (- Latency to approach Puzzle)
Boldness	+ Approaches to leopard + displays to leopard + proximity to leopard + Aggression received
Activity	– Self-scratching + Activity (+ Grooming density given – Time in Proximity to Leopard)

Table 4.5 Variable loadings dimension reduction personality model (from Staes et al., 2016)

	Factor				
Variable	Sociability	Openness	Boldness	Activity	h^2
Grooming Received	0.83	-0.03	-0.03	0.20	0.74
Grooming Density Received	0.76	-0.07	-0.12	0.14	0.68
Number of Neighbours	0.71	0.13	0.13	-0.04	0.54
Grooming Given	0.67	0.18	0.13	0.39	0.69
Latency to Approach Puzzle	-0.66	-0.49	0.02	0.24	0.79
Grooming Density Given	0.64	0.20	0.33	0.42	0.84
Latency to Approach Durian	-0.64	-0.23	-0.01	0.14	0.47
Grooming Diversity Index	0.53	0.12	0.19	0.36	0.67
Autogroom	-0.48	0.10	-0.39	0.01	0.46
Puzzle Number of Approaches	0.08	0.91	0.13	0.06	0.83
Play	-0.07	0.70	0.00	0.22	0.63
Time in Proximity to Puzzle	0.20	0.68	-0.31	0.03	0.59
Approach others	0.05	0.65	0.35	0.27	0.69
Taste Pasta	0.27	0.41	0.20	0.11	0.42
Leopard Number of Approaches	0.02	0.11	0.82	0.02	0.67
Leopard Number of Displays	0.21	0.07	0.62	-0.01	0.48
Time in Proximity to Leopard	0.10	-0.08	0.59	-0.44	0.54
Aggression Received	-0.37	0.12	0.54	0.31	0.54
Scratch	-0.10	-0.17	0.19	-0.69	0.66
Activity	0.29	0.30	0.26	0.53	0.65
Eigenvalue	5.98	2.85	2.59	1.73	
% variance explained	29.92	14.25	12.93	8.65	

Relationship Quality

Measures for relationship quality were determined based on the relationship quality model described in a previous paper on bonobos (J. M. G. Stevens et al., 2015). We extracted dyadic scores for 8 social behavioural variables, which were collected in a naturalistic setting: Aggression frequency, aggression symmetry, counter-intervention, grooming frequency, grooming symmetry, peering frequency, proximity, support (For definitions see table 4.6). We then performed exploratory factor analysis (EFA) with varimax rotation and Kaiser normalization to extract composite measures for these 8 variables. The number of dimensions to extract was determined by inspecting the scree plot and by conducting a parallel analysis (Horn, John, 1965; B. P. O'Connor, 2000). The factors were then subjected to a varimax rotation and variable loadings $\geq |.4|$ were interpreted as salient.

Table 4.6 Behavioural variables, with the corresponding definitions, scored during the naturalistic observations to determine Relationship Quality (see Stevens et al., 2015).

Behavioural variable	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 A and B was calculated using the following formula: A grooms B/(A grooms B + B grooms A). For each dyad, the lowest of the two values obtained reversing A's and B's roles was chosen to represent the degree of symmetry (ranging from 0 to 0.5) [+].
Aggression frequency	Frequency of all aggressive interactions within a dyad
Aggression symmetry	Symmetry of aggression within a dyad (calculated in the same way as grooming symmetry).
Support	Index of agonistic support (frequency of support/opportunity to support). Support was defined as all instances where an individual A intervenes with an aggression within 30s in an agonistic interaction between two other individuals B and C to aid in attack or in defence.
Counter-intervention	Index of counter-intervention (frequency of counter-intervention/ opportunity to intervene). Every support pro for an individual implied a contra support against a victim. The target of a coalition is considered as the receiver of 'counter-intervention'.
Peering frequency	Frequency of peering (i.e., "the actor stares at the receiver's face from very close distance, up to a few centimetres"*)
Proximity	Proportion of scans spent within arm's reach

[+] Fraser et al.; 2008; * Kano, 1992

Linear mixed models

To determine potential associations between relatedness, sex combination, personality profiles and relationship quality measures, we used General Linear Mixed Models with Gaussian error distribution and identity link function (lme4 package 1.1-13 (Bates et al., 2015)) for a total of 90 dyads. Rank difference was not included in our models to reduce the amount of overfitting. Similarity in personality per dyad was determined taking the absolute difference of the personality scores of both individuals of a dyad. The relationship quality components were treated as response variables in two different models. The full models comprised the different personality similarity variables (all z-transformed) and the fixed categorical variable "genetic sex combination" (denoting the demographic nature of the dyad: female-female, female-male, male-male, mother-daughter, mother-son) as predictor variables. Combining relatedness and sex combination in one factor (genetic sex combination) allows us to separate related female-male (mother-son dyads) from unrelated female-male dyads and compare results between them. Only one mother-daughter dyad was included in our sample and was therefore excluded from statistical analyses. The random effects structure consisted of intercepts for each of the two subjects in the dyad and for the location of observation (zoo), including the random slopes of the four personality variables within the subjects and zoo, and the additional random slopes of genetic sex combination (dummy coded) within zoo (Barr et al., 2013; Schielzeth & Forstmeier, 2009). The null model was an intercept-only model, with the same random effects structure as the full model. Given the high number of estimated parameters in relation to the sample sizes (i.e., slight overfitting), we performed simulations to assess the power of our models. Data were corrected for observation time and diagnostic plots (residuals vs. fitted, QQ plots) were used to confirm the assumptions of normality and homogeneity of variances. When any of the assumptions were not met, we used square root, z- or log transformations of our variables. All statistical analyses were conducted using IBM SPSS Statistics 20 and R (version 3.4.3; R Core (Team, 2017).

Given that our models were slightly over-fitted (i.e., n=89, parameters assessed: 27), possibly leading to unstable results and low power, we assessed the stability and power of the models by i) by excluding subjects one at a time from the data and comparing the model estimates derived for these data with those derived for the full data set (indicating no influential subjects to exist), and ii) simulating new instances of the response and computing the frequencies by which simulated large, medium, small and 0-value fixed effects estimates reached significance for the full-null model comparison as well as for individual effects. For each model, we ran 1,000 simulations (script by Roger Mundry, available upon request). The magnitude of the simulated random effects we chose based on the model fitted to the original data (0.2 for the random intercepts and slopes of the two individuals; 0.5 for the random intercept of zoo, and 0 for the random slopes within zoo). If the simulated models, consisting of the same fixed and random effect structures as the original models, yielded high probability of obtaining a significant result for large and medium estimates (power > 0.7), and low probability of obtaining a significant result for 0-value estimates (Type 1 error rate < 0.1), we considered our models to be sufficiently stable for drawing valid inferences.

Ethical statement

No animals were sacrificed or sedated for the purpose of this study. This study was approved by the Scientific Advisory Board of the Royal Zoological Society of Antwerp and the University of Antwerp (Belgium) and endorsed by the European Breeding Program for bonobos. All research complied with the ASAB guidelines (ASAB, 2020).

Results

Relationship Quality

Eight dyadic behavioural variables were included in the first exploratory factor analysis. Sampling adequacy was high (KMO = 0.652) and inter-variable correlations were sufficiently high (Bartlett's test of sphericity: chisq = 275.284, df = 15, p < 0.001). Initial exploration using factor analysis revealed a three-component solution. However only one item, grooming symmetry, loaded on the third dimension, and therefore a new factor analysis was conducted (Budaev et al., 2010) maintaining only two factors. Next, grooming symmetry and aggression symmetry were excluded from the EFA based on low factor loadings (Table 4.7). Varimax- and promax-rotated dimensions did not differ substantially.

Table 4.7 Varimax rotated factor loadings for the components of Relationship Quality

	Varimax rotation	
Variable	Value	Incompatibility
Proximity	**0.945**	-0.114
Grooming Frequency	**0.834**	-0.025
Peering	**0.579**	-0.058
Support	**0.436**	0.062
Counter-intervention	0.058	**0.709**
Aggression frequency	-0.084	**0.595**
Eigenvalue	2.49	1.42
% of variation explained	0.36	0.14

Boldface highlights loadings >|0.4|

The influence of genetic sex combination and similarity in personality on relationship quality

Relationship value

Overall, the set of predictors significantly influenced relationship value (χ2 = 24.8, df = 7, p = 0.001). More specifically, relationship value differed substantially between the genetic sex combinations (χ2 = 15.8, df = 3, p = 0.001) (Fig. 4.1A), such that mother-son dyads had the highest relationship value (mean ± SD = 1.50 ± 0.88), followed by female-female dyads (mean ± SD = 0.40 ± 0.78), unrelated female-male dyads (mean ± SD = -0.33 ± 0.92), and male-male dyads (mean ± SD = -0.41 ± 0.89).

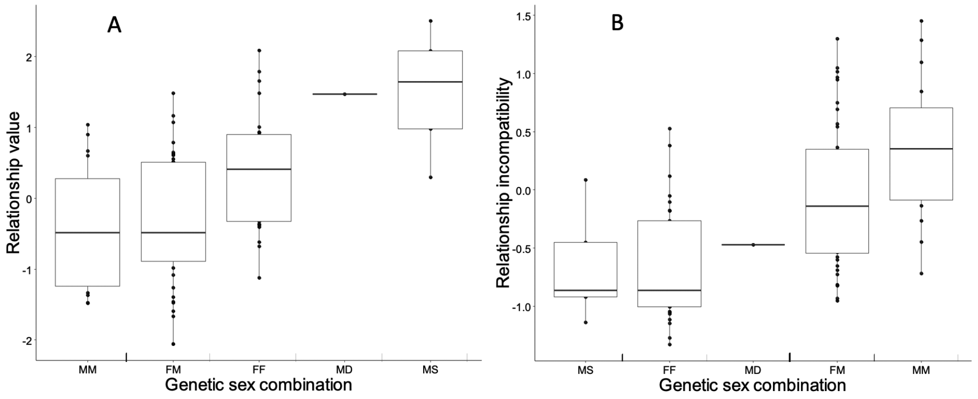

Fig. 4.1 Mean A. relationship value and B. relationship incompatibility of unrelated male-male (MM), unrelated female-male (FM), unrelated female-female (FF), mother-daughter (MD) and mother-son (MS) dyads.

Besides genetic sex combination, similarity in Sociability was also significantly, tough less apparent, associated with relationship value (χ2 = 4.1, df = 1, p = 0.042; Fig. 4.2A), with subjects having more similar Sociability scores exhibiting higher value relationships (estimate ± SD = -0.26 ± 0.09). The other personality traits did not significantly influence relationship value (all p > 0.05) (Table 4.8, Fig. 4.2).

Table 4.8 Factors influencing relationship value, assessed with a General Linear Mixed Model (GLMM).

Fixed variable	Num df	χ^2	β ± SE	*t* value	P
Genetic sex combination	3	15.8	0.347 ± 0.202	1.72	**0.001**
FF vs MF			-0.707 ± 0.174	-4.07	**<0.001**
FF vs MM			-0.611 ± 0.226	-2.71	**0.002**
FF vs MS			0.634 ± 0.469	1.35	0.576
Similarity in Sociability	1	4.1	-0.257 ± 0.090	-2.85	**0.042**
Similarity in Openness	1	1.9	-0.191 ± 0.129	-1.47	0.164
Similarity in Boldness	1	2.1	-0.132 ± 0.083	-1.59	0.145
Similarity in Activity	1	0.1	0.026 ± 0.076	0.34	0.745

Boldface indicates significant p values at the level alpha <0.05.

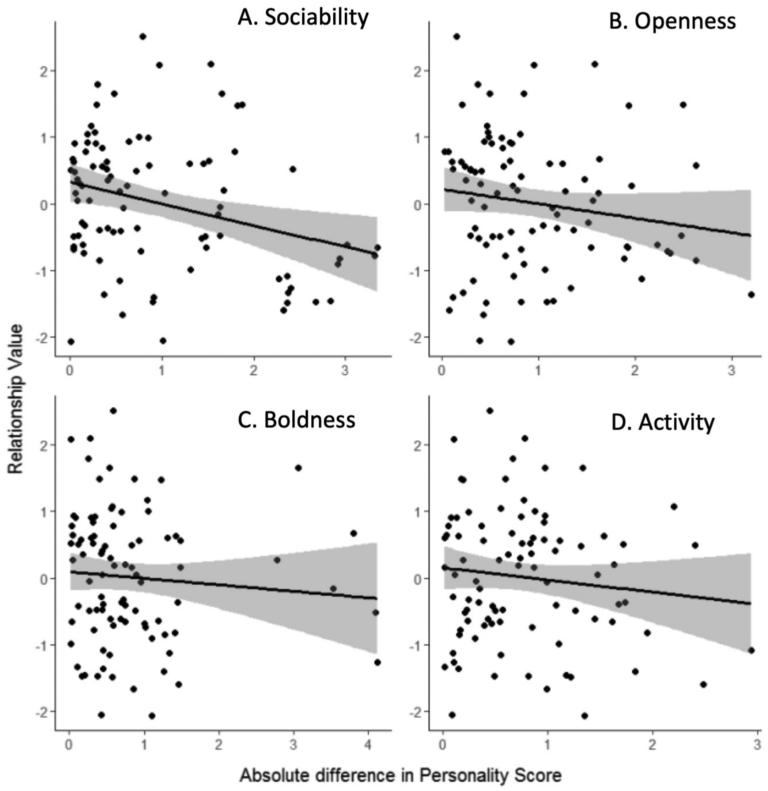

Fig. 4.2 The link between relationship value and the absolute difference in personality score of A. Sociability, B. Openness, C. Boldness and D. Activity per dyad for all genetic sex combinations with corresponding confidence intervals.

Data simulations showed that large and medium-large estimates will be detected in this model with a probability of 1 and 0.80, respectively, indicating high power. The probability of detecting small effects was 0.49, indicating intermediate power. Type 1 error rates were within reasonable boundaries (0.067 and 0.083 for the two 0-value estimates).

Relationship incompatibility

Overall, the set of predictors significantly influenced relationship incompatibility (χ2 = 26.3, df = 7, p < 0.001). Relationship incompatibility differed substantially between the genetic sex combinations (χ2 = 14.75, df = 3, p = 0.002, Fig. 4.1B), with male-male dyads having the most incompatible relationships (mean ± SD = 0.35 ± 0.63), followed by unrelated female-male dyads (mean ± SD = -0.04 ± 0.62), female-female dyads (mean ± SD = -0.64 ± 0.50), and mother-son dyads (mean ± SD = -0.66 ± 0.48). Further, similarity in Activity was significantly associated with relationship incompatibility (χ2 = 5.2, df = 1, p = 0.023), such that subjects with relatively similar Activity traits engaged in more incompatible relationships (estimate ± SD = -0.20 ± 0.07) (Fig. 4.3A). The other personality traits did not influence relationship incompatibility (all p > 0.1, table 4.9, fig. 4.3). The data simulations showed that large and medium-large estimates will be detected in this model with a probability of 1 and 0.81, respectively, indicating high power. The probability of detecting small effects was 0.49, indicating intermediate power. Type 1 error rates were within reasonable boundaries (0.079 and 0.073 for the two 0-value estimates).

Table 4.9 Factors influencing relationship incompatibility, assessed with a General Linear Mixed Model (GLMM).

Fixed variable	Num df	χ^2	β ± SE	*t* value	P
Genetic sex combination	3	14.8	-0.496 ± 0.120	-4.14	**0.002**
FF vs MF			0.416 ± 0.154	2.70	**<0.001**
FF vs MM			0.692 ± 0.227	3.04	**<0.001**
FF vs MS			-0.494 ± 0.246	-2.01	0.889
Similarity in Sociability	1	1.4	0.112 ± 0.069	1.63	0.241
Similarity in Openness	1	0.5	-0.047 ± 0.057	-0.82	0.485
Similarity in Boldness	1	2.2	0.142 ± 0.086	1.65	0.140
Similarity in Activity	1	5.2	-0.199 ± 0.072	-2.77	**0.023**

Boldface indicates significant p values at the level alpha <0.05.

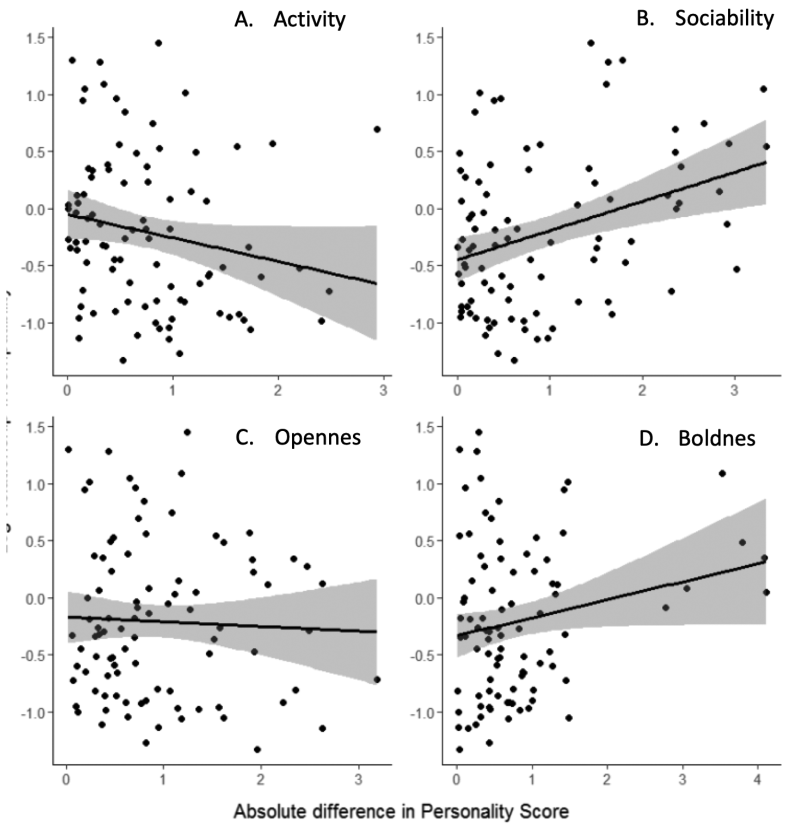

Fig. 4.3 The link between relationship incompatibility (log of the standardized scores) and the absolute difference in personality score of A. Activity, B. Sociability, C. Openness, D. Boldness per dyad for all genetic sex combinations with corresponding confidence intervals.

Discussion

The general aim of this paper was to understand the role of kinship, sex and personality in shaping relationship quality of captive bonobos. Our results indicate that kinship and sex combination, as well as homophily in personality traits Sociability and Activity, affect relationship value and incompatibility in bonobos.

Similar to the relationship quality model previously described, our dimension reduction analysis revealed two components. Due to low item loadings of symmetry in affiliative behaviour, the third factor, 'relationship security', was not retained in this study. Our first component of relationship quality, relationship value, is comparable to the first component in chimpanzees (Fraser et al., 2008; Koski et al., 2012), ravens (Fraser & Bugnyar, 2010), Japanese macaques (Majolo et al., 2010), spider monkeys (Rebecchini et al., 2011), barbary macaques (McFarland & Majolo, 2011), capuchin monkeys (Morton et al., 2015), bonobos (J. M. G. Stevens et al., 2015) and dolphins (Moreno et al., 2017). This component was significantly influenced by genetic sex combination, with mother-son dyads showing the highest value. This is in line with bonobo socio-ecology, where mothers provide agonistic support to their (sub)adult sons against others (Furuichi, 2011; T. Kano, 1992; J. M. G. Stevens et al., 2006), enhance their mating success (Surbeck et al., 2011, 2019) and show high levels of dyadic grooming (J. M. G. Stevens et al., 2006). Similarly, higher relationship values between kin were also previously described in chimpanzees (Fraser et al., 2008; Koski et al., 2012), ravens (Fraser & Bugnyar, 2010), macaques (Majolo et al., 2010) and a previous bonobo study (J. M. G. Stevens et al., 2015). Unrelated female dyads also showed high relationship values, which is in line with higher frequencies of reciprocal support among them, even though they do not always spend more time in proximity and show lower levels of dyadic grooming (J. M. G. Stevens et al., 2006). In addition to genetic sex combination, relationship value was also significantly influenced by homophily in Sociability scores. Our Sociability dimension includes mainly affiliative behaviours (grooming frequency, density and diversity and the number of individuals). Interestingly, while bonobos with similarly high Sociability scores will need to be in proximity to behave affiliative, causing high value relationships, this homophily in Sociability effect also indicates that individuals with similarly low Sociability scores, likewise have high value relationships. Low Sociability individuals, who do not engage in many social interactions, therefore invest a lot in just a few social relations, resulting in rare, but high value relationships. Our Sociability dimension is comparable to the Sociability dimensions found in capuchin monkeys (Morton et al., 2015) and chimpanzees (Massen & Koski, 2014), where similarity in this personality trait also resulted in higher quality relationships with more dyadic affiliation (Morton et al., 2015) and more contact-sitting (Massen & Koski, 2014), respectively. The Sociability dimension most resembles the Extraversion dimension in humans (McCrae & Costa, 1989; D. Watson & Clark, 1997), who also prefer friends that are more similar in Extraversion scores (Nelson et al., 2011; Selfhout et al., 2010). We did not find homophily in any of the other personality traits for relationship value.

Homophily in Openness resulted in high quality relationships in humans (J. L. Holland et al., 1991; Selfhout et al., 2010) and capuchin monkeys (Morton et al., 2015), but no such association was found in our study. Also for Boldness, we did not find any effect of similarity in Boldness on relationship value, while in chimpanzees (Massen & Koski, 2014) and baboons (Carter et al., 2015) dyads with more similar boldness scores showed more contact sitting and grooming, respectively. Chimpanzees with more similar Grooming Equity scores also showed more contact sitting, but only among non-kin (Massen & Koski, 2014). The Grooming Equity factor in this study, however, comprised both grooming density and grooming diversity, two behaviours that were included in our Sociability factor.

Our second relationship quality component, compatibility, was also influenced by genetic sex combination. Unsurprisingly, the highest compatibility scores were found between mother-son dyads followed by unrelated female-female dyads, female-male dyads and male-male dyads. Aggression is most common between males and from females to males but rarely happens between females or from males to females (Furuichi, 2011; T. Kano, 1992; Surbeck et al., 2012). Also in chimpanzees (Fraser et al., 2008; Koski et al., 2012), ravens (Fraser & Bugnyar, 2010), macaques (Majolo et al., 2010) and a previous bonobo (J. M. G. Stevens et al., 2015) study higher compatibilities were found between related individuals. Relationship compatibility was also significantly influenced by personality, albeit less clear given the high spread of our data. Similarity in Activity resulted in lower compatibility scores meaning that individuals with similar Activity scores engage in more counter-interventions against each other and behave more aggressively against one another. Our Activity trait had a high positive loading for activity and a negative one for self-scratching. In addition, grooming density, and time spent in proximity to the leopard had loadings >|0.4| on Activity but were attributed to Sociability and Boldness, respectively, due to higher loadings on these factors.

In chimpanzees, activity and self-scratching loaded on two separate personality factors: Activity and Anxiety (Koski, 2011; Massen & Koski, 2014). Similarity in these personality traits resulted in stronger friendships in unrelated chimpanzees (Massen & Koski, 2014), while similar Activity levels in bonobos here result in less compatible relationships. This effect might partly be explained by an underlying sex bias in Activity scores. Additional analyses for sex effects on bonobo personality dimensions (see Supplementary materials) indicate that bonobo males score significantly higher on Activity than females. In chimpanzees, higher levels of self-directed behaviours in males, have been suggested to reflect the stress of their male dominated society (Koski, 2011). Considering that female bonobos occupy the higher ranks (J. M. G. Stevens et al., 2007; Vervaecke, de Vries, et al., 2000a), our results are in line with potential dominance-related influences on personality. However, further studies are needed to confirm the link between Activity, self-scratching and rank. If these effects are present, dyads with more similar Activity scores and small rank differences would show higher dyadic frequencies of aggression and therefore have less compatible relationships. However, these effects are not linear, as shown by the high distribution of data points on the graph. Similarity in Sociability, Boldness and Openness did not influence relationship compatibility in our study.

While our bonobo personality factors, based on behavioural observations, are comparable to the personality factors in humans (Izard, 1960; Selfhout et al., 2010) and chimpanzees (Massen & Koski, 2014) different results concerning the effect of personality on friendships were found. One apparent explanation is that we implemented a different and perhaps more inclusive composite model to measure relationship quality (Cords & Aureli, 2000). In chimpanzees (Massen & Koski, 2014), contact-sitting was used as a simple measure for friendship, while in humans, questionnaire answers were used instead of behavioural observations to determine relationship quality (Selfhout et al., 2010). Studying the influence of personality on the composite measure for relationship quality in chimpanzees (Fraser et al., 2008) might be an interesting next step to further our understanding of the evolution of homophily in friendships in these two closely related species.

While the relationship between personality and friendship is clear in several species, less is known about its underlying mechanism. Do individuals choose others with similar personalities to form friendships or do personalities of individuals become more similar over time due to shared experiences? This attraction and/or convergence comparison (Morton et al., 2015) requires a long-term study to compare personalities and relationship quality at consecutive points in time. Further, the role of personality in friendships seems to be trait-specific, as opposed to all traits being similar between friends, and the importance of different traits appears to be species-specific. Further research is therefore needed to study which benefits result from similarity in certain personality traits and whether the evolutionary fitness of dyads with similar personalities is higher than dissimilar dyads in both captive and wild populations.

In conclusion, we found that the quality of social bonds between bonobos is influenced by the genetic sex combination of both partners and their personality similarity, more specifically in Sociability and Activity. Homophily in Sociability is likely to be a shared feature in ourselves and our closest relatives, chimpanzees and bonobos. While similarity in Sociability might promote reliable high quality relationships through reciprocity in similarly affective behavioural tendencies, lower compatibility levels of dyads with more similar Activity scores may be a by-product of rank differences.

Self-interest precludes prosocial juice provisioning in a free choice group experiment

Jonas Verspeek
Edwin J. C. van Leeuwen
Daan W. Laméris
Jeroen M. G. Stevens

In revision in Primates

Abstract

Previous studies on prosociality in bonobos have reported contrasting results, which might partly be explained by differences in experimental contexts. In this case study, we implement a free choice group experiment in which bonobos can provide fruit-juice to their group members at a low cost for themselves. Four out of five bonobos passed a training phase and understood the set-up, and provisioned fruit juice in a total of 17 dyads. We show that even in this egalitarian group with a shallow hierarchy, most pushing was done by the alpha female, who monopolised the set-up and provided most juice to two adult females, her closest social partners. Nonetheless, the bonobos in this study pushed less frequently than the chimpanzees in the original juice-paradigm study, suggesting that bonobos might be less likely than chimpanzees to provide benefits to group members. Moreover, in half of the pushing acts, subjects obtained juice for themselves, suggesting that juice provisioning was partly driven by self-regarding behaviour. Our study indicates that a more nuanced view on the prosocial food provisioning nature of bonobos is warranted but based on this case study, we suggest that the observed sex differences in providing food to friends corresponds with the socio-ecological sex difference in cooperative interactions in wild and zoo-housed bonobos.

Introduction

Prosociality has been defined as “any behaviour performed by one individual to alleviate the needs of other individuals or to improve their welfare, without the actor necessarily incurring extra costs to provide these benefits” (Amici et al., 2014; Cronin, 2012b). It has been suggested to be the promoting driver of cooperation (Burkart et al., 2014; Fehr & Fischbacher, 2003; Jaeggi, Burkart, & van Schaik, 2010; Silk, 2012). Humans’ species-unique psychology allows them to possess unique levels of prosociality and to engage in a vast variety of cooperative interactions (Fehr & Fischbacher, 2003; Powers et al., 2021; Tomasello & Vaish, 2012). To pinpoint the psychological predispositions of human prosociality an increasing number of studies have investigated to what extent our closest living relatives, chimpanzees and bonobos, show comparable levels of prosocial behaviour. According to the self-domestication hypothesis, natural selection has increased the expression of prosocial behaviour in both humans and bonobos (Hare, 2017; Hare et al., 2012). Therefore, bonobos have been explicitly proposed as an ideal species to study the phylogenetic origins of human prosociality (Hare, 2017; Hare & Yamamoto, 2017; Maclean, 2016; Tan & Hare, 2017). However, sex differences within the species are often overlooked in this context. In the wild, male and female bonobos differ in their cooperative and prosocial behaviour. Male bonobos do not patrol territorial boundaries, do not hunt individually, do not form strong bonds among each other and seldomly share food (Furuichi & Ihobe, 1994; Ihobe, 1992b; Surbeck & Hohmann, 2013). Female bonobos on the other hand form alliances, co-defend and share food and provide coalitionary support to each other (Surbeck & Hohmann, 2013; Tokuyama & Furuichi, 2016; Yamamoto, 2015). Experimental prosociality studies in captive bonobos have also yielded mixed results. Bonobos showed targeted helping in some (Hare & Kwetuenda, 2010; Nolte & Call, 2021; Tan et al., 2017; Tan & Hare, 2013), but not all studies (Bullinger et al., 2013; Liebal et al., 2014). They voluntarily handed food to others (Krupenye, Tan, et al., 2018), while failed at the prosocial choice test (Amici et al., 2014; Tan et al., 2015) and showed limited social tolerance and co-feeding in a group setting (Cronin et al., 2015; Jaeggi, Stevens, et al., 2010). These inconsistent results may be partly explained by different approaches in the experimental context (House et al., 2014), including the set-up and individual and social characteristics of the study subjects. For example, the quality of social bonds and the position in the dominance hierarchy influenced tolerance and food-sharing in other primates (Cronin et al., 2017; Marshall-Pescini et al., 2016; Tan & Hare, 2017). Most prosociality and food sharing studies in bonobos thus far have tested preselected dyads which may lead to ecologically less relevant conditions. To investigate more naturally occurring social interactions between subjects, studies should implement experimental paradigms that allow for free partner choice and participation (Cronin et al., 2017; Marshall-Pescini et al., 2016). We presented a group of zoo-housed bonobos with a free choice group experiment, that has previously been used to study prosociality in chimpanzees (van Leeuwen et al., 2021). Using this juice-paradigm in a group setting, we aimed to investigate whether such a naturalistic experimental context gives rise to the tolerant donation of a preferred resource in bonobos. Next, we also compared the level of juice-provisioning with the previously reported juice-provisioning in chimpanzees (van Leeuwen et al., 2021). Based on bonobo socio-ecology, we expect female bonobos to participate more often than males and to find similar juice provisioning frequencies as chimpanzees.

Materials and Methods

Subjects and housing

Nine bonobos (5F, 4M) from one social group housed at ZOO Planckendael (Belgium) participated (Table 5.1). At the time of the study, they were housed in an enclosure that consisted of nine interconnected rooms of various sizes (between 15 and 65 m^2). The bonobos were fed four times per day and water was available ad libitum.

Table 5.1 Subject information and the corresponding dominance scores. Individuals are ordered according to their dominance rank. Rank was not assessed for adolescents, juveniles and infants and these are ordered according to age.

Individual	Sex	Age (years)[a]	Parents	Normalised David's score[b]
Djanoa	Female	24	Santi x Yala	3.38
Hortense	Female	41	Unknown	2.50
Habari	Male	13	Vifijo x Djanoa	2.50
Busira	Female	15	Birogu x Eja	2.49
Vifijo	Male	25	Kidogo II x Hortense	2.32
Zamba	Male	21	Kidogo II x Hortense	1.81
Nayoki	Female	7	Louisoko x Djanoa	NA
Kikongo	Male	5	Bolombo x Hortense	NA
Sanza	Female	2	Lucuma x Busira	NA
Sakana[c]	Female	1	Lucuma x Djanoa	NA

Individuals in bold passed the training criterium.
[a] Individual's age when the study took place
[b] Based on fleeing upon aggression
[c] Died between the period of observations and the experiment
NA: dominance ranks in juveniles and infants were not assessed

Dominance hierarchy and social relations

We collected behavioural data during experimental-free days to determine relationship quality and the dominance hierarchy between the adult subjects (total of 96 hours and 42 mins). The dominance hierarchy was determined by constructing a win-lose matrix based on the behaviour fleeing upon aggression (J. M. G. Stevens et al., 2007; Vervaecke, de Vries, et al., 2000a). Using this matrix, we calculated normalised David's scores, which were used to calculate the steepness of the hierarchy (De Vries et al., 2006).

Relationship quality

Relationship quality was determined based on the relationship quality model described in previous bonobo papers (J. M. G. Stevens et al., 2015; Verspeek et al., 2019). For the fifteen adult-adult dyads of this study, we extracted dyadic scores for eight social behavioural variables, collected during the experimental-free days: Aggression frequency, aggression symmetry, counter-intervention, grooming frequency, grooming symmetry, peering frequency, proximity, support (for definitions see table 5.2). We added these data to the existing dataset including all other bonobo groups of the European zoos (Verspeek et al., 2019) resulting in 169 unique dyads. From this entire dataset, we extracted composite measures for relationship quality using exploratory factor analysis (FA) with varimax rotation and Kaiser normalisation. The number of dimensions to extract was determined by conducting a parallel analysis (Horn, John, 1965; B. P. O'Connor, 2000). After varimax rotation, variable loadings ≥ |0.4| were interpreted as salient. For each of the fifteen adult-adult dyads of this study, we extracted the component scores for relationship quality.

Table 5.2 Behavioural variables, with the corresponding definitions, that were used to determine Relationship Quality (See Stevens et al., 2015).

Behavioural variable	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 A and B was calculated using the following formula: A grooms B/(A grooms B + B grooms A). For each dyad, the lowest of the two values obtained reversing A's and B's roles was chosen to represent the degree of symmetry (ranging from 0 to 0.5) [+].
Aggression frequency	Frequency of all aggressive interactions within a dyad
Aggression symmetry	Symmetry of aggression within a dyad (calculated in the same way as grooming symmetry).
Support	Index of agonistic support (frequency of support/opportunity to support). Support was defined as all instances where an individual A intervenes with an aggression within 30s in an agonistic interaction between two other individuals B and C to aid in attack or in defence.
Counter-intervention	Index of counter-intervention (frequency of counter-intervention/ opportunity to intervene). Every support pro for an individual implied a contra support against a victim. The target of a coalition is considered as the receiver of 'counter-intervention'.
Peering frequency	Frequency of peering (i.e., "the actor stares at the receiver's face from very close distance, up to a few centimetres"*)
Proximity	Proportion of scans spent within arm's reach

[+] Fraser *et al.*; 2008; * Kano, 1992

Experimental set-up

The set-up consisted of a button that when pushed, released juice (75% water, 25% apple juice) from a distant fountain. Before testing, the bonobos were familiarised with the set-up. In a first training phase, the button and juice fountain were positioned 0.5 m apart so that by pushing, subjects could obtain juice for themselves. In the following training phase, the button and fountain were positioned 2 m apart so that pushing and drinking by the same subject was impossible, but subjects could clearly see the consequence of pushing. Subjects passed the training phases as soon as they reliably pressed the button at least seven times in the same session. Five out of nine bonobos passed this criterion and were included as subjects. All nine bonobos participated as possible recipients. In the experimental phase, the button and fountain were 5 m apart to avoid simultaneous pushing and drinking by the same subject. The experiment was repeated fifteen times (total of 23 hours and 37 minutes). Each testing session started when the button was uncovered and lasted until the juice-container was depleted (on average 1h 30 mins ± 29 mins). Each session was videorecorded with one camera focused on the button and another on the fountain.

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[9] See also table 9.1 Overview of the study subjects p 144

Behavioural coding

All occurrence observations of agonistic behaviours and pushing and drinking of the juice were collected using a combination of live scoring and video-coding in the Observer software (Noldus version XT 10, the Netherlands). Aggressive interactions were coded to monitor competition around the set-up. Each time the button was pushed, we coded the identity of the subject and the receiver of the juice. After a subject stopped pushing, some juice remained in the hose-system of the fountain. Therefore, subjects could also get a limited benefit for themselves by going toward the fountain to suck the leftover juice out of it. Thus, we scored each pushing event also in terms of potential motivation: self-motivated, i.e. when subjects moved over to the fountain to get juice, or non-self-motivated, i.e. when subjects pushed the button but did not move over to the fountain to get juice.

Data analysis

To determine whether individual pushing frequencies increased over time, we used Spearman's rank correlation. To investigate the distribution of self-motivated pushing, we determined whether self-motivated pushing increased with the number of test sessions, using a Pearson correlation.

Results

Dominance hierarchy and social relations

During experimental-free days, we observed 78 instances of fleeing upon aggression among the adult bonobos, resulting in a dominancy hierarchy with a shallow slope of 0.24 (p = 0.02). The highest position in the hierarchy was occupied by a female, followed by a cohort of individuals with very similar dominance scores (Table 5.1).

Based on parallel analysis, two components for relationship quality were extracted. The first factor explained 38.9% of the total variance and had positive loadings for proximity, grooming frequency and peering. This component is very similar to the relationship value component of previous bonobos studies (J. M. G. Stevens et al., 2015; Verspeek et al., 2019) and was therefore labelled Relationship Value. The second component explained 10.3% of the total variance, had positive loadings for grooming reciprocity and aggression frequency and was thus labelled Relationship Incompatibility (J. M. G. Stevens et al., 2015; Verspeek et al., 2019). In order to make further interpretation easier, we reversed the sign of the component and relabelled it compatibility (Table 5.3).

Table 5.3 Varimax rotated factor loadings for the components of Relationship Quality.

	Varimax rotation	
Variable	Value	Compatibility
Proximity	**0.917**	-0.125
Grooming frequency	**0.776**	0.036
Peering	**0.577**	-0.037
Grooming reciprocity	**0.404**	-0.546
Aggression frequency	-0.075	**-0.447**
% of variation explained	38.897	10.331
Eigenvalue	2.375	1.139

Boldface highlights loadings > |0.4|.

The differences in factor loadings between our study and the previous bonobo studies might be due to the limited amount of aggressive interactions and especially in coalitionary support that were observed. In this study, we were able to extract two components that were comparable to many other species (Fraser et al., 2008; Fraser & Bugnyar, 2010; Koski et al., 2012; McFarland & Majolo, 2011; Morton et al., 2015) and can therefore be used to study the effect of relationship quality on prosociality. We found the highest Values between female-female dyads (Djanoa-Hortense and Djanoa-Busira) and the lowest Values for the dyads that included the lowest ranking adult male (Zamba) (Fig 5.1)

We found the highest pushing frequencies between dyads with the highest Relationship Values, i.e. strongest bonds (Djanoa – Hortense and Djanoa – Busira). The highest Relationship Values were found between unrelated female-female dyads.

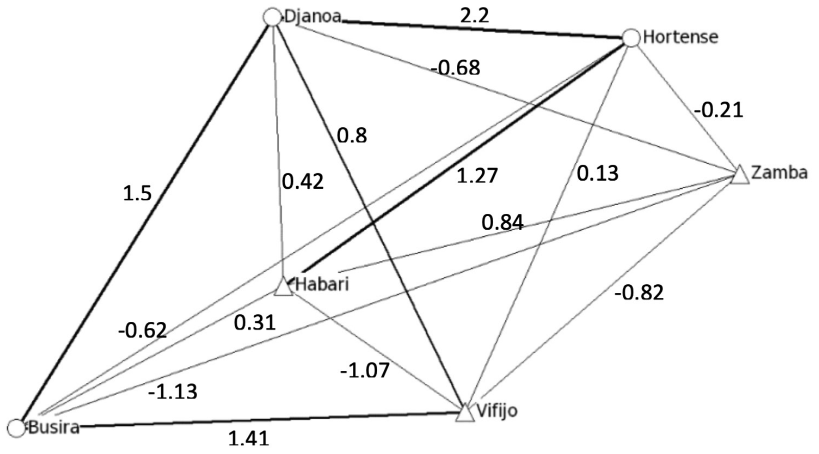

Fig. 5.1 Sociogram of Relationship Value in adult-adult dyads. The circles and triangles (nodes) represent respectively females and males and the weight of the lines (edges) connecting the nodes represents Relationship Value between the dyads.

Juice-experiment

We observed few aggressive and competitive interactions during the experiment (4 cases of contact aggression; 21 cases of noncontact aggression and only 14 instances of fleeing upon aggression), suggesting that there was no overt competition over the fruit juice.

Four out of five bonobos that passed the training criterium, provided juice to a group member. We recorded a total of 522 pushing-events were recorded in 17 unique dyads. Pushing was mostly done by the alpha female (Djanoa), (91.7%, n = 478, 6 partners), followed by her adolescent daughter (Nayoki) (5.4%, n = 28, 5 partners), a subadult male (Kikongo) (2.5%, n = 13, 5 partners) and the most dominant male, son of the alpha female (Habari) (0.4%, n = 2, 1 partner) (Tables 5.4 & 5.5). Seven out of nine bonobos received juice by pushing of others at least once. The two main receivers of juice were the adult females (Hortense and Busira). the two lowest ranking adult males (Vifijo and Zamba) never obtained juice.

Table 5.4 Total number of pushes and self-motivated pushes of the subjects towards each possible partner and Relationship Value and Compatibility between each dyad.

Subject	Receiver	Total number of pushes	Total number self-motivated pushes	Relationship Value	Relationship Compatibility
Djanoa	Hortense	145	40	2.293	-0.175
	Busira	192	145	1.496	-0.874
	Vifijo	0	0	0.844	-1.924
	Habari	32	24	0.416	-1.934
	Zamba	0	0	-0.679	-0.353
Habari	Djanoa	1	1	0.416	-1.934
	Hortense	0	0	1.265	-0.979
	Busira	0	0	0.314	-0.682
	Vifijo	0	0	-1.067	-0.439
	Zamba	0	0	0.844	-1.924
Vifijo	Djanoa	0	0	0.844	-1.924
	Hortense	0	0	0.132	0.587
	Busira	0	0	1.405	-0.407
	Habari	0	0	0.399	-1.793
	Zamba	0	0	-0.824	-0.300

Table 5.5 Distribution of pushing events for the subjects that passed the training phase

Subject	Receiver									
	Djanoa	Habari	Vifijo	Nayoki	Kikongo	Hortense	Busira	Zamba	Sanza	No partner°
Djanoa	-	32	0	43	28	145	192	0	11	27
Habari	1	-	0	0	0	0	0	0	0	1
Vifijo	0	0	-	0	0	0	0	0	0	0
Nayoki	14	1	0	-	3	7	1	0	0	2
Kikongo	6	1	0	1	-	1	3	0	0	1

° Pushing events where subjects started to push when no receiver was present

Pushing frequencies did not increase over the course of the experiment (rs = -0.06, df = 31, p = 0.75), indicating that bonobos did not adjust their juice-provisioning throughout the experiment (Fig. 5.2a). In 55% of the pushing events, subjects drank from the juice nipple after pushing, which may indicate that they acted self-motivated. Over the course of the experiment, the proportion of self-motivated pushing events increased, although not significantly (r(13) = 0.21, p = 0.24) (Fig. 5.2b).

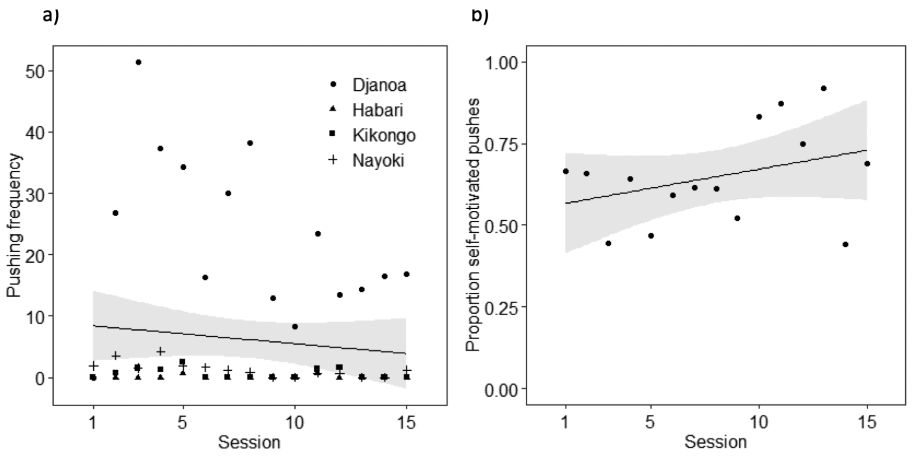

Fig. 5.2 Bonobos' pushing frequencies over the course of the experiment: a) Total individual pushing frequencies per session; b) Total proportion of self-motivated pushing per session.

Discussion

This experimental case study of fruit juice provisioning in a naturalistic group setting shows that juice was provided and received mainly by female bonobos. The bonobos pushed less frequently than all three chimpanzee populations in the original juice-paradigm study (van Leeuwen et al., 2021). This is surprising, as according to the self-domestication hypothesis bonobos have been suggested to show more cooperative and prosocial behaviour than chimpanzees, including instrumental helping and food sharing, (Hare, 2017; Hare et al., 2007; Melis, 2018; Tan & Hare, 2017). The majority of studies reporting positive food sharing and tolerance in bonobos, which have shaped the popular view of the tolerant and food-sharing bonobo, are largely based on experimental studies that tested subadult and juvenile bonobos (reviewed inCronin et al., 2015; Verspeek et al., 2022 - see Chapter 6). Studies that did include adult subjects in their experiments often failed to find supporting evidence for their tolerant and prosocial nature around food (Amici et al., 2014; Bullinger et al., 2013; Cronin et al., 2015; Jaeggi, Stevens, et al., 2010). Our data suggest that adult bonobos might be equally or even less likely as adult chimpanzees to share food benefits with conspecifics in experimental contexts [Jaeggi et al., 2010a; Cronin et al., 2015]. Note that although the original juice study included chimpanzees of different ages, all subjects lived in Chimfunshi, a sanctuary in Zambia (van Leeuwen et al., 2021). Their pushing behaviour could therefore reflect the prosocial behaviour of a-typically raised chimpanzees. Additional studies using a comparable set-up in other social groups should clarify how rearing and background of individuals influences their levels of prosociality. It is likely that “enculturated” apes who spent more time with humans (cfr Bering, 2004), have been, even unintentionally, conditioned to participate with humans or with other apes.

Although free choice of participation and partner allows for more ecologically relevant interactions (House et al., 2014), group experiments often suffer from reduced participation of certain individuals due to competition in the group (Cronin et al., 2017). This was also evident in our study. The majority of pushing (91.7 %) was done by the group’s alpha female, suggesting that she monopolised the set-up. She occupied the button rather than the actual resource, the juice, which might have hindered the subordinates to approach and push the button. Indeed, we found that in 57.3 % of her pushing events, the alpha female obtained juice herself, indicating that her pushing could (partly) be selfishly motivated. While she secured access to the button, other high-ranking females were able to monopolise the fountain, impeding the opportunity for lower ranking individuals to participate. Interestingly, the alpha female showed similar pushing frequencies as the most prosocial individual of the least tolerant chimpanzee group, but participation of the other bonobos was much more limited than the chimpanzees, resulting in overall lower pushing frequencies (van Leeuwen et al., 2021). This suggests that either tolerance around the set-up and/or motivation to benefit others was lower in the bonobo group than the least tolerant chimpanzee group. Although differences in the experimental context, like the inability of the chimpanzees to obtain juice after pushing and/or the more central position of the set-up in the chimpanzee enclosure, could explain part of the species differences (see also House et al., 2014), our data provide additional evidence for the need of a more nuanced view on the prosocial behaviour of bonobos (Verspeek et al., 2022 - see Chapter 6).

We found a very shallow dominance hierarchy when comparing with previous bonobo studies (Jaeggi, Stevens, et al., 2010; J. M. G. Stevens et al., 2007), which indicates an egalitarian society (De Vries et al., 2006). The highest rank was occupied by a female, but we found very similar dominance scores for the highest ranking male (Habari, son of the alpha female) and the two other adult females (Hortense and Busira). While both offspring of the alpha female (Habari and Nayoki) also pushed the button, they were not the main receivers of the juice when their mother pushed. The two other adult females received most of the juice. Because of the shallow dominance hierarchy in our study, the limited participation of bonobo males cannot only be attributed to their position in the dominance hierarchy. The lower participation of males in our study corresponds with the socio-ecological sex difference in cooperative and prosocial behaviour in bonobos. While females engage in several cooperative and prosocial interactions like coalitionary support, food sharing and bond formation, males do not (Furuichi & Ihobe, 1994; Surbeck & Hohmann, 2013; Yamamoto, 2015). Moreover, the highest pushing frequencies were observed in female-female dyads, the dyads with the most Valuable relationships. As a result, our findings not only correspond to the female-centred bonobo society but are also in line with previous results in bonobos and chimpanzees, in which food sharing and collaboration happened more often between closely bonded individuals (Cronin et al., 2014; de Waal, 1989b; Moscovice et al., 2017).

Our experimental design did not allow to discriminate between motivations or preferences underlying the pushing behaviour. Due to the lack of an additional control condition, where pushing would produce juice from a fountain outside the enclosure (cfr. van Leeuwen et al., 2021), we could not discriminate prosocial pushing form other forms of pushing behaviour like for example self-motivated pushing or pushing out of interest. Also, only few subjects participated in the experiment, resulting in a very limited sample size. However, while this study does provide information on the determinants of prosocial behaviour in bonobos, we should be careful in drawing strong conclusions. We show that when implementing experiments in a naturalistic setting, the corresponding participation may reflect the socio-ecological characteristics of the respective species. Also, even though the study group included mother-son dyads and closely bonded female-female dyads, adult bonobos pushed less frequently and more self-motivated than chimpanzees. In conclusion, we demonstrate that instead of showing heightened levels of prosociality, the dominant female monopolised the set-up and seemed to behave out of self-interest. Therefore, this study provides support for the important nuance to the existing but largely age-biased knowledge on prosocial food provisioning in bonobos (see also Verspeek et al., 2022 - see Chapter 6).

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Statement of Ethics

No animals were sacrificed or sedated for the purpose of this study. The research adhered to the legal requirements of the country in which the research was conducted (Belgium) and was approved by the Scientific Advisory Board of the Royal Zoological Society of Antwerp and the University of Antwerp (Belgium) and endorsed by the European Breeding Program for bonobos. All research complied with the ASAB guidelines (ASAB, 2020).

Author Contributions

JV, EJCvL and JMGS developed the study. Formal statistical analyses and investigation were done by JV and DWL. JV wrote the manuscript with editing from all co-authors involved.

Adult bonobos show no prosociality in both prosocial choice task and group service paradigm

Jonas Verspeek
Edwin J. C. van Leeuwen
Daan W. Laméris
Nicky Staes
Jeroen M. G. Stevens

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Abstract

Previous studies reported contrasting conclusions concerning bonobo prosociality, which are likely due to differences in the experimental design, the social dynamics among subjects and characteristics of the subjects themselves. Two hypotheses have been proposed to explain the occurrence of prosociality in animals: the cooperative breeding hypothesis and the self-domestication hypothesis. While the former predicts low levels of prosociality in bonobos because they are non-cooperative breeders, the latter predicts high levels of prosociality because self-domestication has been proposed to select for high levels of tolerance in this species. Here, we presented a group of thirteen bonobos with two platform food-provisioning tasks: the prosocial choice task (PCT) and the group service paradigm (GSP). The latter has so far never been applied to bonobos. To allow for free choice of participation and partner, we implemented both tasks in a group setting. Like in previous PCT studies, bonobos did not choose the prosocial option more often when a group member could benefit vs not benefit. In the GSP, where food provisioning is costly, only subadult bonobos showed a limited amount of food provisioning, which was much lower than what was previously reported for chimpanzees. In both experiments, adult subjects were highly motivated to obtain rewards for themselves, suggesting that bonobos behaved indifferently to the gains of group members. We suggest that previous positive food-provisioning prosociality results in bonobos are mainly driven by the behaviour of subadult subjects. The lack of prosociality in this study corresponds to the hypothesis that proactive food provisioning co-occurs with cooperative breeding and suggests that proactive prosociality might not be part of the self-domestication syndrome in bonobos.

Introduction

Non-human animals (henceforth “animals”) engage in a variety of cooperative interactions, like border patrolling, cooperative hunting, grooming, coalition formation and food sharing (Clutton-Brock, 2009a). Prosociality has been suggested as the main facilitating evolutionary driver of cooperation (Fehr & Fischbacher, 2003; Jaeggi, Burkart, & Van Schaik, 2010; J. S. Martin et al., 2021; Silk, 2012), and has been defined as “any behaviour performed by one individual to alleviate another’s need or to improve their welfare, without the actor necessarily incurring extra costs to provide these benefits” (Amici et al., 2014). It has been suggested that humans show unique levels of prosociality, including both reactive prosociality, i.e. in response to directed signals of need, and proactive prosociality, i.e. in the absence of recipient’s signals of need, because of a unique set of socio-cognitive traits that humans typically possess (Jaeggi, Burkart, & van Schaik, 2010). To gain insight into the evolutionary basis of human prosociality, and to investigate to what extent animals show comparable levels of prosociality, an increasing number of studies has investigated prosociality in animals. Most experimental prosociality studies have focused on primates (reviewed in Marshall-Pescini et al., 2016), but more recent research has also demonstrated prosociality in other species, including rodents (Hernandez-Lallement et al., 2015; Lalot, Liévin-Bazin, et al., 2021; Márquez et al., 2015; Schweinfurth & Taborsky, 2018), canids (Dale et al., 2016; Dale, Despraz, et al., 2019; Dale, Palma-Jacinto, et al., 2019; Quervel-Chaumette et al., 2015), cetaceans (Nakahara et al., 2017; Lalot, Delfour, et al., 2021), corvids (Horn et al., 2016, 2020; Massen et al., 2020), parrots (Krasheninnikova et al., 2019; Brucks and von Bayern, 2020; Laumer et al., 2021) and fish (Satoh et al., 2021). However, other studies found no evidence for prosociality (e.g. in chimpanzees (Silk et al., 2005; Vonk et al., 2008), capuchin monkeys (Drayton & Santos, 2014; Santos, 2011), cotton-top tamarins (Cronin et al., 2009), meerkats (Amici et al., 2017), corvids (Di Lascio et al., 2013; Horn et al., 2021; M. L. Lambert et al., 2017)). These contrasting findings have sparked the interest in which factors could explain the variability in the expression of prosociality. The most extensive comparative prosociality study tested 15 primate species, including humans. The results showed that the level of allomaternal care was the best predictor for the level of proactive prosociality ((Burkart et al., 2014) yet, for some nuance see (van Leeuwen, 2021)), providing evidence for the cooperative breeding hypothesis, i.e. “cooperative breeding is accompanied by psychological changes leading to greater prosociality” (Burkart et al., 2009). For cooperatively breeding to work, caretakers must proactively seek opportunities to provide food to others (Burkart & van Schaik, 2010). However, other experimental studies showed negative prosociality results in cooperatively breeding species (e.g. cotton-top tamarins (Cronin et al., 2009; J. R. Stevens, 2010), meerkats (Amici et al., 2017), carrion crows and azure-winged magpies (Horn et al., 2021)), while others also found prosociality in independently breeding species (e.g. cichlids (Satoh et al., 2021), long-tailed macaques (Massen, van den Berg, et al., 2010), capuchin monkeys (Lakshminarayanan & Santos, 2008), chimpanzees

(Melis, Warneken, et al., 2011; van Leeuwen et al., 2021; Warneken & Tomasello, 2006), bonobos (Krupenye, Tan, et al., 2018; Tan et al., 2017; Tan & Hare, 2013). This suggests that cooperative breeding is not a prerequisite for prosocial behaviour (Cronin, 2017). Also, it remains debated what social or cognitive effects cooperative breeding might have had on humans and to what extent humans are cooperative breeders (Bogin et al., 2014; Thornton et al., 2016; Thornton & Mcauliffe, 2015). Another factor that positively correlated with the level of prosociality was a high level of social tolerance, as measured by the extent of equal access to food by group members in the GSP (Burkart et al., 2014). This fits with the self-domestication hypothesis (Hare, 2017; Hare et al., 2012), which states that prosociality arises as a by-product of selection against aggression and selection for increased tolerance ((Wrangham, 2019) but see (Sánchez-Villagra & van Schaik, 2019)). Both the cooperative breeding hypothesis and the self-domestication hypothesis suggest a link between social tolerance and prosociality, but emphasize different influential factors. Since prosociality is a diverse and flexible trait (Decety et al., 2016; Dunfield et al., 2011; Tomasello & Vaish, 2012), both hypotheses may complement each other to explain different facets of prosocial behaviour rather than being mutually exclusive (Decety et al., 2016; Horn et al., 2020).

The variety of task designs, experimental contexts and reward distributions has led to a large variation in reported prosociality within and between-species (Jensen, 2016a; Marshall-Pescini et al., 2016; Tan & Hare, 2017). Two main types of experimental paradigms have been used to study prosociality in animals: the targeted helping paradigms and food provisioning tasks, each with its own advantages and disadvantages (House et al., 2014; Marshall-Pescini et al., 2016; Melis, 2018; Tennie et al., 2016). Targeted helping paradigms examine whether subjects help others in situations that they cannot resolve on their own (Yamamoto & Takimoto, 2012). They require a certain degree of perspective taking, since subjects have to understand the goals and needs of others to react to it, which could explain why sustainable targeted helping is only found in species with higher levels of such cognitive capacities like great apes, dolphins and elephants (de Waal, 2008; Yamamoto & Takimoto, 2012). In food provisioning tasks, subjects can choose whether to provide food to a recipient or not. The most commonly used food provisioning task is the cost-free prosocial choice task (PCT) (Jensen et al., 2006; Silk et al., 2005), in which subjects can choose between a selfish (1/0) and a prosocial option (1/1). Subjects gain identical payoffs for the same effort in either option, so they should prefer the prosocial option (1/1) if they have a prosocial preference. Two main approaches of the PCT exist: platforms and tokens. In the platform PCT, the two choices are presented on sliding platforms, allowing for a physical choice by the subject. In the token PCT, the two choices are represented symbolically with tokens (Amici et al., 2014; Dale et al., 2016; de Waal et al., 2008; Emigh et al., 2020; Horner et al., 2011; Krasheninnikova, Brucks, Blanc, et al., 2019).

Importantly, to allow for comprehensive comparisons of prosociality within and between species, several methodological issues should be considered. A first concern is task complexity. Subjects must understand the contingencies of the task. Some studies have incorporated contingency training phases to ensure task comprehension, but this can lead to overtraining of the subjects and an overestimation of prosocial behaviours (Jensen, 2012; Marshall-Pescini et al., 2016; Tennie et al., 2016). As an alternative, ‘knowledge’ self-tests can be incorporated to test the subject’s understanding of the task. Here, the reward distribution is changed so that subjects can access the better reward by choosing the option with the most food rewards (Burkart et al., 2007; Claidière et al., 2015; Jensen, 2016b; Tan et al., 2015). The PCT has been suggested to be cognitively too demanding (Burkart & Rueth, 2013; Claidière et al., 2015; Melis, 2018; Tan et al., 2015). Therefore, an alternative version has been proposed: the group service paradigm (GSP) (Burkart et al., 2014; Burkart & van Schaik, 2013; Cronin et al., 2010; House et al., 2014; van Leeuwen et al., 2021). In this costly version of the PCT, subjects can choose whether to deliver food only to a partner or to provide no food at all, which has also been referred to as a single-choice (go) task (Jensen, 2016b). The GSP is considered as cognitively less demanding compared to the PCT, because subjects only need to consider the payoff of one food item (instead of three in the PCT) (Burkart et al., 2014). The adjusted payoffs in the GSP essentially turn the standard PCT into an instrumental helping task, since only recipients receive a reward at a low cost for the subject, i.e. the energetic cost to pull the handle (House et al., 2014; Tan et al., 2015). A second limitation of most PCTs and helping studies, is that mainly preselected, compatible or tolerant dyads have been tested, often with the deliberate intent to increase the chance to detect prosociality (e.g., Melis, Schneider and Tomasello, 2011; Taglialatela et al., 2020; Nolte and Call, 2021). However, several studies showed the importance of free partner choice in experimental studies (Cronin et al., 2017; Melis et al., 2008; Suchak et al., 2014; van Leeuwen et al., 2021). Therefore, experiments that maintain the social group dynamics during testing should be implemented to improve the socio-ecological validity and make biologically relevant conclusions (Cronin et al., 2017; House et al., 2014; Marshall-Pescini et al., 2016; Massen et al., 2019). More recently, the GSP has successfully been implemented in a group setting in a variety of species (Burkart et al., 2014; Burkart & van Schaik, 2013; Horn et al., 2016, 2020; J. S. Martin et al., 2021; van Leeuwen et al., 2021), providing additional evidence for the importance of free choice of partner (J. S. Martin et al., 2021).

The bonobo, one of humans’ closest living relatives, is a very interesting independently breeding species to investigate the two hypotheses regarding the evolutionary origins of prosociality. Most prosociality studies in great apes have focused on chimpanzees because, among other things, they are more numerous in captivity (Melis, 2018; Tennie et al., 2016). Bonobos are stated to be more peaceful, tolerant and cooperative than chimpanzees (Hare, 2017; Hare et al., 2012; Maclean, 2016) and have been suggested to have undergone the process of self-domestication (Hare, 2017; Hare et al., 2012). Because of this, and their close genetic relatedness to humans, they have been explicitly proposed as an ideal species to study the biological predispositions of prosociality in humans (Hare, 2017; Hare & Yamamoto, 2017; Maclean, 2016; Tan & Hare, 2017). Experimental studies of prosocial behaviour in bonobos, however, are rare and have so far yielded mixed results. Moreover, all these studies have worked with preselected instead of freely interacting dyads. Bonobos showed targeted helping in some (Hare & Kwetuenda, 2010; Nolte & Call, 2021; Tan et al., 2017; Tan & Hare, 2013), but not all studies (Bullinger et al., 2013; Liebal et al., 2014). They voluntarily handed food items to others (Krupenye, Tan, et al., 2018), but they did not behave prosocially in a token and platform variant of the PCT (Amici et al., 2014; Tan et al., 2015). To date, bonobos have not been tested on the GSP.

Our aim was therefore to study bonobo prosociality using both the PCT and the GSP in the same bonobo group. This study will be the first to implement the GSP in bonobos, and will contribute to the cross-species comparative framework of prosociality research that employs an identical experimental paradigm (Burkart et al., 2014; Horn et al., 2020). Using both the PCT and GSP approach, we aim to rule out that cognitive limitations resulting from PCT complexity are at the base of negative results in previous bonobo studies (Burkart & Rueth, 2013; Melis, 2018; Tan et al., 2015). We will, for the first time in bonobos, use the stacked platform PCT rather than the horizontal platform PCT that has been previously used but showed negative results (Amici et al., 2014; Tan et al., 2015). It has been suggested that the horizontal platform PCT task can cause false positives through local enhancement, which can be avoided if the rewards are stacked in a stacked platform PCT (Amici et al., 2014; Tan et al., 2015). Finally, we implement both tasks in group context rather than in preselected dyads, to allow for free choice of participation, resulting in more naturalistic partner choices that will allow for more biologically relevant conclusions (Cronin et al., 2017). Based on the cooperative breeding hypothesis, low to intermediate levels of proactive prosociality are expected in bonobos given that they are an independently breeding species, while the self-domestication hypothesis predicts high levels of prosociality in this species if prosociality indeed co-evolved with selection for higher tolerance and lower aggression.

Materials & Methods

Subjects & Housing

This study included 13 bonobos (6M:7F) housed at Zoo Planckendael (Belgium) (mean age 15.77 ± 3.12 years, Table 6.1 See also table 9.1 Overview of the study subjects p 144). They were housed in an indoor enclosure consisting of ten interconnected rooms of varying sizes (from 11 to 100m² total size: 422m²). No animals were separated for testing. The test apparatus was presented in a central room (35m²), which could be directly accessed from six adjacent rooms. During testing, all animals had access to the apparatus, and could freely move through the entire building. Although we attempted to increase participation by calling the subjects to the central room, participation was always voluntarily. Therefore, individuals varied substantially in the number of trials they participated in (see below). The testing apparatus, baiting process, distribution of food rewards and reward consumption were always visible to the bonobos. To maximise subject's motivation, we used grape halves as highly favoured food, as this was confirmed to be the preferred food in a previous study (Verspeek & Stevens, 2020 - see Chapter 2). JV videotaped and coded all recordings. No animals were sacrificed or sedated for the purpose of this study. This non-invasive research adhered to the legal requirements of the country in which the research was conducted (Belgium) and was approved by the Scientific Advisory Board of the Royal Zoological Society of Antwerp (EC-3/SGZ(10-12-19)) and the University of Antwerp (Belgium) and endorsed by the European Breeding Program for bonobos. All research complied with the ASAB guidelines (ASAB, 2020).

Setup and procedure

Experiment 1: Prosocial choice task (PCT)

The PCT set-up was based on the original chimpanzee study (Silk et al., 2005): subjects could deliver benefits to group members at no cost for themselves (Jensen et al., 2006; Silk et al., 2005). They could choose between a prosocial option, providing a reward to subject and receiver (1/1) and a selfish option, where only the subject obtains a food reward (1/0). The apparatus consisted of two platforms, each with one handle attached to it, that were stacked on top of each other and which were colour coded to improve discrimination by the subjects (Figure 6.1). When a subject pulled a handle, the corresponding platform moved forward and brought the food rewards within reach.

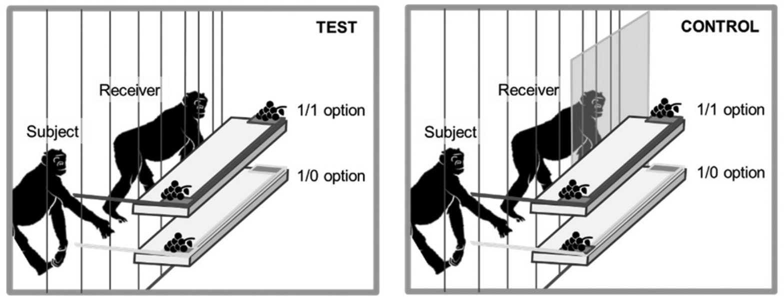

Fig. 6.1 Schematic drawing of the PCT set-up. The handle can be pulled to bring the platform within reach. Each trial, only one bar could be pulled. In the control sessions, the receiver's reward was unreachable due to a plexiglass panel (online version in colour).

Subjects were able to only reach food rewards on their side since the food item on the receiver's side of the tray was more than two arm's lengths (approximately 3m) away from the pulling side. Monopolisation of both food items by the subject was impossible because pulling of the handle, repositioning to obtain the reward through the mesh and eating the reward took longer than it took the receiver to obtain its reward. Prior to the testing, we included a knowledge self-test to show that each subject could maximise its own benefit (Jensen, 2016b; Marshall-Pescini et al., 2016; Tan et al., 2015). In the self-test, subjects were tested individually and were presented with identical options as in the actual experiment (i.e., prosocial 1/1 and selfish 1/0, counterbalanced across platforms) but had the possibility to access both sides of the tray. In this case, choosing the 1/1 option would result in an extra reward, because they could reach and eat the food items at both sides. Only seven bonobos that chose the 1/1 option in 8 of 10 consecutive trials were considered to pass the self-test and were included as subjects in the actual experiment (see Table 6.1). All bonobos acted as receivers throughout the entire experiment. Therefore, although only seven bonobos acted as subjects, they participated with the different potential receivers, resulting in 49 unique (unidirectional) pairs (mean 7 ± 2 partners per subject).

Table 6.1 Subject information of the prosocial choice task

Individual	Sex	Age[a]	Prosocial choice task Number of trials Test	 Control	Group service paradigm Amount of pulls Test	 Control	 Deliveries
Hortense°	Female	41	-	-	0	0	-
Banya°+	Female	29	-	-	-	-	-
Vifijo°	Male	25	-	-	0	0	-
Djanoa	Female	24	90	20	4	0	0
Zamba°	Male	21	-	-	0	0	-
Busira	Female	15	103	19	0	0	-
Kianga	Female	14	118	20	5	0	0
Habari	Male	13	99	20	10	0	0
Nayoki	Female	7	50	3	32	1	2
Mokonzi	Male	6	12	20	14	1	1
Kikongo	Male	5	22	20	38	0	5
Moko°+	Male	3	-	-	-	-	-
Sanza°+	Female	2	-	-	-	-	-

[a] Individual's age when the study took place, based on the studbook data (Stevens & Pereboom, 2020)
°Individuals that did not pass the training criterion to act as a subject in the PCT
+Individuals that did not pass the training criterion to act as a subject in the GSP
Names in *italic*: individuals younger than 8 years were considered as subadults

The PCT was conducted during twelve different sessions, in which subjects could freely choose to participate. Therefore, the number of trials per session differed between sessions as individuals varied in their participation levels between sessions. Before each trial, the handles were pulled back and the platforms were baited. Trials started as soon as the experimenter, who was seated behind the apparatus, made the handles available by pushing the handles forward. In each trial, subjects could only choose one option because the space between both handles made it impossible for the bonobos to grab them with one hand to pull and because the other handle was pulled back as soon as the subject chose one option. To make sure that only one animal at a time could act as a subject, and to increase the chance of only testing one receiver, handles were only made available when one individual was present at the subject side and another individual sat in front of the receiver side of the apparatus. The experiment consisted of two types of sessions: test sessions and control sessions. Over ten test sessions, each bonobo had the possibility to act as a subject in maximal 20 trials with each receiver of the group (a maximum of 240 trials in total). In the two control sessions, the receiver side of the apparatus was positioned behind a plexiglass panel to block access to the food on the receiver's side. Control trials were also freely accessible and each subject could participate in maximal 20 trials. The two control sessions were conducted after the ten test sessions to avoid that subjects would lose interest in the receiver's side of the apparatus. The top/bottom position of the 1/1 option was randomised and counterbalanced across test and control trials. No trials were excluded from the analyses.

Experiment 2: Group service paradigm (GSP)

We copied the setup of the original GSP studies (Burkart et al., 2014; Burkart & van Schaik, 2013). Subjects could choose to either pull and deliver a grape half to a group member or not pull and provide nothing (Figure 6.2). The apparatus consisted of one slidable platform with a handle at one side of the platform. When a subject pulled the handle, the platform moved within reach. As soon as the subject released the handle, the platform slid back out of reach due to the attached counterweight. To deliver food to a receiver, a subject had to pull the handle and keep it in place. During test trials, the distance between the handle and the grape was more than two arm's lengths, making it impossible for a subject to both pull and obtain the grape (cfr., Burkart and Van Schaik, 2013; Burkart et al., 2014). The only way to obtain food was when another individual pulled and held onto the handle (0/1).

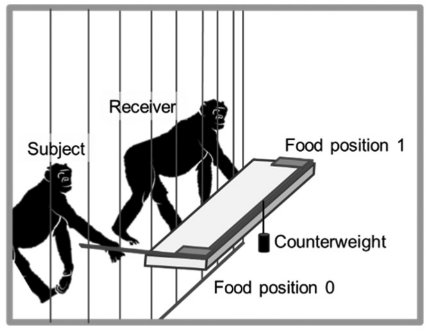

Fig. 6.2 Schematic drawing of the GSP set-up. The handle can be pulled to bring the platform within reach. When the handle is released, the platform slides back due to the counterweight. Food can be placed on position 0 (motivational trials) and 1 (test trials). Food in position 1 can only be obtained by an individual if another individual pulls the handle and holds it in place (online version in colour).

Prior to testing, we included a knowledge self-test. In this self-test, the distance between the handle and the grape was only one arm length, allowing subjects to pull and obtain the grape themselves. Subjects passed the self-test if they were able to pull the handle, hold it and obtain the grape in at least seven trials during one session (cfr., Burkart and Van Schaik, 2013) (see Table 6.1). All bonobos acted as receivers throughout the entire experiment.

During the actual experiment, we alternated five test sessions with five control sessions (cfr., Burkart and Van Schaik, 2013; Burkart et al., 2014). Each test session consisted of 70 test trials in which a grape half was placed on food position 1 (Figure 6.2). Trials ended either when the grape was obtained, or after 1 minute passed since the beginning of the trial. If the grape piece was not taken, the experimenter started the next trial by holding the grape up, attracting the bonobos' attention and replacing the grape on food position 1. Control sessions were implemented to make sure that the bonobos did not pull simply to play or to explore the apparatus. Each control session consisted of 35 trials. Instead of placing a grape, the experimenter held up a stick, touched the apparatus at food position 1 and drew the bonobos' attention verbally. To keep the individuals interested throughout the test and control sessions, every 6th trial a motivation trial was introduced. In motivation trials, a grape was placed on food position 0 and could be obtained by the pulling subject, resulting in a selfish outcome (cfr., Burkart and Van Schaik, 2013; Burkart et al., 2014). Because of practical restrictions, we could not conduct the blocked control phase (phase V of the original GSP studies (Burkart et al., 2014; Burkart & van Schaik, 2013)).

Coding and analyses

To determine whether bonobos behaved prosocially in the PCT, we ran a logistic regression analysis using a generalised linear mixed model (GLMM) with binomial error structure and logit link function using the R package "Ime4"(Bates et al., 2014). The response variable was the binary variable that captured whether the prosocial 1/1 choice was chosen (coded as "1") or not (coded as "0"). To investigate whether bonobos pulled more often in the test than control trials, we included 'condition' (control vs test trial) as fixed factor. We also added position as a fixed effect to determine whether the 'position' (top vs bottom) of the receiver's reward influenced the choice of the subject. Subject identity was added as a random intercept effect to control for the non-independence of observations. We used likelihood ratio tests (R function anova with argument "test" set to "Chisq" (Dobson & Barnett, 2018)) to test the fixed effects by excluding each predictor at a time and comparing this reduced model to the respective full model using the function drop1 (Barr et al., 2013). To assess the influence of possible collinearity between independent variables, the variance inflation factors (VIF) of each model were evaluated with the function vif of the R package "car" (Fox & Weisberg, 2019). None of the variables were rejected from the model (all VIF > 5) (O'Brien, 2007). We used diagnostic plots to examine assumptions of normality and homogeneity and tested uniformity and dispersion of the residuals using the "DHARMa" package (Hartig, 2020). To check whether our conclusions were robust to different forms of analyses, we also repeated the PCT analyses using Wilcoxon signed-ranks tests.

To test whether bonobos behaved prosocially in the GSP, we assessed whether subjects pulled more often during the test versus the control trials using Wilcoxon signed-ranks test. Next, we analysed the trials in which subjects delivered food to group members, i.e., where the handle was pulled long enough to allow recipients to take the grape. All analyses were performed using R version 4.0.2 (R Core Team, 2016).

Results

Prosocial choice task

Bonobos chose the prosocial option on average in 53% (s.e. = 1.4) of the test trials (when receivers could obtain the reward) and in 49% (s.e. = 3.1) of the control trials (when no receiver could obtain the reward) (Fig. 6.3a). Overall, the logistic regression model showed that the likelihood of choosing the prosocial option was not significantly influenced by condition ($\chi^2 = 0.21$, df = 1, $p = 0.65$), but by position of the food reward ($\chi^2 = 50.32$, df = 1, $p < 0.001$) (Table 6.2). This means that subjects did not choose the prosocial option more often in the test than control trials and that the likelihood of choosing the prosocial option was affected by the position of the reward at the receiver's side. Overall, subjects were more likely to choose the prosocial option when it was positioned on the bottom platform (Table 6.2, Fig. 6.4). Also at the individual level, none of the actors chose the 1/1 option more often in the test than control trials (all $p > 0.05$) (Fig. 6.4). We did find that for some individuals the likelihood of choosing the 1/1 option was significantly influenced by the position of the receiver's reward, indicating that these individuals preferred one of both handles of the apparatus (Table 6.3, Fig. 6.4).

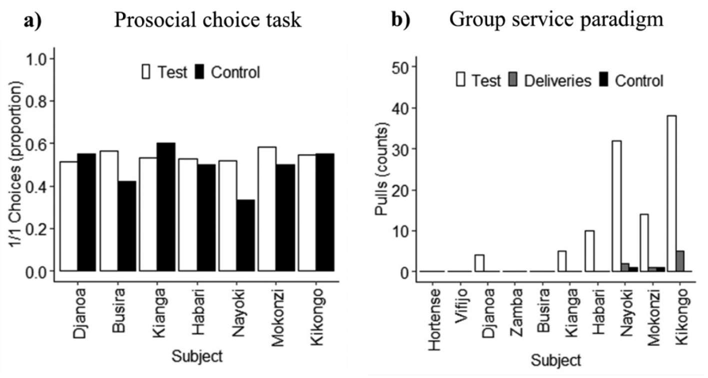

Fig. 6.3 Prosociality results. a) Proportion of 1/1 choices made by each subject in the PCT. Black bars represent control trials, white bars represent test trials. None of the subjects chose the 1/1 option more often in the test than the control trials (GLMM's: all $p > 0.05$; see Table 6.3); b) Total amount of pulls by each subject in the group service paradigm. Black bars represent control trials, grey bars represent deliveries and white bars represent test trials. Subjects pulled significantly more often during test than control trials ($p < 0.05$, Wilcoxon signed rank test).

Table 6.2 Factors that influenced the likelihood of choosing the 1/1 option in the PCT

Factor	Estimate	Standard error	z-value	p-value	Odds ratio	95 % CI	
						Lower	Upper
Condition	0.097	0.212	0.457	0.647	0.908	0.6	1.37
Position	-1.204	0.170	-7.094	<0.001	3.33	2.39	4.65

Variables are coded so that odds ratios exceed 1 for condition if actors were more likely to choose the 1/1 option when the receiver's reward was blocked than when the receiver's reward could be obtained by group members. Position was coded so that odds ratios larger than 1 indicate that actors were more likely to choose 1/1 option when positioned on the bottom platform of the set-up.

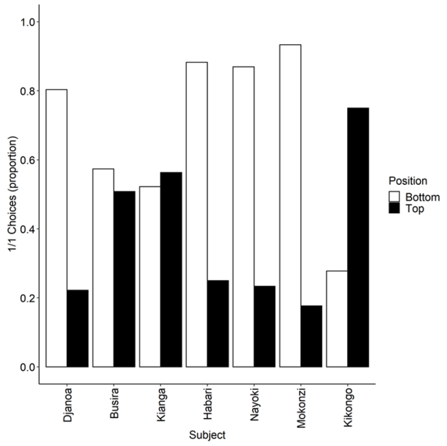

Fig. 6.4 Proportion of 1/1 choices made by each subject in the PCT. White bars represent trials where the prosocial option (1/1) was positioned on the lower platform and black bars represent trials where the prosocial option was positioned on the upper platform.

Table 6.3 Factors that influenced the likelihood of choosing the 1/1 option in the PCT for each subject.

Subject	Factor	Estimate	Standard error	z-value	p-value	Odds Ratio	95% CI	
							Lower	Upper
Busira	Condition	0.57	0.51	-1.12	0.26	0.57	0.21	1.53
	Position	-0.26	0.37	0.7	0.48	1.29	0.63	2.65
Djanoa	Condition	-0.28	0.61	0.45	0.65	1.32	0.40	4.35
	Position	-2.67	0.47	5.67	<0.001	14.4	5.74	36.3
Habari	Condition	0.28	0.64	-0.44	0.66	0.76	0.22	2.66
	Position	-3.12	0.52	6.02	<0.001	22.8	8.23	63.0
Kianga	Condition	-0.27	0.49	0.55	0.58	1.31	0.50	3.45
	Position	0.17	0.34	-0.49	0.62	0.85	0.43	1.65
Kikongo	Condition	-0.37	0.72	0.51	0.61	1.45	0.35	5.99
	Position	2.12	0.73	-2.92	0.004	0.12	0.03	0.50
Mokonzi	Condition	1.48	1.27	-1.17	0.24	0.23	0.02	2.75
	Position	-4.65	1.41	3.30	0.001	104	6.62	1646
Nayoki	Condition	0.82	1.63	-0.51	0.61	0.44	0.02	10.2
	Position	-3.09	0.76	4.07	<0.001	22.0	4.97	97.2

Variables are coded so that odds ratios exceed 1 for condition if actors were more likely to choose the 1/1 option when the receiver's reward could be obtained by group members than when the receiver's reward was blocked. Position was coded so that odds ratios larger than 1 indicate that actors were more likely to choose 1/1 option when positioned on the bottom platform of the set-up.

Additional analyses to confirm the results of the GLMM of the PCT study

To show that the results of the generalised mixed models are not the result of underpowered analyses, we conducted additional analyses. We used Wilcoxon signed rank tests to compare the preferences between and within conditions. We found that subjects did not prefer the prosocial 1/1 to the selfish 1/0 option in the test nor the control trials (test: mean = 0.53 ± 0.02; self: mean = 0.47 ± 0.02; N = 7, Z = -1.54, p = 0.108; control: mean = 0.49 ± 0.03; self: mean = 0.51 ± 0.03; N = 7, Z = 0, p = 1, Wilcoxon signed-ranks). Also, the proportion of prosocial choices 1/1 did not differ between the test and control trials (N = 7, Z = -0.76, p = 0.447, Wilcoxon signed-ranks test). The subjects' preferences did not differ between the first 20 and the last 20 test trials (first: mean = 0.44 ± 0.04; last: mean = 0.59 ± 0.05; N = 7, Z = 1.90, p = 0.06, Wilcoxon signed rank test). These results show that subjects did not prefer the prosocial option to the selfish option in both the test and control trials. Although the GLMM results show that on a trial basis, some of the subjects preferred one of both handles, the position of the prosocial option was counterbalanced between the top and bottom platform, overcoming any false positives due to the handle preference. Therefore, these results show that bonobos did not behave prosocially in the PCT.

We also ran an additional GLMM, which was identical to the other model but also included the interaction term between condition and position. The logistic regression model showed that the likelihood of choosing the prosocial 1/1 option was significantly influenced by the interaction term between condition and position ($\chi^2 = 7.78$, df = 1, p = 0.005). The model showed that subjects were more likely to choose the bottom handle than the top handle in the test and control trials (control: p < 0.001; test: p < 0.001) and that the odds of doing so were bigger in the control than the test trials (Table 6.4).

Table 6.4 Factors that influenced the likelihood of choosing the 1/1 option in the PCT

Factor		Probability	Standard error	z-value	p-value	Odds ratio	95 % CI	
							Lower	Upper
Condition								
Test	Bottom	0.660	0.031	5.191	< 0.001	2.63	1.83	3.8
	Top	0.42	0.03					
Control	Bottom	0.780	0.054	5.336	< 0.001	9.57	4.18	22.0
	Top	0.270	0.031					

Position was coded so that odds ratios larger than 1 indicate that actors were more likely to choose 1/1 option when positioned on the bottom platform of the set-up.

Pulling behaviour in the first 20 test trials

In the PCT study, we included much more test than control trials. To determine whether this may have influenced our results, we conducted the same analyses only including the first 20 trials of each subject. For Mokonzi only 12 trials were included as he only participated in 12 test trials. Bonobos chose the prosocial 1/1 option on average 52% (s.e. = 1.8) in the first 20 test trials. The logistic regression model showed that the likelihood of choosing the prosocial 1/1 option was significantly influenced by the interaction between condition and position ($\chi^2 = 10.33$, df = 1, p = 0.001). Post-hoc analysis showed that in the control trials, subjects were more likely to choose the lower handle than the upper handle (p < 0.001), while in the test trials the bonobos did not choose one handle more often than the other (p = 0.18) (Fig. 6.5).

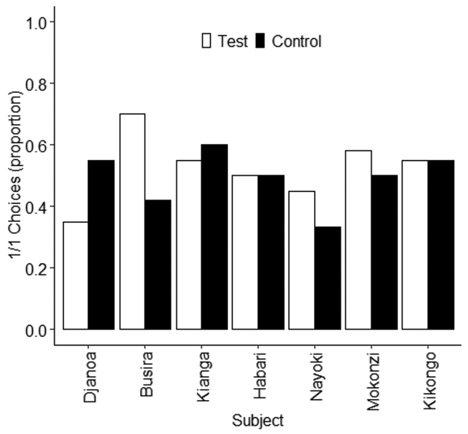

Fig. 6.5 Proportion of 1/1 choices made by each subject in all control trials and the first 20 test trials of the PCT. Black bars represent control trials, white bars represent test trials.

Group service paradigm

During motivation trials, all food items were taken. Two females monopolised the apparatus and obtained all the grapes. During the control and test sessions, bonobos rarely pulled the platform (Fig. 6.6).

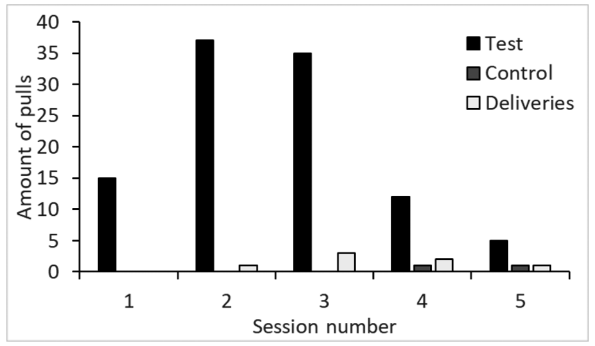

Fig. 6.6 Number of pulls in test and control session and the number of deliveries across the five sessions. Black bars represent pulls in the test sessions, grey bars represent pulls in the control sessions and white bars represent food deliveries.

Table 6.1 shows the number of pulls in test and control trials and the amount of food deliveries for each of the thirteen bonobos. Out of the ten bonobos, that had passed the training criterium, four bonobos never pulled the handle during the experiment. Out of the six subjects that did pull the handle, one adolescent and one juvenile also pulled once during a control trial. Most pulling was done by the adolescent female and two juvenile males (Fig. 6.3b). Overall, subjects pulled more often in the test than the control trials (test: mean = 10.3 ± 5.26; control: mean = 0.2 ± 0.16; N = 10, Z = 0.66, p = 0.04, Wilcoxon signed ranks test), suggesting that pulling was deliberate. Subjects pulled the handle in 29.4% of the test trials and in 1.1% of the control trials. In only 2% of all test trials (8 out of 350), however, grapes were successfully delivered to another individual. All successful deliveries were performed by the adolescent female and two juvenile males. One food item was delivered from the adolescent female to her mother, while seven deliveries happened between unrelated individuals (Table 6.5).

Table 6.5 Distribution of successful food deliveries for each dyad (food given vs received)

	DJ	KG	BY	HO	HB	BS	ZA	NY	VI	MZ	KK	MO	SA	Total given
DJ	-	0	0	0	0	0	0	0	0	0	0	0	0	0
KG	0	-	0	0	0	0	0	0	0	0	0	0	0	0
BY	0	0	-	0	0	0	0	0	0	0	0	0	0	0
HO	0	0	0	-	0	0	0	0	0	0	0	0	0	0
HB	0	0	0	0	-	0	0	0	0	0	0	0	0	0
BS	0	0	0	0	0	-	0	0	0	0	0	0	0	0
ZA	0	0	0	0	0	0	-	0	0	0	0	0	0	0
NY	1	0	0	0	0	0	0	-	0	0	0	1	0	2
VI	0	0	0	0	0	0	0	0	-	0	0	0	0	0
MZ	1	0	0	0	0	0	0	0	0	-	0	0	0	1
KK	0	0	0	0	2	0	0	3	0	0	-	0	0	4
MO	0	0	0	0	0	0	0	0	0	0	0	-	0	0
SA	0	0	0	0	0	0	0	0	0	0	0	0	-	0
Total received	2	0	0	0	1	0	0	3	0	0	0	1	0	7

Subjects are ordered according to their dominance rank. HO= Hortense, VI = Vifijo, ZA = Zamba, KK = Kikongo, BY = Banya, MO = Mokonzi, DJ = Djanoa, HB = Habari, NY = Nayoki, BU = Busira, SA = Sanza, KI = Kikongo, MK = Moko

To investigate whether the limited amount of pulls and successful deliveries was not result of the absence of possible receivers, we collected data on the number of individuals in the testing room throughout the experiment. We used instantaneous group scan sampling with a fixed time interval of five minutes and collected data on the location of each of the individuals. For each instantaneous scan sample, we calculated the proportion of individuals that was present in the testing room. We found that in each scan sample during the test trials, at least 30% of the individuals, i.e. 4 potential participants, were present in the testing room (Figure 6.7). These data show that although potential receivers were present, subjects were not motivated to donate food items.

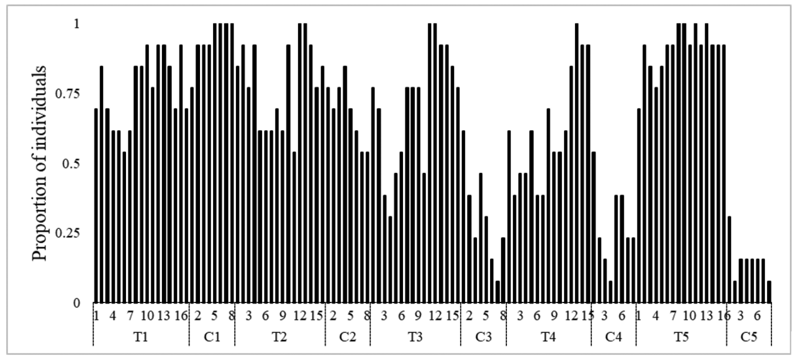

Fig. 6.7 Proportion of individuals that was present during each instantaneous scan sample (T = test session, C = control session).

Discussion

Overall, the adult bonobos in this social group did not behave prosocially in two free choice group experiments. The adult bonobos were clearly motivated to obtain a reward for themselves the PCT and GSP but they did not choose to provision partners above chance level; in the PCT, they did not pull more often in the test than the control sessions; and in the GSP, they never delivered food items. This suggests that in these food provisioning tasks, bonobos did not behave prosocially, but were rather indifferent to the gains of group members.

In the stacked platform PCT, bonobos did not choose the prosocial option more often in the test than the control trials. Our results therefore support previous studies that showed a lack of prosociality in bonobos in the horizontal and token PCT (Amici et al., 2014; Tan et al., 2015). During the test trials, the bonobos in our study chose the prosocial option in roughly half of the trials, which is higher than what a previous horizontal PCT study reported (± 18%) but much lower than the levels in another horizontal PCT study (± 79%) (Tan et al., 2015), which could be attributable to intergroup differences in prosocial tendencies between these bonobo populations. However, it is noteworthy that in the latter study, subjects chose the prosocial option in ± 79% of the test and in ± 84% of the control trials, which is likely the result of local enhancement due to overtraining during the self-regard pre-test (Tan et al., 2015).

Our findings are also comparable with PCT studies that showed an absence of prosociality in chimpanzees (Claidière et al., 2015; Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008). Also in chimpanzees, the likelihood of choosing the prosocial 1/1 option was influenced by position of the reward, but not condition of the trials (Silk et al., 2005). One of the criticisms of the PCT is that it might be cognitively too demanding, leading to false results (Melis, 2018; Tan et al., 2015). This would suggest that subjects in our study understood how to obtain food for themselves, but not that they could deliver rewards to group members. However, the self-test phase showed that each of the subjects understood the consequences of each choice. The implementation of the stacked platform PCT in our study not only allowed for the knowledge self-test, it also controlled for any location bias, avoiding false positives due to local enhancement (Amici et al., 2014; Tan et al., 2015).

We found that in five out of seven bonobos, the prosocial option was more likely to be chosen when the receiver's reward was positioned on a specific tray, meaning that these subjects developed a preference for one of the two handles. These choices seemed to be individualistic, i.e., not all seven subjects showed the same preference. Four of the bonobos chose the prosocial 1/1 option more often when positioned on the lower tray; one individual chose the prosocial 1/1 option more often when positioned on the upper tray, and two subjects did not show any preference for the upper or lower tray. The individual handle preference combined with the benefits of using the stacked platform PCT set-up (Tan et al., 2015), leads us to conclude that neither overtraining of the bonobos nor local enhancement explained the lack of prosociality in the PCT. Note that individual preferences for one handle over the other might have made it more difficult for the bonobos to show their potentially (non-)prosocial tendencies.

Using the GSP for the first time in bonobos, we found that there were no deliveries by adults, but subadult bonobos on several occasions delivered food to their group members. All subjects pulled more often in the test than control trials, suggesting that they pulled deliberately. Although subjects pulled the handle in 29.4% of the trials, food provisioning was low (2% over all five sessions and 2.02% during the last two sessions). This rate is much lower than reported for chimpanzees in the original GSP study (12% during the last two sessions; (Burkart et al., 2014)). This suggests that bonobos in our study group behaved much less prosocially in the GSP compared to chimpanzees. Subjects needed to pull the handle long enough to deliver the grape to a conspecific. Similar to the capuchins and the macaques in the original GSP study, the majority of pulls by the bonobos did not result in a delivery (Burkart and Van Schaik, 2013). In most events, subjects stopped pulling and released the handle before the receiver could obtain the reward. These results support the conclusion that while the bonobos were able to benefit group members, only subadults persisted in the pulling behaviour until the food was delivered in a limited amount of trials. One explanation for why the adult bonobos did not provide food to group members in this task, could be that behaving prosocially in the GSP creates inequity between subject and receiver. By refraining from providing food to group members, adult bonobos may have avoided the emergence of inequity, to which they might be averse (Verspeek & Stevens, in prep.- see Chapter 7). The motivation to provide benefits to others is then lower than the motivation to avoid inequity. Although a previous study found no conclusive evidence that bonobos showed aversion to inequity (Bräuer et al., 2009), our own results in this study group show that the bonobos react to receiving less than a partner in a token exchange task and refuse to participate (Verspeek & Stevens, in prep. - see Chapter 7). Although more GSP and inequity studies are needed, this hypothesis is supported by the findings that primate species showing the lowest levels of proactive prosociality in the GSP (chimpanzees, macaques, capuchin monkeys, bonobos) also responded to inequity (Brosnan and de Waal, 2003; Van Wolkenten, Brosnan and De Waal, 2007; Brosnan et al., 2010; Takimoto, Kuroshima and Fujita, 2010; Massen et al., 2012; Hopper et al., 2014 but see Bräuer, Call and Tomasello, 2009), while species that showed relatively high levels of proactive prosociality in the GSP (e.g. callitrichids) were not found to be averse to inequity (reviewed in Brosnan and de Waal, 2014).

Overall, our study shows that bonobos did not take advantage of the opportunity to deliver food rewards to group members, even at little cost for themselves. Our findings are therefore comparable to previous food-based studies that tested for prosociality in the Pan species implemented food provisioning experiments in preselected pairs of chimpanzees (dyadic level: Silk et al., 2005; Jensen et al., 2006; Vonk et al., 2008; Amici, Visalberghi and Call, 2014; Tan, Kwetuenda and Hare, 2015; group level: Burkart et al., 2014; House et al., 2014 but see van Leeuwen et al., 2021). This seems surprising and controversial, since bonobos have been observed sharing food with related and unrelated individuals in the wild (e.g., White, 1994; Hohmann and Fruth, 1996; Hirata et al., 2010; Yamamoto, 2015) and behaved prosocially in several other experimental studies (e.g. Hare et al., 2007; Hare and Kwetuenda, 2010; Tan and Hare, 2013). We propose two possible explanations for these contrasting findings. First, in the majority of the food sharing events, food was acquired by stealing and tolerated theft (i.e. the owner of a food item does not facilitate taking but tolerates the recipient's taking) (Jaeggi, Stevens, et al., 2010; Yamamoto, 2015), and shared food items were usually abundant or too large to consume by one individual. In situations with a surplus of food, owners can afford to pay a little cost by sharing only small portions of their food item (Yamamoto, 2015), while in food provisioning studies the limited food rewards may induce a more competitive context (Jaeggi, Burkart, & Van Schaik, 2010). Second, the contrasting findings in the prosociality experiments in bonobos may be caused by an age effect. Previous experimental studies that reported prosociality in bonobos mainly included subadults and even juveniles in their helping and food sharing experiments (Hare et al., 2007; Hare & Kwetuenda, 2010; Tan & Hare, 2013). Additional instrumental helping studies that also reported prosocial tool and food transfers only tested juvenile, adolescent and young adult bonobos (Krupenye, Tan, et al., 2018; Nolte & Call, 2021; Tan & Hare, 2017). Moreover, studies that replicated some of the experimental designs in a more diverse bonobo group (i.e. consisting of individuals of a wider age range and different backgrounds), failed to find the previously reported high levels of social tolerance, cofeeding and prosociality in bonobos (Bullinger et al., 2013; Cronin et al., 2015; Jaeggi, Stevens, et al., 2010) (for an overview of the ages of the study subjects see table 6.6 – p 103). Our data support this age effect hypothesis, since most pulling and prosocial acts in our study were done by subadults and juveniles. This corresponds with studies that suggested that younger bonobos may have higher other-regarding levels (Clay & de Waal, 2013a) and higher tolerance levels (Cronin et al., 2015), perhaps as a result of their lower development of inhibitory control (Clay & de Waal, 2013b). The lower inhibitory control could also explain why in the door-opening paradigm, subadults and juveniles behaved more prosocially (Hare & Kwetuenda, 2010) than older bonobos (Bullinger et al., 2013). Although the subadults were able to differentiate between the test and control trials in the GSP, their lower levels of inhibitory control might make them more prone to local enhancement when food is involved (test trials), thus resulting in the food deliveries. This study does not allow to differentiate prosociality from such alternative explanations for the pulling behaviour in subadults, because of the missing blocked-control (phase V in (Burkart et al., 2014; Burkart & van Schaik, 2013)). However, the very low levels of food deliveries do provide evidence for a low motivation to provision group members. Future studies with more diverse and a larger number of study subjects are needed to confirm our findings on the low levels of food provisioning in adult bonobos and to specifically address the possible age effect on bonobos' prosocial behaviour. Also, although the GSP does not allow to investigate the motivation behind pulling behaviour, it is possible that the limited pulling by adult bonobos could have served as re-examinations of the task contingencies. After they started pulling, their self-inhibiting capacity might have allowed them to stop holding on the handle as soon as they realised that a conspecific would benefit from their action, hence avoiding food delivery and more frequent pulling. This would mean that the adult bonobos actively chose not to provide a resource to any of their group members.

An additional limitation of this study was that the experimental procedures involved high levels of manipulation by the experimenter. Although we aimed to use an open test setting that allowed free choice of participation, the current paradigms may have influenced naturally occurring patterns and therefore participation of certain individuals. Ideally, open group experiments should use an apparatus with automatic baiting to avoid any experimenter bias (e.g. see (van Leeuwen et al., 2021)). Also, because the experiments were performed in a group setting, some pairs of subjects never participated. This could be the result of a lack of motivation to participate but is also likely that competition or interference by group members may have hindered participation of certain subjects. Only one receiver could obtain the reward, but we cannot rule out that the presence of multiple possible receivers in the testing room may have influenced the subject and receiver behaviour. Providing multiple apparatuses at the same time may overcome this reduced participation in a group setting (Cronin et al., 2017).

Despite the popular view of the prosocial bonobo, the implementation of both paradigms shows a lack of prosociality in food-based experiments in this group of bonobos. The adult bonobos did not show prosociality in a context where behaving prosocially did not incur a cost to the actor (PCT) and neither did they in a cognitively less demanding food provisioning task (GSP). By including the self-regard pre-tests and the counterbalanced trials in the stacked PCT set-up, we overcame the suggested constraints intrinsic to the PCT (Tan et al., 2015). In addition, although the GSP payoff is suggested to resemble instrumental helping paradigms (Tan et al., 2015), our findings contrast with the positive targeted helping of young bonobos (e.g., Hare and Kwetuenda, 2010; Tan and Hare, 2013; Tan, Ariely and Hare, 2017), while they do correspond with the negative helping results in older bonobo groups (Bullinger et al., 2013; Liebal et al., 2014).

Therefore, our results correspond with the predictions of the cooperative breeding hypothesis, as the non-cooperatively breeding bonobos show a very limited amount of proactive prosociality (Burkart et al., 2014). It also suggests that although bonobos do show signatures of self-domestication (Hare, 2017; Hare et al., 2012), proactive prosociality might not be part of this domestication syndrome. Although the cooperative breeding hypothesis explains the negative proactive food provisioning results in independently breeding species like capuchin monkeys, macaques, bonobos, chimpanzees, it fails to explain the presence of reactive prosociality in these species (reviewed in (Jensen, 2016b; Marshall-Pescini et al., 2016)). In contrast to cooperative breeders, independent breeders do not need to proactively seek opportunities to provide food to others (Burkart & van Schaik, 2010). As a result they might need explicit signals of a need or a goal of others in order to show prosocial behaviour like helping or comforting (Jensen, 2016b). Therefore, rather than focusing on one prosocial behaviour and extrapolating the conclusions to explain prosocial behaviour as a whole, future studies should aim to investigate the multidimensional nature of prosocial behaviour in each species by including different pre-validated paradigms. Although additional research is needed to pinpoint whether the contrasting conclusions regarding bonobo prosociality are due to studying different facets of prosocial behaviour, or the age of the subjects, our study provides an important nuance in the existing field of prosociality research in bonobos.

Conclusions

In contrast to the popular view of the prosocial and food sharing bonobo, we show that adult bonobos do not behave prosocially in two food provisioning paradigms. This suggests that proactive prosociality may not be part of the self-domestication syndrome in bonobos. Since food provisioning studies likely evoke competitive behaviour around the limited food rewards (Jaeggi, Burkart, & Van Schaik, 2010), instrumental helping tasks or token variants of the prosociality paradigms could offer alternatives to study reactive prosocial behaviour in independently breeding species. Additional prosociality research in more diverse social groups is needed to expand our knowledge on the specific contexts that elicit prosociality in bonobos.

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Table 6.6 Summary of prosociality and food sharing experiments in bonobos. Task refers to the kind of paradigm that was used. Result summarises the findings of the study. Prosocial reports whether the study found a positive or negative result.

Study	Task	Sample size	Age range	Mean age	Result	Prosociality
Hare et al. (2007)	Dyadic co-feeding[a]	20	5 - 22	9.6 ± 5.7	Tolerant cofeeding	+
Hare & Kwetuenda (2010)	Door-opening paradigm[a]	8	°	°	Food sharing with group members	+
Tan & Hare (2013)	Door-opening paradigm[a]	14	4 - 12	7.5 ± 2.5	Food sharing with strangers	+
Tan et al. (2017)	Helping task[a]	16	5 - 15	9.2 ± 3.1	Prosocial helping	+
Krupenye et al. (2018)	Helping task[a]	12	5 - 15	10.2 ± 3.2	Food transfer	+
Nolte & Call (2021)	Helping task	6	5- 16	12.2 ± 4.5	Object transfer	+
Jaeggi et al. (2010)	Group co-feeding	9	10 - 30	21.0 ± 7.9	Limited cofeeding	-
Bullinger et al. (2013)	Door-opening paradigm	6	6 - 28	15.0 ± 7.7	Prefer to feed alone	-
Amici, Visalberghi, et al. (2014)	Lateral PCT	9	+	+	No prosociality	-
	Token PCT	9	+	+	No prosociality	-
Tan et al. (2015)	Lateral PCT[a]	10	6 - 11	8.2 ± 1.8	No prosociality	-
	Lateral PCT[a]	9	6 - 11	8.4 ± 2.1	No prosociality	-
Cronin et al. (2015)	Group co-feeding	8	5 - 27	13.1 ± 6.9	Limited cofeeding	-
Krupenye et al. (2018)	Helping task[a]	18	3 - 15	8.4 ± 3.3	No object transfer	-
This study: experiment 1	Stacked PCT	13	2 - 41	15.8 ± 11.2	No prosociality	-
This study: experiment 2	GSP	13	2 - 41		No prosociality	-

°Not provided but similar subjects as Hare et al. (2007) and Tan & Hare (2013)
+Not provided but some similar subjects as Bullinger et al. (2013)
[a] The majority of the tested dyads involves at least one adolescent or even juvenile

Behavioural and physiological response to inequity in bonobos (Pan paniscus)

Jonas Verspeek
Jeroen M. G. Stevens

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Abstract

Inequity aversion (IA), the affective, cognitive and behavioural response to inequitable outcomes, allows individuals to avoid exploitation and therefore stabilizes cooperation. The presence of IA varies across animal species, which has stimulated research to investigate factors that might explain this variation, and to investigate underlying emotional or affective responses. Among great apes, IA is most often studied in chimpanzees. Here, we investigate IA in bonobos, a reputedly tolerant and cooperative ape species for which few IA studies are available. We describe how bonobos respond to receiving a less preferred reward than a partner in a token exchange task. We show that bonobos do respond to receiving less preferred rewards by refusing tokens and rewards, and by leaving the experimental area. Bonobos never refused a trial when receiving the preferred reward, and thus showed no advantageous IA. We also investigate the variability in the disadvantageous IA response on a dyadic level, because the level of IA is expected to vary, depending on factors like the sex and relative rank of the subjects and the relationship quality between individuals. Like in humans and chimpanzees, we show that the tolerance towards inequity was higher in bonobo dyads with more valuable relationships. To study the affective component of IA, we included behavioural and physiological measures of arousal: a displacement behaviour (rough self-scratching) and changes in salivary cortisol levels. Arousal levels were lower in subjects that received less than their partner, but higher in subjects that received more than their partner. This suggests that although overcompensated bonobos showed no behavioural response, they were more aroused. These data support the cooperation hypothesis on both an interspecific and intraspecific level. We suggest that the variability in IA can be explained by the socio-ecology of the species, which should be considered in designing and analysing future IA studies.

Introduction

Humans have been claimed to be unique in their vastly more and distinctly cooperative interactions as a result of a species-unique psychology (Fehr & Fischbacher, 2003; Henrich et al., 2005; Powers et al., 2021; Tomasello & Vaish, 2012). Cooperation can be observed in a wide variety of contexts but can only be evolutionary stable when the benefits outweigh the costs (Clutton-Brock, 2009). Therefore, individuals that are able to compare their own effort and reward to their partners may avoid exploitation by ceasing interactions with an unfavourable outcome for themselves (Brosnan & Bshary, 2016). According to the cooperation hypothesis, inequity aversion (IA), i.e. the affective, cognitive and behavioural response to inequitable outcomes (Oberliessen et al., 2016), may have evolved as a mechanism to stabilize cooperation and avoid unfavourable cooperation partners (Brosnan & de Waal, 2014; Fehr & Schmidt, 1999). In human populations, both disadvantageous IA (i.e. disliking that another individual receives more than yourself, i.e. undercompensated) and advantageous IA (i.e. disliking if you receive more than another individual, i.e. overcompensated) (Fehr & Schmidt, 1999) have been found across different populations (e.g. Blake et al., 2015; Rochat et al., 2009), but its occurrence is influenced by various factors like culture (Henrich et al., 2001), personality (Colquitt et al., 2006; Wiesenfeld et al., 2007) and relationship quality between the individuals that cooperate (Clark & Grote, 2003). To better understand the evolutionary origins of IA, its occurrence has been studied in a variety of animal species across different taxa, including birds, mammals and mostly non-human primates (reviewed in Brosnan & de Waal, 2014; McGetrick & Range, 2018; Sosnowski et al., 2021; Talbot et al., 2016). In the first study of IA in non-human animals, capuchin monkeys (Sapajus apella) had to exchange tokens for a food reward (Brosnan & de Waal, 2003), which has now become a standard method to study IA in animals. Subjects always received a less preferred reward for a token exchange, while their partner either received the same type of reward (equity condition) or a more preferred reward (inequity condition) for a token. The capuchin monkeys refused the less-preferred reward when a partner received the more preferred food item for the same task. The authors concluded that capuchin monkeys were averse to disadvantageous inequity, suggesting that IA has an early evolutionary origin (Brosnan & de Waal, 2003). However, later studies were not always able to replicate these original findings (Dubreuil et al., 2006; Roma et al., 2006 but see Van Wolkenten et al., 2007), sparking a lively debate about IA in animals and how to study it (review in Bräuer & Hanus, 2012; Brosnan, 2006; Oberliessen & Kalenscher, 2019; Price & Brosnan, 2012). Despite several methodological improvements in subsequent IA studies (review in Bräuer & Hanus, 2012; Price & Brosnan, 2012), not every species responds negatively to receiving less than a conspecific, even within primates (Brosnan & de Waal, 2014). The species that do respond to disadvantageous inequity, habitually cooperate with kin and non-kin in a variety of contexts. Therefore, the cooperation hypothesis also explains the interspecific variation in disadvantageous IA (reviewed in Massen et al., 2019; Price & Brosnan, 2012). However, also within species the responses to inequity differ. For example in chimpanzees (Pan troglodytes), some studies found evidence for disadvantageous IA while others have not (Bräuer et al., 2006, 2009; Brosnan et al., 2010, 2015; Hopper et al., 2014), and even within the same study, one group of chimpanzees showed IA while the other group did not (Brosnan et al., 2005). Interestingly, advantageous IA has only been reported for one group of chimpanzees (Brosnan et al., 2010). The question then rises why groups of the same species vary in their IA responses. To address this question, the influence of various individual and social factors on the expression of IA have been investigated, including sex, dominance rank, personality, relationship quality or length (Talbot et al., 2016). In terms of individual factors, sex of the subject has often been investigated as influencing factor, but the effect varied across studies, also within the same species (Brosnan, 2006b; Brosnan et al., 2010; Freeman et al., 2013; Hopper et al., 2014; Mustoe et al., 2016; Talbot et al., 2011). When tested in same-sex pairs, male chimpanzees were more sensitive to IA in one study (Brosnan et al., 2010), but not another (Brosnan, 2006b). Female chimpanzees, when tested in same-sex and mixed pairs, showed a higher level of IA in one study (Hopper et al., 2014), but lower in another (Brosnan et al., 2015). Given that the pair composition differed between studies and that cooperative interactions involve more than one individual, the dyadic sex-combination rather than the individual sex of the subject might play a role in the response to inequity in the dyadic token exchange paradigm. This suggests that studies should investigate factors based on the socio-ecology of the study species, which could help in explaining contradictory findings across studies (review in McGetrick & Range, 2018; Oberliessen & Kalenscher, 2019; Price & Brosnan, 2012).

While several studies found that dominant individuals were more sensitive to inequity than subdominants (Bräuer et al., 2006; Brosnan et al., 2010; Dale et al., 2020; Essler et al., 2017; Oberliessen et al., 2016), others have found no such rank effects (Brosnan & de Waal, 2003; Massen et al., 2012; Range et al., 2012; Sosnowski et al., 2021; Van Wolkenten et al., 2007). Again, the socio-ecology of the species could explain these differing results. In groups with a clear and despotic dominance hierarchy, resources are often distributed unequally, with the most dominant individuals having access first (Van Schaik, 1989). When roles are reversed, i.e. when the dominant individual receives less than a partner, this likely results in a violation of expectation in the dominant individual and therefore a stronger IA response is expected (Essler et al., 2017).

Finally, the relationship quality between subjects also influences the level of IA. Human friends tolerate a certain level of disadvantageous inequity, while people in negative relationships do not and become even more tolerant of advantageous inequity (Clark & Mills, 2004; Loewenstein et al., 1989). Also in animals, group members that have lived together for a longer time and/or with stronger bonds showed lower levels of IA (Brosnan et al., 2005, 2015; Hopper et al., 2014; Mustoe et al., 2016; Range et al., 2012). However, another study that explicitly tested the effect of relationship quality in long-tailed macaques (Macaca fascicularis) did not find a difference in the expression of IA between friends and nonfriends (Massen et al., 2012).

In general, IA studies measure the overt (behavioural) reaction of subjects in response to an unequal situation. However, the absence of a behavioural IA response in certain subjects or species does not (necessarily) prove absence of IA. It is possible that while noticing inequity, subjects might simply fail to respond or do not want to respond (Talbot et al., 2016). This has led to a research focus on the emotional mechanisms that underly responses to inequity (Massen et al., 2019; McGetrick & Range, 2018). In humans, inequity heightened activity in brain areas related to emotions and cognition (Sanfey et al., 2003) and IA has been associated with negative emotions such as anger, guilt, spite and jealousy (Cubitt et al., 2011; Matsuzawa & Tanimoto, 2018; McAuliffe et al., 2014). This suggests that the inequity response in experimental studies may also be emotionally mediated rather than an objective deduction of what is fair (Brosnan, 2009; Massen et al., 2019; Talbot et al., 2016). Thus, the trial refusals may be the result of a state of frustration across experimental trials, instead of trial-based comparisons. Therefore, in addition to the behavioural response of IA, a shift in the subjects' arousal is expected, which can be studied by collecting physiological measures (Massen et al., 2019), or by behavioral indicators. In primates, rough self-scratching is a self-directed behaviour that is often used as a behavioral indicator associated with anxiety, frustration or social arousal (Baker & Aureli, 1997; Maestripieri et al., 1992; Troisi, 2002). On the physiological level, cortisol is one of the most commonly used markers for arousal after a specific event (O'Connor et al., 2000). So far neither measure for arousal has been included in IA studies.

While the majority of IA research in great apes has focused on chimpanzees, bonobos make a very interesting study species to investigate advantageous and disadvantageous IA. Bonobos are often said to be very peaceful, tolerant, prosocial and empathic (Furuichi, 2011; Hare et al., 2007; Maclean, 2016; Parish & de Waal, 2000 but see Cronin et al., 2015; Jaeggi et al., 2010; J. M. G. Stevens et al., 2008; Verspeek et al., 2022), and have been shown to cooperate in experimental food retrieval studies in the lab (Hare et al., 2007; Nolte & Call, 2021). Under the cooperation hypothesis it could be expected that IA may be equally expressed in bonobos compared to chimpanzees. Also, if bonobos are more empathic and sensitive to the needs of others, advantageous IA is expected. However, the one study on IA on five bonobos during a token exchange task found that they did refuse more rewards during the inequity than equity condition, and did so more than orangutans and chimpanzees, but the difference was not significant because of low statistical power (Bräuer et al., 2009). In comparative research there is a great need for replication studies (J. R. Stevens, 2017), and since there has been great variability in the IA response across chimpanzee populations (see above), more data are needed on different groups using a similar methodology for a better understanding of IA in bonobos. Moreover, the socio-ecology of bonobos may allow to disentangle the differential effects of sex, kinship and relationship quality on the expression of IA. Similar to chimpanzees, bonobos are a male-philopatric species, meaning that males stay in their natal groups, while females migrate to other communities when they reach maturity (Hashimoto et al., 2007; Kano, 1992). Unlike chimpanzees however, female bonobos engage in strong cooperative bonds among each other as well as with their adult sons (Hohmann & Fruth, 2002; Parish, 1994; J. M. G. Stevens et al., 2006; Surbeck & Hohmann, 2008), resulting high value relationships between females, but not between males [Stevens et al., 2015; Verspeek et al., 2020]. Males on the other hand do not form strong bonds among each other and only rarely engage in cooperative interactions (Furuichi & Ihobe, 1994; Hohmann & Fruth, 2002; Kano, 1992; Surbeck et al., 2017), and show low value relationships [Stevens et al., 2015; Verspeek et al., 2020]. As the frequency of cooperative interactions depends on the relationship quality between individuals, the level of IA is expected to vary accordingly.

The present study has three aims. First, we want to investigate the IA response in 15 unique dyads of bonobos, who all lived in the same captive group. Following more recent studies (Bräuer et al., 2009; Brosnan et al., 2010, 2015; Hopper et al., 2014), we implemented some methodological changes aimed at improving the original IA study in chimpanzees (Brosnan et al., 2005): 1) before exchanging, subjects were always shown what reward they would receive for an exchange (cfr. Hopper et al., 2014; Van Wolkenten et al., 2007), allowing them to refuse to participate without any effort, i.e. refusing the token; 2) to avoid false expectations of receiving the preferred reward due to presenting it in front of the subjects (cfr. individual contrast (Brosnan et al. 2005; 2010; Van Wolkenten et al., 2007; Hopper et al., 2014), the preferred food item was always visible to the subjects, but was never held in front of the animals before exchanging in the equity condition (cfr. Bräuer et al., 2009); 3) we randomized the order of experimental conditions to avoid order effects (cfr. Bräuer et al., 2009; Brosnan et al., 2010, 2015; Hopper et al., 2014); and 4) subjects were tested in the same room, so they could easily see the actions of the partner and to allow for free social interactions between the participants (cfr. Brosnan et al., 2010, 2015; Hopper et al., 2014). If bonobos are sensitive to differential rewarding, we expect them to show IA by a) refusing to exchange tokens and food rewards; b) staying away from the researcher. Second, we investigate how the factors sex, relative dominance rank of the subject and relationship quality influence the response to inequity in bonobos. Based on the socio-ecology of bonobos, we expect the level of IA to vary depending on the relationship quality between subjects. The highest tolerance towards inequity, measured as the lowest level of refusals, is expected in dyads with stronger bonds, i.e. higher relationship quality. The influence of the relative rank of the subject is expected to depend on the steepness of the dominance hierarchy. As a shallow dominance hierarchy is expected in this bonobo group, we predict that the relative dominance rank of the subject will not have an influence on the level of IA. Third, we investigate the emotional component of IA by analysing a behavioral and a physiological measure of arousal. We expect to find higher arousal levels in under- and overcompensated animals, as measured by rough self-scratching and salivary cortisol level change.

Methods

Ethics Statement

No animals were sacrificed or sedated for the purpose of this study. The research adhered to the legal requirements of the country in which the research was conducted (Belgium) and was approved by the Scientific Advisory Board of the Royal Zoological Society of Antwerp and the University of Antwerp (Belgium) and endorsed by the European Breeding Program for bonobos. All research complied with the ASAB guidelines (ASAB, 2020).

Subjects and Housing

All tests were conducted between September 2018 and June 2019. We included seven bonobos (mean age 21.9 ± 3.4, Table 7.1[11]) that lived in a social group of fourteen individuals in Zoo Planckendael (Belgium). During this study, they were housed in an enclosure that consisted of nine interconnected rooms of various sizes (between 15 and 65 m²), all of which included a number of platforms and ropes for enrichment. The bonobos were fed four times per day, and water was available ad libitum. Prior to this study, all subjects had been trained to be separated in subgroups and individually and had been trained to deliver saliva samples (see Verspeek et al., 2021 for details – Chapter 3). All tests were conducted in the largest enclosure of 65 m² and subjects and partners were not physically separated.

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[11] See also table 9.1 Overview of the study subjects p 144

Table 7.1 Subject information

Individual	Sex	Age (years)[a]
Hortense	Female	41
Vifijo	Male	25
Djanoa	Female	24
Zamba	Male	21
Busira	Female	15
Kianga[b]	Female	14
Habari	Male	13

[a] Individual's age when the study took place
b Did not provide saliva samples

Social bond strength and dominance relations were determined using observational data that were collected during the two months before the start of the experiments. The quality of the social bonds between each of the dyads was measured by determining the relationship value of each dyad. Full details of how the relationship value component was determined, can be found in (J. M. G. Stevens et al., 2015; Verspeek et al., 2019).

The dominance hierarchy was determined by constructing a win-lose matrix based on the behaviour fleeing upon aggression (Vervaecke et al., 2000). Using this matrix, we calculated normalised David's scores, which were used to calculate the steepness of the hierarchy (De Vries et al., 2006). We observed 78 instances of fleeing upon aggression among the adult bonobos, resulting in a dominancy hierarchy with a shallow slope of 0.24 ($p = 0.02$). For each subject in a dyad, we determined its dominance rank relative to the partner (dominant or subdominant).

Experimental testing procedure

Prior to the experiment all subjects had been trained to return a plastic token (22cm by 2cm) to the experimenter to receive a food reward, and to deliver saliva samples (as described in Verspeek et al., 2021). Based on a previous food preference study on the same subjects (Verspeek & Stevens, 2020), we used grapes as a high-value and parsnip as a low-value food reward. During all test sessions, two transparent plastic boxes stood in front of the testing room and were clearly visible to the subjects, one containing similar sized parsnip pieces and the other containing similar sized grapes.

In each session, subjects exchanged alternatingly until each individual had the opportunity to participate in 25 trials per session (cfr. Bräuer et al., 2009; Brosnan et al., 2005, 2010, 2015). A testing session started when the experimenter took a token and the appropriate food reward, depending on the test condition, raised them in front of himself and called the name of one of the subjects. Next, the experimenter handed the token over to that subject. After the bonobo had taken the token, the experimenter opened his hand as a sign that he wanted the token back. When the bonobo returned the token, the experimenter explicitly said 'thank you' and handed the food reward (grape or parsnip) over to the subject while saying its name. Next, the experimenter repeated this process with the next subject and exchanged the token for the appropriate food item according to the test condition. If a subject refused the token, the experimenter put it against the mesh, called the subject's name again and rattled the token against the mesh. If subjects did not return the token after 30 sec, a new trial was started with the other bonobo. If a subject did exchange the token, but refused the food, the experimenter called the subject's name and showed the food item again. In case subjects did not take and consume the food within 30s, a new trial was started with the other bonobo (cfr. Hopper et al., 2014). A test session was ended 5 sec after the last food item was consumed. Testing conditions remained the same throughout the entire test session, and each subject only participated in one session per day.

Test Conditions

Following Bräuer et al. (2009), subjects were tested in three different experimental conditions: disadvantageous inequity, equity and advantageous inequity. In the equity condition, both individuals received identical less-preferred parsnip in exchange for the token. In the disadvantageous inequity condition, the subject got the less-preferred parsnip in exchange for the token, while the partner received the preferred grape. In the advantageous inequity condition, the subject exchanged for the preferred grape, while the partner exchanged for the piece of parsnip. Throughout the experiment, we aimed to test each subject with all possible combinations of partners in each condition, meaning that each pair would be tested in three sessions, as in the equity condition both apes received identical payoffs (cfr. Bräuer et al., 2009). The order of conditions was randomized between dyads to avoid order effects (Bräuer et al., 2009; Brosnan et al., 2015; Hopper et al., 2014). Separation of the subjects from the group happened on voluntary basis. In total, 15 unique pairs could be tested, resulting in 57 dyadic tests and on average 242 ± 38 opportunities to exchange for each individual (see table 7.2).

Table 7.2 Number of trials per dyad in the tested conditions

Subject	Sex of subject	Partner	Sex partner	Relative dominance of subject	Number of trials in each condition		
					Disadv.°	Equity	Advant.°
Busira	F	Djanoa	F	Subdominant	25	25	24
Busira	F	Habari	M	Subdominant	25	25	25
Busira	F	Hortense	F	Subdominant	25	25	25
Busira	F	Vifijo	M	Dominant	25	24	25
Djanoa	F	Habari	M	Dominant	25	25	25
Djanoa	F	Hortense	F	Dominant	25	25	0
Djanoa	F	Kianga	F	NA	25	0	0
Djanoa	F	Vifijo	M	Dominant	25	25	25
Djanoa	F	Zamba	M	Dominant	0	0	25
Habari	M	Hortense	F	Subdominant	0	25	24
Habari	M	Vifijo	M	Dominant	24	25	25
Habari	M	Zamba	M	Dominant	25	25	0
Hortense	F	Vifijo	M	Dominant	0	0	25
Hortense	F	Zamba	M	Dominant	25	25	25
Vifijo	M	Zamba	M	Dominant	25	0	0

° The disadvantageous inequity condition for the subject was the advantageous inequity condition for the partner and vice versa (cfr. Bräuer et al., 2009).

Dependent variables and analyses

Behavioural responses of inequity aversion

All 38 sessions were video-recorded and coded afterwards using The Observer software package (Noldus Information Technology, Wageningen, The Netherlands). As a first measure for disadvantageous IA, we compared the proportion of trial refusals between the equity and disadvantageous inequity condition (Bräuer et al., 2009; Brosnan, Talbot, et al., 2010). Trials were coded as 'accepted' if subjects accepted the token within 30 sec after the experimenters offering and accepted and ate the food reward within 30 sec after having received it. Trials were coded as 'refused' if subjects (a) did not return the token within 30 sec after the experimenters offering or (b) did not eat the food reward within 30 sec after offering (cfr. Hopper et al., 2014).

As a second behavioural measure for IA, we compared the duration of absence, i.e. the proportion of the testing duration during which subjects were not present in the testing area in front of the experimenter where they could exchange and obtain food rewards, between the conditions (cfr. Bräuer et al., 2009).

Affective component of inequity aversion

In addition to the two standard behavioral measures of inequity aversion, we also aimed to measure the affective component of IA. Therefore, as a behavioral measure for social arousal, we compared the frequency of rough self-scratching, defined as "raking one's own hair or skin with fingernails including large movements of arm" (Baker & Aureli, 1997) between the three conditions. We further included salivary cortisol as a physiological measure of arousal (Baker & Aureli, 1997; Maestripieri et al., 1992; O'Connor et al., 2000). Before (cort_pre) and after (cort_post) each dyadic test session, we collected Saliva samples of each subject were taken by sweeping the Salivette (Ref 51.1534, Sarstedt, Numbrecht, Germany) through the mouth of the subject, a procedure which took approximately 30 sec. After collection, saliva samples were immediately placed in Salivette tubes (Ref 51.1534, Sarstedt), and stored at – 20 °C until analysis. Saliva sample preparation and cortisol measurement was done following a pre-validated protocol (Verspeek et al., 2021). We removed any outliers from the cortisol dataset based on the median plus or minus 2.5 times the median absolute deviation (Leys et al., 2013). To determine whether unequal payoffs during the token exchange task result in physiological changes, we compared the relative change of salivary cortisol levels between the equity, disadvantageous and advantageous inequity conditions. The relative salivary cortisol change was calculated as the change in salivary cortisol over the test session divided by the level of salivary cortisol before the test ((cort_post-cort_pre)/cort_pre). Positive values would represent an increase of cortisol levels.

Data analyses

We ran multiple Generalized Linear Mixed Models (GLMMs) and used a hypothesis-driven approach to determine how bonobos react to inequity. In the first GLMM the proportion of refusals for each individual was the response variable, test condition (disadvantageous inequity and equity) and sex of the subject the fixed effects and identity of the subject the random factor. Using Wilcoxon signed ranks tests, we determined whether subjects rejected more tokens than food and whether token refusal alone also differed between conditions. We ran a second GLMM with the proportion of refusals by each subject in the disadvantageous inequity condition, for the different partners as response variable, the sex of the subject, the sex combination of the dyad (i.e. female-female, female-male, male-male, mother-son), the relative rank of the subject and relationship value of the dyad as fixed factors and subject and dyad identity as random factors. The third GLMM had the proportion of absence per session as response variable, condition and sex of the subject as fixed factors and subject and dyad identity as random factors. For the frequency of rough self-scratching, we ran a GLMM with rough self-scratching frequency as response variable and condition, sex of the subject and relationship value as fixed factors and subject and dyad identity as random factors. Finally we ran a GLMM with the relative salivary cortisol change per session as response variable and condition, the proportion of absence during the session and relationship value as fixed factors and subject and dyad identity as random factors.

All analyses were done using RStudio (1.0.136) (Team, 2020). Models that assessed proportions used a binomial distribution with a logit link function using the 'glmer' function and models assessing frequencies used a negative binomial distribution and log link function using the glmmTMB package (Brooks et al., 2017) and included the number of observation hours as offset to correct for the sampling effort. Random factors were added to correct for repeated measures. In addition to the main effects, we also included two-way interactions between the main effects as fixed effects. Significance of fixed effects was determined by comparing the full model with the respective null model, excluding the fixed effect but retaining the random effects, using a likelihood ratio test. Non-significant interaction terms were excluded and the reduced model was used for hypothesis testing. Multicollinearity between independent variables was tested based on a variance inflation factor (VIF). None of the variables showed multicollinearity (VIF>5) (O'Brien, 2007).

Results

Behavioural measures of inequity aversion

Bonobos refused more trials in the disadvantageous inequity than the equity condition, but never refused any of the trials in the advantageous inequity (Fig. 7.1a). Overall, the proportion of refusals differed significantly between the conditions disadvantageous inequity (mean: 0.15 ± 0.05) and equity (mean: 0.03 ± 0.01) (χ2 = 39.667, df = 1, P <0.001) but not between the sexes (χ2 = 1.400, df = 1, P = 0.237). Overall, subjects rejected more tokens (mean: 0.09 ± 0.04) than food rewards (mean: 0.01 ± 0.01) (Wilcoxon signed-ranks test: N = 6, Z = -2.01, P = 0.04) and token refusal alone also differed between disadvantageous inequity (mean: 0.14 ± 0.05) and equity (mean: 0.02 ± 0.01) (Wilcoxon signed-ranks test: N = 6, Z = -2.15, P = 0.03) (Fig. 7.1b).

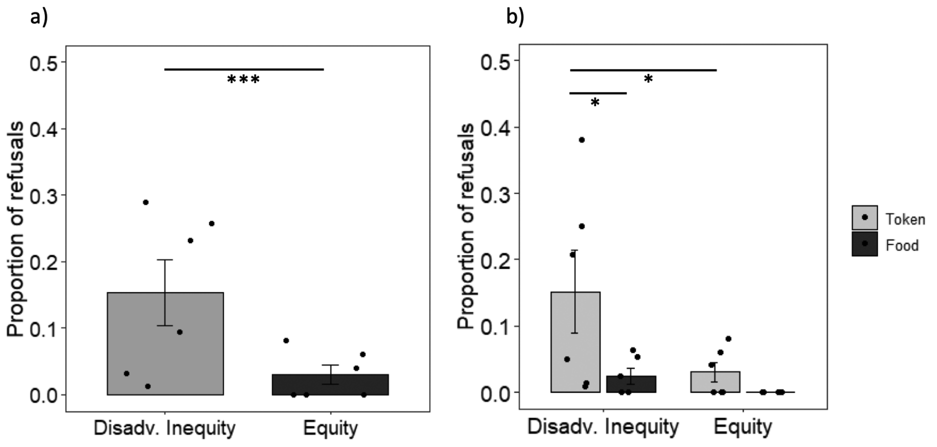

Fig. 7.1 Average proportion of a) trial refusals and b) refusals of tokens and foods separately in the disadvantageous inequity and equity condition. (***P < 0.001 and *P < 0.05).

With respect to learning and order effects (Brosnan & de Waal, 2003), we compared the proportion of trial refusal during the first half of the test sessions (first 15 trials of each session) with the second half of the test sessions (the last 10 trials of each session). The proportion of trial refusals did not differ between the first and second half of the test sessions (Wilcoxon signed-ranks test: N = 12, Z = -0.47, P = 0.64).

On the dyadic level, we found that trial refusal in the disadvantageous condition was influenced by the relationship value (χ2 = 4.16 df = 1, P = 0.041) but not by the genetic sex combination of the dyad (χ2 = 1.72 df = 3, P = 0.632), the sex of the subject (χ2 = 0.05, df = 1, P = 0.816) or the relative rank of the subject (χ2 = 0.55, df = 1, P = 0.459). The proportion of refusals decreased with increasing relationship value (Fig. 7.2).

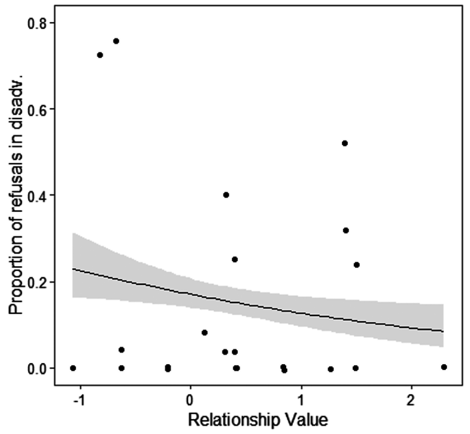

Fig. 7.2 Relationship between the proportion of trial refusals in the disadvantageous inequity and the relationship values of the dyads.

Regarding the duration of absence, we found a significant interaction effect between condition and sex of the subject ($\chi 2 = 1103.002$, df = 2, $P < 0.001$). Both female and male subjects were absent longer in the disadvantageous inequity than the equity and advantageous inequity condition (all $p < 0.001$) and males were absent longer than females in the equity and advantageous inequity conditions (all $p < 0.001$) (Fig. 7.3).

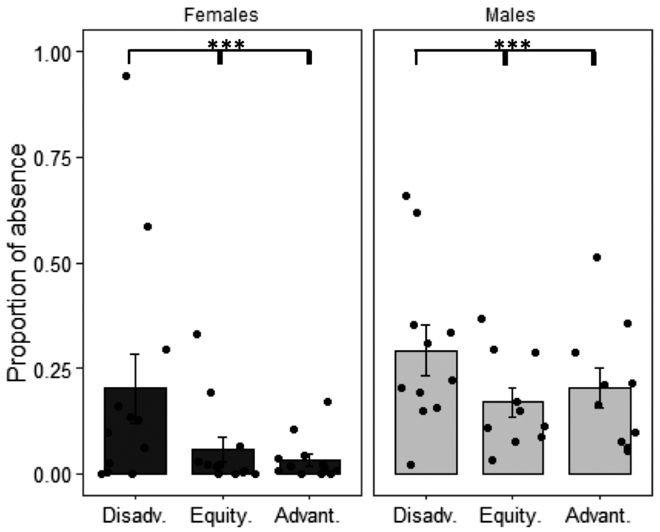

Fig. 7.3 Average duration of absence (expressed as proportion of trial duration) in each condition by female and male bonobos (Disadv.: disadvantageous inequity, Advant.: Advantageous inequity). Significant differences between conditions are indicated by a hatch and between sexes within each condition by a bold hatch. (All $P < 0.001$).

Affective component of inequity aversion

The model for rough self-scratching showed a trend for the interaction between condition and sex of the subject ($\chi 2 = 5.352$, df = 2, $P = 0.069$) but no significant effect for the interaction between condition and relationship value ($\chi 2 = 4.254$, df = 2, $P = 0.119$) (Fig. 7.4a). The model for salivary cortisol change, showed significant effects of condition ($\chi 2 = 7.157$, df = 2, $P = 0.028$), the proportion of absence ($\chi 2 = 7.435$, df = 1, $P = 0.006$) and relationship value ($\chi 2 = 4.480$, df = 1, $P = 0.034$). Salivary cortisol levels increased during advantageous inequity conditions, but decreased during disadvantageous inequity conditions (Fig. 7.4b). Salivary cortisol also increased when subjects were absent longer (Fig. 7.5a), and in subjects that were paired with more closely bonded partners (Fig. 7.5b).

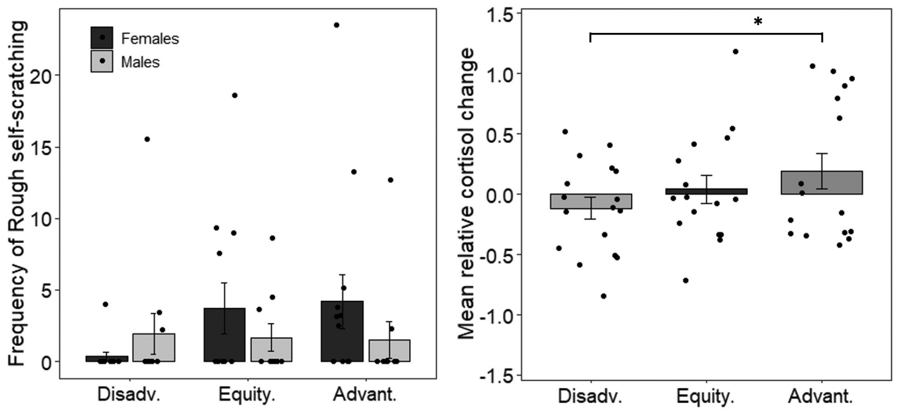

Fig. 7.4 Average a) Frequency of rough scratching during the three conditions; b) Relative salivary cortisol change during sessions for the three conditions. (Disadv.: Disadvantageous inequity; Advant.: Advantageous inequity). Significant differences between conditions ($p < 0.05$) are indicated by a hatch.

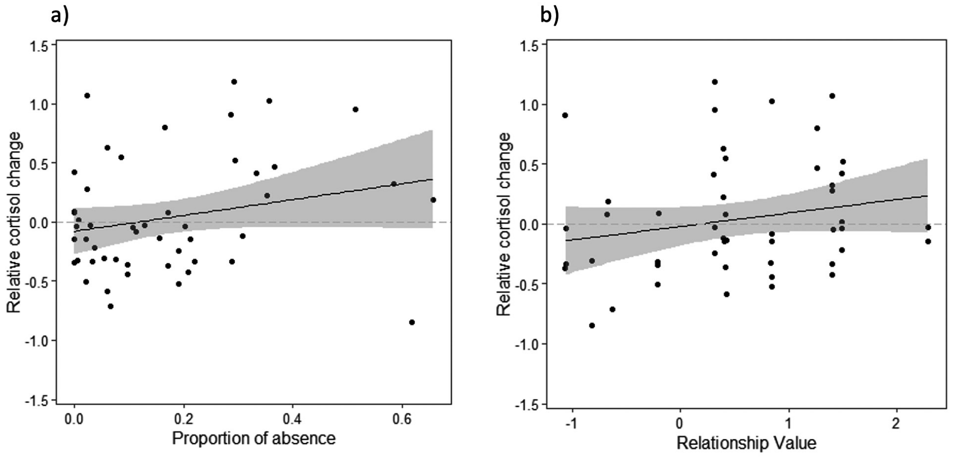

Fig. 7.5 Relation between relative cortisol change during test sessions and a) proportion of absence and b) relationship value.

Discussion

This is the first study to show that bonobos respond negatively to disadvantageous inequity in the token exchange paradigm, by refusing trials and by staying away from the experimental area. Also, subjects were less likely to refuse trials when paired with closely bonded partners. We found no behavioral evidence for advantageous IA in bonobos. However, arousal levels were higher in overcompensated but not undercompensated individuals, suggesting the presence of a physiological response to advantageous inequity.

A previous study, using a similar methodology no clear IA in bonobos, although they were more likely to show IA than the other great ape species tested (Bräuer et al., 2009). The bonobos in our study showed similar refusal levels in the disadvantageous inequity condition as this previous study and studies reporting on IA in chimpanzees (Bräuer et al., 2009; Brosnan et al., 2005; Brosnan, Talbot, et al., 2010; Hopper et al., 2014), but also showed lower refusal levels in the equity condition (Bräuer et al., 2009; Brosnan, Talbot, et al., 2010). The low refusal levels in the equity condition are expected, as subjects knew which reward they would receive before the exchange, so we avoided any violation of expectation, and therefore ruled out frustration effects. Indeed, the bonobos did not reject participation, and rarely refused the food in our study, but refused more tokens than food rewards, as has also been reported for chimpanzees by Hopper et al (2014). These findings contrast with earlier studies that reported much higher proportions of food refusal than token refusal in chimpanzees and bonobos (Bräuer et al., 2009; Brosnan, 2006b; Brosnan et al., 2005). This is surprising because food refusal after the exchange even exacerbates inequity (Henrich, 2004). Both in our study and the chimpanzee study of Hopper et al (2014) subjects knew before exchanging which reward they would receive, and therefore could refuse to ‘work’ for an unfair offer, which demonstrates the importance of this methodological improvement over earlier studies (Bräuer et al., 2009; Brosnan et al., 2005; Brosnan, Talbot, et al., 2010). Nevertheless, in some of the disadvantageous inequity trials, the undercompensated bonobos in our study still exchanged the token, but rejected the food reward. The majority of these food refusal trials were observed when the undercompensated subject, after having refused to exchange in multiple consecutive trials, returned towards the experimental area and exchanged one more token. When the subject then again received the less preferred food item, it would refused the food reward and moved away. One possible explanation could be that in these cases the bonobos re-evaluated the reward distribution by the experimenter to determine whether to continue to exchange or not.

Our findings on the duration of absence are in contrast with previous findings (Bräuer et al., 2009) but further support the idea that when being undercompensated, bonobos refused to participate in the interaction. Undercompensated bonobos were absent longer in the disadvantageous inequity condition than the equity condition. Bonobos thus respond to inequity by refusing trials and moving away from the experimenter, which can be seen as a way to avoid the unequal interaction with the experimenter. The bonobos could not influence the experimenters behavior in this study, so their only solution was to walk away from the experiment (Brosnan & Bshary, 2016), and stop to put effort in the unequal interaction. Leaving the exchange task therefore reflects the partner choice mechanism of animals in naturalistic interactions (Brosnan & Bshary, 2016). Surprisingly, subjects never reacted aggressively, angry or frustrated towards the experimenter during the entire experiment. Although bonobos regularly redirect their aggression and frustration towards keepers and researchers during feedings and other social interactions (personal obs.), they never did so in this study. This supports the idea of the limited effect of the exchange task on the arousal levels in bonobos.

The relative rank of the bonobos did not influence the level of disadvantageous IA. This corresponds with the prediction that in groups with a shallow dominance hierarchy, rank effects on IA might be smaller. This also suggests that not the dominance rank, but other factors may explain the intra-species variability in IA. Indeed, the proportion of refusals in the disadvantageous inequity condition varied depending on the quality of the relationship between subjects. While the sample size is arguably small, our results show that the proportion of refusals decreased with increasing relationship value. These results are similar to studies in chimpanzees and dogs that showed that social closeness inhibited the expression of IA (Brosnan et al., 2005; Range et al., 2009), and fit the hypothesis that like in humans, closely bonded pairs tolerate inequity while weaker bonded pairs prefer more equal distributions (Clark & Mills, 2004; Loewenstein et al., 1989). Therefore, our data provide support for the cooperation hypothesis not only on the interspecific level but also on the intraspecific level, suggesting that variation in the inequity response within cooperative species can be explained by their socio-ecology. The closest and most affiliative bonds in bonobos, i.e. with the highest relationship values, are formed between mothers and their sons and among unrelated females (J. M. G. Stevens et al., 2015; Verspeek et al., 2019).These dyads also show the most cooperative interactions in the wild and captivity such as coalitionary support and food sharing (Moscovice et al., 2019; J. M. G. Stevens et al., 2006; Surbeck et al., 2011; Surbeck & Hohmann, 2008; Yamamoto, 2015). Such frequent interactions within strongly bonded dyads are often characterized by emotionally and attitudinally mediated reciprocity (Brosnan & de Waal, 2002; G. R. Brown & Silk, 2002; Massen et al., 2019), in which the need to monitor the partners’ investment and to react to unequal payoffs to avoid exploitation is smaller (Price & Brosnan, 2012). Our data therefore suggest that the differential effects of sex, rank and relationship value act on the dyadic level corresponding to the socio-ecology of the species (Hopper et al., 2014).

Regarding the affective component of IA, both the behavioral (rough self-scratching) and physiological (salivary cortisol) data were very variable across conditions. The rough self-scratching results seem to indicate that bonobos were more aroused in the equity and advantageous inequity conditions, and possibly show different effects between the sexes. Female bonobos scratched more often in the equity and advantageous inequity condition than in the disadvantageous inequity condition, while males overall showed lower but constant levels of scratching across conditions. Overall, salivary cortisol levels increased during the advantageous inequity conditions, but decreased in the disadvantageous inequity condition. These results on suggest that even though bonobos did not react behaviorally to being overcompensated, they got more aroused when receiving the more valuable reward. Alternatively, the salivary cortisol increase in the advantageous inequity condition could also reflect their excitement about receiving a valuable food item (Verspeek & Stevens, 2020). Across conditions, salivary cortisol levels increased in subjects that were absent longer, which suggests that subjects that were more aroused were also more likely to stay away longer. Surprisingly, we also found that salivary cortisol levels were more likely to increase in subjects that were paired with close friends, i.e. dyads with higher relationship values, while decrease in dyads with a low relationship value. This finding is likely the result of the limited sample size since only few dyads with a low relationship value participated in the experiments. Also, arousal levels were variable and relatively low, suggesting that the testing condition did not create much arousal or frustration. While psychological stressors can elicit cortisol activation, the size of the cortisol effects varies substantially depending on the characteristics of the stressor, i.e. a stressor-physiology 'specificity" (Dickerson & Kemeny, 2004). For example, several studies showed that uncontrollable stressors lead to greater cortisol responses than controllable ones (reviewed in (Dickerson & Kemeny, 2004)). This suggests that the test sessions in this study might not evoke a strong response because they allowed sufficient individual control, as subjects could always freely move though the testing room and the connected rooms and decide to refrain from the interaction whenever they wanted. While we previously showed that in bonobos, salivary cortisol increased strongly in response to a highly stressful event (Verspeek et al., 2021), it might not rise as sharply in response to inequity. The sampling interval between the two samples in this study was on average 44.2 ± 9.8 mins and the post-test saliva sample was taken 14.0 ± 7.1 mins after the end of the session. In bonobos, salivary cortisol levels rose between 10 to 40 minutes after a psychological stressor, while maximal levels were reached 160 minutes after the stressor (Verspeek et al., 2021 - see Chapter 3). While the sampling interval in this study is long enough to detect cortisol changes after an event, the post-test saliva sample might have been taken too early to detect the accumulating frustration effect over the 25 trials of the test sessions. Also, subjects show individual variation in their level of IA but also in the activation of the HPA-axis. The limited effect of the unequal rewarding on both measures of arousal may have been masked by the inter-individual variability in the level of rough self-scratching, the high sensitivity of salivary cortisol (Kirschbaum & Hellhammer, 2000; Laudenslager et al., 2006b) and the inter-individual variability in HPA-axis activity (Sheriff et al., 2011). To overcome this, future studies should aim to take multiple samples after the experimental session and include alternative physiological markers for arousal like for example infrared thermography. Infrared thermography records the electromagnetic radiation emitted by body parts, which allows to indirectly assess the sympathetic and parasympathetic activity without influencing the subjects' behavior or physiological response (reviewed in Travain & Valsecchi, 2021).

Because of a missing non-social control condition in our study (cfr. Dubreuil et al., 2006; Hopper et al., 2014; Neiworth et al., 2009) and a missing contrast control (cfr. Brosnan et al., 2010; Hopper et al., 2014; Sosnowski et al., 2021), we cannot differentiate social IA two alternative non-social explanations. While the IA hypothesis predicts that subjects feel treated unfairly in relation to a conspecific, some hypotheses have been proposed to explain the negative reaction of subjects in the exchange paradigm. The social disappointment hypothesis states that subjects are disappointment by the experimenters as they did not reward the subject as well as they could have (Engelmann et al., 2017) and subjects attribute this negative state to the experimenter. However, others suggests that is can still be considered a form of IA (Oberliessen & Kalenscher, 2019). The reward expectation hypothesis, states that subjects who see a valuable reward being manipulated when the conspecific receives a more valuable reward, will expect also to receive the same valuable reward (Bräuer et al., 2006; Dubreuil et al., 2006; Neiworth et al., 2009). The assumption that perceiving rewards delivered to conspecifics elevates expectations about own-reward, requires the existence of social comparison processes, which implies social cognition (Oberliessen & Kalenscher, 2019). However, while these two hypotheses consider different sources of IA, they both suggest that the exchange task itself does measure whether subjects are able to recognize and respond to differences in food rewards (Oberliessen & Kalenscher, 2019), which are the first evolutionary steps toward the evolution of IA as we know it in humans (Brosnan, 2006a, 2009). It is possible that also in our study, bonobos were disappointed by the experimenter's behaviour and only responded to the manipulation of the preferred food item in the disadvantageous inequity condition. To clarify this and obtain evidence for the existence of social IA in bonobos, future studies should implement the necessary control conditions.

In conclusion, we showed that bonobos react to inequity by refusing to participate in an exchange task and that the tolerance towards inequity increases with social bond strength between partners, suggesting that the cooperation hypothesis explains inter- and intraspecific variation in the IA response. Future studies on IA, but also cooperation, should therefore take the socio-ecology of the species into account when designing experiments and interpreting results. Regarding the affective component of IA, we showed a limited effect of inequity on the level of arousal in bonobos but suggest that future research should aim to implement more samples and alternative physiological measures to complement the standard behavioral measures of IA.

Author's Contributions

JV and JMGS developed the study. Formal statistical analyses were done by JV. The manuscript was written by JV with editing from JMGS.

Acknowledgements

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General discussion

The main goal of my PhD thesis was to complement the existing knowledge about the proximate mechanisms of cooperation in bonobos. By implementing different experimental paradigms, I aimed to explain the variability in the level of prosociality and inequity aversion from a socio-ecological perspective. For the experimental part of my study, I focused on the bonobo group of Zoo Planckendael. Although this social group consists of individuals of both sexes and different age classes and backgrounds, the results obtained from one study group should not be generalised to the species level. Additional research is therefore required to complement my findings in order to make conclusions about the species (see below). I used a combination of novel and pre-validated experiments and collected behavioural and physiological data to obtain a multi-dimensional understanding of the proximate mechanisms of cooperation in bonobos. As a general framework, I used an adjusted version of the cooperation model by de Waal and Suchak (2010) and Yamamoto and Takimoto (2012), which links prosociality and inequity aversion as the proximate mechanisms of cooperation with tolerance and the preference for similarity as additional relevant factors. Before focusing on prosociality and inequity aversion, I conducted three studies to establish some methodological aspects. In the following section, I will briefly discuss the general findings and will discuss how they relate to the general cooperation framework and the socio-ecology of bonobos. In the last section, I will focus on some limitations of this study and future perspectives.

Methodology matters

When I set about this PhD, one of my main concerns was to avoid pitfalls that had been identified in previous prosociality and inequity aversion studies in primates. Often critics argued that some methodological issues were at the base of contrasting and negative results. These include the actual setups or paradigms, which will be discussed later, but also involve measures of food preference, methods to quantify social bond strength and the complex relationship between physiology, stress and the affective component of inequity aversion. Therefore, I aimed to study some of these basic premisses before I would endeavour to investigate prosociality and inequity aversion itself.

To determine which food items to use in the experimental paradigms of this thesis, I investigated the food preference of bonobos (Chapter 2). I showed that bonobos preferred fruits over vegetables and that their food preference correlated with the total energy and carbohydrate content of the food items. These results support the idea that food preference of bonobos follows the general pattern of other great apes and that their common preference for the same nutrients may have shaped their frugivorous diets (Hohmann et al., 2010; Remis, 2002; Ungar, 1995). The results of this study are of course not totally unexpected, and any zookeeper could tell me that bonobos prefer fruit, or sugar rich food items over most vegetables. Already in the 1970 and 1980s, field ecologists like Claude Marcel Hladik, Katharine Milton and David J. Chivers have demonstrated that primates select their foods based on the nutritional contents while avoiding toxins, as well as on availability of the food items in space and time (e.g. Chivers et al., 1986; Chivers & Hladik, 1980; Hladik, 1978; Milton, 1979, 1981, 1984). And because it is a central component of a species' biology, feeding ecology is a huge subdiscipline in primatology (Hohmann, 2009; Hohmann et al., 2012; Raubenheimer et al., 2015; Righini, 2017). Also for wild bonobos and chimpanzees it has been shown that they select food items high in non-structural carbohydrate content while avoiding foods with high levels of antifeedants (e.g. Hohmann et al., 2006, 2010; Reynolds et al., 1998; Wrangham et al., 1998). The data analysed in my PhD merely roughly scratched the surface of food preference in bonobos, and one could write an entire PhD on this topic. However, I still decided to include food selection as part of my PhD because data for captive bonobos had not been published, while they are available for other ape species (e.g. Berkson, 1962; Remis, 2002, 2006) and because I wanted to know which food items I could use for the behavioural experiments later in the study.

The moderate to strong positive correlations between food preference and energy and carbohydrate content show that, as could be predicted and has been reported for other primate species, bonobos indeed prefer sugar and energy rich food (Hickmott et al., 2021; F. Y. Huang et al., 2021; Laska, 2001; Laska et al., 2000; Remis et al., 2001; Remis & Kerr, 2002; Visalberghi et al., 2003). The negative correlations between food preference and several micronutrients are likely by-products of the bonobos' overall preference for energy-rich food items, but also suggest that the bonobos do not actively seek to consume these nutrients in the food choice experiments in captivity. In the wild, however, bonobos have been shown to consume food items potentially to meet micro nutritional or mineral dietary requirements. For example, bonobos in Luikotale eat aquatic plants presumably to supplement their diet with iodine (Hohmann et al., 2019) and in Kokolopori, bonobos appear to consume fungi to increase their energy uptake but potentially also to supplement their diet with sodium (Lucchesi, Cheng, Wessling, et al., 2021).

Food choices are based on food availability, chemical defence and nutritional content (J. E. Lambert & Rothman, 2015). Food availability in the wild varies in time and space and is the most fundamental factor influencing an individual's feeding choice (J. E. Lambert & Rothman, 2015; van Schaik et al., 1993). The chemical defence of foods evolved through natural selection for thwarting herbivory. Flowering plants produce a diversity of defensive plant chemicals, i.e. secondary metabolites, that either inhibit digestion or are true toxins (Feeny, 1976; Harborne, 2001; Iason et al., 2013). The ways in which these plant chemical defence impacts primate feeding decisions is to a large extent still unknown. Although differences between species exist, in general, primates are predicted to avoid these secondary metabolites (Ganzhorn, 1989; J. E. Lambert & Rothman, 2015; Milton, 1979). In addition to the food availability and defensive chemistry of foods, animals must also cope with the variability of the nutritional content of food items. Nutrients not only vary between plants but also with the stage of the plant and ripeness of the fruits (J. E. Lambert & Rothman, 2015). Wild animals respond to variation in nutrient supply or demand by compensatory adjustments in their foraging behaviour and physiological processing of nutrients (J. E. Lambert & Rothman, 2015; Raubenheimer et al., 2012). While ripe fruits are typically high in easily digestible sugars, contain moderate amounts of fibrous material and are lower in secondary metabolites, young leaves contain lower levels of sugar but higher levels of protein (Houle et al., 2014). The weekly diet of the bonobos at Planckendael consists of 23 commercially available food items, with differing nutritional compositions to meet the nutritional requirements of bonobos (J. M. G. Stevens, 2020). The food items include ripe fruits and vegetables that have been bred for increased sweetness and palatability and thus contain high levels of sugar and energy but are low in secondary metabolites (B. Holland et al., 1991; Milton, 1999; Rafert & Ono Vineberg, 1997). In addition to the mixture of vegetables and fruits, the bonobos have daily access to browse. Thus, the bonobos are not expected to experience a deficiency in certain nutrients in their diet. The question rises whether bonobos, that have access to this abundant, balanced buffet of highly palatable and nutritious food items, would select for specific nutrients during the relatively short and artificial paired-choice tests. Rather than to balance their nutritional intake, the bonobos may simply select tasty foods. Whereas sweetness is expected to contribute to the preference among primates, astringency, bitterness or sourness may reflect alkaloids or tannins and therefore may be the cause of food rejection (Hayakawa, 2015; Nishida et al., 2000; Rozin & Vollmecke, 1986). Great apes, including humans, and other primates show some between-species differences in taste perception of alkaloids and tannins but have a broadly similar threshold and preference for sweetness (Hladik & Simmen, 1996; Remis, 2006; Remis & Kerr, 2002; Simmen & Charlot, 2003; Vigues et al., 2009). Thus, like chimpanzees, gorillas and humans (Remis, 2006; Remis & Kerr, 2002; Sclafani, 2001), the bonobos in my study likely used sugar as criterion for food selection. Also, several nutritious foods of the human diet, such as potatoes, nuts and most plants parts that contain high levels of starch, fat or proteins have little taste. In contrast to the clear response to soluble sugars, there is no clear taste response to these highly nutritious compounds, which has been related to the relatively recent radiation of flowering plants. While sugar has always been present in plant metabolic pathways and may have been concentrated in fruit of the early angiosperms, fatty fruits evolved more recently (Hladik & Simmen, 1996). Some have suggested that tactile cues rather than a typical taste may motivate humans and animals to select for these nutrients (Heinze et al., 2015; F. Y. Huang et al., 2021; Mccrickerd & Forde, 2016). Taste perception of amino acids and proteins is also unclear. No clear link has been found between the role of essential amino acids and their palatability and protein intake by primates may to a large extent be regulated by the post-ingestive effects of proteins (R. J. Haefeli & Glaser, 1990; Robert J. Haefeli et al., 1998; Larsson et al., 2014). This supports the idea that the food choices in the paired-choice food test in zoo housed bonobos are almost entirely based on the sweet taste, and therefore sugar content, of the food items. Although this is outside of the scope of my study, to fully investigate the relationships between different nutrients and how bonobos balance their nutritional intake by selecting upon specific nutrients, a more multi-dimensional data analysis tool could be implemented. Graphical approaches, like the right-angels mixture triangle (RMT) and the amounts-based nutritional geometry (ABNG), have been proposed as complementary geometric frameworks for nutritional analysis, in which various facets of animal nutrition can be interrelated (J. E. Lambert & Rothman, 2015; Raubenheimer, 2011; Raubenheimer et al., 2015). Using these methods, numerous studies have demonstrated the importance of several macro and micronutrients in different species (reviewed in Nie et al., 2015; Raubenheimer et al., 2009).

There are of course drawbacks to my study design. The nutritional content of each of the food items I used, was obtained from an available databank, which is regularly updated and contains extensive information on the nutrient content of foods commonly consumed in the UK (B. Holland et al., 1991). While this information represents the average nutritional content of many items of the same food type, intraspecific variation in nutrient composition is inevitable. Ideally, nutritional analyses of each of the used food items of each food type should have been carried out to avoid this potential bias. However, since the paired-choice tests were conducted over several months, many different food items of the same food type were used. To correlate the actual nutritional content of each of the items of the same food type to the food preference results of that food type, we would need to analyse the nutritional content of each item and calculate an average nutritional value for each food type, which is very similar to how the dataset, that I used for the nutritional information, was created (B. Holland et al., 1991).

To determine food preferences in animals, researchers typically investigate which of two food items subjects move toward first, reach for first or select manually (Fernandez et al., 2004; Finestone et al., 2014; Laska et al., 2000; Remis, 2002; Sánchez-Amaro et al., 2019; Shorland et al., 2019). I also chose to use the paired-choice food test because it only requires very limited training of the subjects and does not involve technical and expensive set-ups. An important drawback of this manual method for testing preferences is their vulnerability of cueing effects (Beran, 2012). The researcher might for example hold one item closer to the animal than the other or may (unintentionally) look longer at a certain food item. These subconscious cueing effects may impact the behavioural responses of the subjects and therefore bias the food choices (Hopper et al., 2019). Bonobos have been shown to follow conspecific gaze but also follow the gaze of humans (Herrmann et al., 2010; F. Kano & Call, 2014). Gaze following has been suggested to be a reflexive response that evolved for its adaptive benefits like guiding the gaze follower to important resources, such as food (Krupenye, MacLean, et al., 2018; Tomasello et al., 1998). Therefore, bonobos are expected to be very sensitive to cuing effects. An additional drawback of this method is the visibility of the food items. Food rewards are highly potent stimuli (see also below) and subjects may reach for an item and thus quickly choose a food item without evaluating the other option (Hopper et al., 2019). In order to avoid these impulsive choices, cognitive studies have often covered the food rewards (e.g. Claidière et al., 2015; Horner et al., 2011) or represented them with symbols (Boysen et al., 1996; Tanaka, 2003). To avoid the biases and confounds introduced by these manual tests, alternative approaches have used eye-tracking (Howard et al., 2017; Wallis & Miller, 2003) or touch-screen devices (Hopper et al., 2019; Huskisson et al., 2020; Vonk et al., 2022). During the food preference trials, I also showed the photograph of each food item to the individual to help subjects to choose when the distinction between the cubes of the actual food items was unclear (Huskisson et al., 2020; Tabellario et al., 2020). Initially, I also aimed to use these photographs in a touchscreen food choice paradigm (cfr. Hopper et al., 2019; Huskisson et al., 2020; Vonk et al., 2022) to compare the food preference results between methods. However, touchscreen methods for assessing preferences also require validation of the presented photographs to demonstrate that subjects perceive the images as representing the actual items depicted (Vonk et al., 2022). Due to practicalities and time constraints, I was therefore unable to implement this touchscreen task in my PhD project.

The bonobos' preference for the familiar food types is likely based on their previous experiences with those food types (Yeomans, 2006). The novel food items were labelled novel because they were not part of the weekly bonobo diet in Zoo Planckendael. However, it is not unthinkable that several of the bonobos had experienced the novel food items prior to my study. Bonobos are long-lived species and the diets in zoos varied across the years, and are updated regularly. Some individuals in my study have moved between zoos because of breeding strategies, and likely experienced different diets in different zoos (J. M. G. Stevens & Pereboom, 2020). Finally, some of the novel food items used in my study, like for example grapes and pumpkin, are occasionally added to the weekly diet as an extra treat (personal obs.). Thus, the ten food items that were not part of the weekly diet should perhaps be considered 'rare' rather than completely novel or unknown. Although this nuance is important when investigating the effect of novelty on individual food choices, the aim of my study was to determine which food items to use in future experimental paradigms. The food rewards for the experimental paradigms of prosociality (Chapter 6) and inequity aversion (Chapter 7) were selected based on the relative preferences of the different individuals. To avoid interference with the daily feeding sessions, I chose to select green grapes as the high value and parsnip as the low value food items, because here the preference was conspicuous across all individuals. For some food types, large inter-individual differences in food preference were found. For example, dried apricot would have been a useful high value food reward, since it contains a lot of sugar, and is practical to buy and store, but one individual in my sample had an absolute aversion for this food item and never selected the dried apricot. Since taste perception depends on the expression of chemosensory receptors, which differs between but also within species, differences in receptor genes could explain these individual preferences for certain foods (Hladik & Simmen, 1996; Parry et al., 2004; Remis, 2006). This supports the use of elaborate paired-choice tests to determine which food items to use in future experiments. Without such objective comparisons, assuming similar preferences for all subjects of the species may lead to selection of inappropriate food rewards for the experimental paradigms, which might have an important impact on the participation and motivation of certain individuals.

It had been suggested that looking at endocrinological responses in cooperation studies might be useful to better understand proximate causes of cooperative behaviour (e.g. Soares et al., 2010). In my PhD, I focused on cortisol to measure the level of arousal and stress (see also below). To obtain a biological validation for the use of salivary cortisol as a non-invasive measure of stress and arousal in bonobos, I investigated the urinary and salivary cortisol response after a psychological stressor (Chapter 3). The time-lag between the stressor and the maximal cortisol concentration was similar in both media (after 160 min). Urinary cortisol levels reached their maximal levels much quicker than what was reported for peak excretion of cortisol in primates after injection (Bahr et al., 2000). The time-lag in salivary cortisol rise after the stressor was much longer in my study than the reported delay of 30 to 45 minutes after the injection of cortisol in humans and chimpanzees (Gozansky et al., 2005; Heintz et al., 2011; Kirschbaum & Hellhammer, 2000). These differences are likely due to the different time course of cortisol in response to a physiological and psychological stimulus (Dayas et al., 2001; Jacobson, 2005; Oswald et al., 2004). I also found inter-individual variability in the cortisol patterns during the control and stress day, which emphasizes the importance of including individuals as their own control in a repeated measures design (Honess & Marin, 2006). The results suggested that salivary cortisol can be used as a non-invasive measure to detect the short-term effect of a specific event and that the relevant sampling window to detect a change is 15 to 40 minutes after the event. However, the inter-individual variability in the stress-response and the high sensitivity of salivary cortisol should be considered when interpreting results. Note that the cortisol increase in this study occurred in response to a severe stressor: the veterinarian who walked through the building with a blowpipe while calling each bonobos' name. It is likely that the vocalisations of the conspecifics towards the veterinarian might have increased the cortisol response in the bonobo subjects, prolonging the effect of the stimulus. This could explain the strong and relatively longer cortisol response that we found in our study, but also raises the question whether a similar response is expected in situations with a less severe social stressor. While previous studies looked at the effect of a variety of events on the cortisol levels in great apes (Behringer et al., 2009a, 2013, 2020, 2022; Wobber et al., 2010), additional research is needed to expand our knowledge on the sensitivity and the pattern of urinary and salivary cortisol to a wide variety of stimuli.

Although stable inter-individual differences in HPA-axis activation have been shown (Mormède et al., 2007; Sheriff et al., 2011; Taff et al., 2018), healthy individuals are expected to have an appropriate regulation of glucocorticoid levels (Taff et al., 2018). Cortisol excretion in response to a stressor serves to restore homeostasis. Therefore, cortisol level rise reflects a threat to homeostasis but also an organism's ability to restore homeostasis (Karatsoreos & McEwen, 2010; L. M. Romero & Beattie, 2022). An interruption of the diurnal decrease in cortisol has therefore been interpreted as a potential HPA axis dysfunction or as an indication of a long-term stressor (De Jong et al., 2000; Ross et al., 2014). Atypical cortisol patterns in humans for example have been linked to posttraumatic stress disorder (Yehuda et al., 2005), depression (Hsiao et al., 2010) and history of maltreatment (Valentino et al., 2021). Therefore, the aberrant cortisol patterns in the study subject Hortense, the only wild-caught animal in my study, might be indicative of underlying issues with her homeostatic regulation potentially due to historical events during her life.

One drawback of this study is that we did not take the urination interval into account. By implementing the regular urine sampling every hour, we limited the accumulation of urinary cortisol over a longer period. However, cortisol accumulates over a shorter time if the bonobos urinated more often than once per hour. For example, while every subject might have urinated more frequently, Hortense is always very motivated to provide urine samples to get a reward. During the second day of the experiment, the test day, the presence of the keepers and researchers in the corridor might have stimulated her even more to provide urine samples in the morning, resulting in a lower urinary cortisol increase when comparing with the other individuals. Ideally, in future studies the urination frequency of each subject should be considered to investigate the urinary cortisol response.

While urinary and salivary cortisol provide an insight into the HPA-axis activation in response to the psychological stressor, the HPA activation is only one aspect of the stress response. The other major physiological responses are 1) the activation of the Autonomic-Nervous System (ANS), including the Sympathetic Nervous System (SNS) and the Para-Sympathetic Nervous System, and 2) The immune system (Moberg & Mench, 2000). Therefore, additional stress markers should be used to obtain a more comprehensive view on an individuals' stress response (Ali & Pruessner, 2012; Fuentes et al., 2011; MacDougall-Shackleton et al., 2019). For example, the salivary enzyme alpha amylase (sAA) has been suggested to be a good proxy for the activation of the sympathetic nervous system (Rohleder et al., 2004). In bonobos, an increase in sAA activity has been linked to a variety of stressors, such as giving birth, a transfer and an integration of new group members (Behringer et al., 2012). In non-stressful conditions, sAA levels were correlated with salivary cortisol levels while in stressful situations this was no longer the case. Other studies investigated the cortisol to sAA ratio to investigate the relationship between the HPA axis and SNS. They showed that for example in humans and rhesus monkeys, early life adversity resulted in an asymmetry in the cortisol-sAA ratio (Gordis et al., 2008; Petrullo et al., 2016). Dehydroepiandrosterone (DHEA) is also secreted during the stress response and has an opposite effect to cortisol in regulation of HPA axis activity (Ebeling & Koivisto, 1994; Ferrari et al., 2008; Majewska et al., 1990). Another physiological stress marker is chromogranin A (CgA), which is a glucoprotein pro-hormone that is released along with catecholamines from the adrenal medulla and the sympathetic nerve endings when the SNS is stimulated (Dimsdale & O'Connor, 1992). The use of salivary CgA has therefore been used as biomarker of the SNS in several mammalian species (Dai et al., 2020; Y. Huang et al., 2017; Lensen et al., 2019). To conclude, future studies should aim to use panels of different biomarkers, ideally from multiple systems that respond to stress, to obtain a more comprehensive view of the stress response (e.g. Filaire et al., 2009).

The cooperation model (Fig 1.1. p 15) starts with the premise that cooperation is based on the psychological mechanisms that stimulate a preference for similarity. Animals, including humans, prefer to associate and interact with genetically related individuals and with unrelated individuals that are more similar in traits like age, sex and personality (Carter et al., 2015; de Waal & Luttrell, 1986; Gerber et al., 2021; McPherson et al., 2001). These frequent interactions can result in long-term social bonds that are often characterized by regular exchanges of benefits and successful cooperation. Thus, the proximate mechanisms of cooperation, prosociality and inequity aversion, are also expected to rely on the preference for similarity (Yamamoto & Takimoto, 2012). Therefore, I aimed to investigate the preference for similarity in zoo-housed bonobos. More specifically, I studied whether relationship quality in bonobos was influenced by the genetic sex combination of the subjects and the similarity in personality between friends. I showed that a composite measure of relationship quality, which had been previously used in zoo-housed bonobos (J. M. G. Stevens et al., 2015), could reliably be replicated on an entirely different dataset of 39 bonobos, and could be used to test a preference for similarity in personality (Chapter 4). First, as can be expected, I found more valuable relationships between related bonobo dyads, including mother-son and mother-daughter dyads (Chapter 4). Genetically related individuals benefit from strong and affiliative associations through indirect fitness benefits (Hamilton, 1964b, 1964a). Associations with kin increase the chance of more successful cooperative partners and decrease the chance of defection. In bonobos, both in the wild and in zoos, the strongest bonds are found between mothers and their adult sons (Furuichi & Ihobe, 1994; T. Kano, 1992; J. M. G. Stevens et al., 2006; Surbeck et al., 2011). These strong mother-son preferences largely influence association patterns in bonobos (Surbeck, Girard-buttoz, et al., 2017). The strong associations promote agonistic support from bonobo mothers, allowing the sons to increase their dominance rank and their mating success (Furuichi, 1997; Furuichi & Ihobe, 1994; T. Kano, 1992; Surbeck et al., 2011, 2019). For the mothers this might be a way to increase their number of grand-offspring through support of their adult sons, resulting in an indirect fitness benefit for themselves (Furuichi, 1997; Schubert et al., 2013; Surbeck et al., 2011). Based on this, high levels of prosociality and low levels of inequity aversion are expected between mother-son dyads. Second, I found high quality relationships among females, which corresponds to the homophily principle, that predicts same-sex dyads to form strong bonds (McPherson et al., 2001). Female-female friendships in zoo-housed bonobos were equally compatible, but were less valuable than mother-son dyads. This corresponds to the fact that female-female interactions in bonobos are tolerant, but involve lower levels of affiliation than mother-son relationships females (Hohmann et al., 1999; Hohmann & Fruth, 2002; J. M. G. Stevens et al., 2015). Thus, high levels of prosociality and low levels of IA are expected between female-female bonds, which would result in more successful cooperation, like for example agonistic coalitions (see below). Third, the relationship quality results confirmed the weak social bonds among bonobo males that only rarely engage in positive interactions or within-group coalitionary support (Hohmann & Fruth, 2003b; Ihobe, 1992a; T. Kano, 1992; Surbeck et al., 2012; Tokuyama & Furuichi, 2016). Male-male dyads are therefore expected to show lower levels of prosociality and higher levels of inequity aversion, which would explain the lower levels of successful cooperation. Finally, I also showed, for the first time that, similar to other species, including humans, (Carter et al., 2015; Laakasuo et al., 2020; Massen & Koski, 2014; Morton et al., 2015), zoo-housed bonobos were more likely to form valuable relationships with individuals that were similar in personality, more specifically their level of Sociability. The preference for individuals with similar personalities might result in bonds that are more trustworthy (Massen & Koski, 2014). In this case, similarity in Sociability might result in reliable and valuable relationships through reciprocity in the similarly affective behavioural tendencies. It can be predicted that bonobo dyads with more similar Sociability scores would be inclined to show more prosociality and less inequity aversion, which eventually would lead to more successful cooperation (see Chapter 1).

Although the popularity of using multidimensional measures of relationship quality and personality has increased, it is important to evaluate the biological relevance of the different composite measures. First, social relationships are often asymmetric (Silk, 2002b). Group members differ in their resource holding potential, i.e. the capacity to obtain and preserve a resource, and their competitive power based on dominance or rank or other factors, like supporting group members (Smith & Parker, 1976). Dominant individuals are more likely to display aggressive behaviours than subordinates, which may result in asymmetric relationships in terms of the value that individuals attach to their relationship with their partner (Schino et al., 2003; Silk, 2002b). Additionally, individuals may also trade different resources following a biological market (L. Barrett et al., 1999; Noë & Hammerstein, 1994, 1995). Thus, individuals of a dyad may exchange different behaviours or in different frequencies, which may increase the degree of asymmetry in their relationship. To measure the asymmetrical nature of relationships, the bidirectional behavioural measures like grooming and aggression frequency should be decomposed into individual scores for behaviours given by and received from each member of the dyad (Majolo et al., 2010; McFarland & Majolo, 2011). Since relationships between friends are based on emotionally mediated reciprocity, highest asymmetries are expected to be found in the most valuable relationships (Roberts, 2005; Schino & Aureli, 2010).

Second, the question remains to whether the composite structure of social relationships is reflected in how individuals perceive their own relationships. While partners are not expected to consciously distinguish among the three components, different emotional responses preceding and following social interactions may be expected and each component may be important in a different situation (Majolo et al., 2010). Overall, the results of chapter four show that also bonobos prefer to associate with more similar individuals, which has been suggested to be the basic psychological trait of the cooperation model (de Waal & Suchak, 2010; Yamamoto & Takimoto, 2012). The model predicts that strongly bonded partners will show higher levels of tolerance, more prosociality and less inequity aversion, which could eventually lead to more successful cooperative interactions. Indeed, the female preference to associate with their adult sons and with other females results in tolerant and highly successful cooperative interactions against other males (Furuichi, 1997; T. Kano, 1992; Parish, 1994; Surbeck et al., 2011; Tokuyama & Furuichi, 2016). Following socioecology theory, individuals are also expected to form strong affiliative relationships with their cooperative partners (Sterck, 1997). While this is true for mother-son dyads, agonistic support between female bonobos is not correlated to the strength of relationships but simply facilitated by being associated in the same party (Moscovice et al., 2017; Tokuyama & Furuichi, 2016). This suggests that female bonobos seem to choose female coalition partners rather opportunistically instead of forming closely bonded alliances (Nurmi et al., 2018; Surbeck & Hohmann, 2013; Tokuyama & Furuichi, 2016). Agonistic support by males against other males has occasionally been observed in wild (Ryu et al., 2015) and zoo-housed bonobos (Furuichi & Ihobe, 1994; Idani, 1990b; J. M. G. Stevens et al., 2006; Surbeck, Girard-buttoz, et al., 2017). While we found that bonobo females are likely to form high value relationships with other females, it is also reported that young immigrant female bonobos associate with the older resident females, i.e. the specific senior females, of a bonobo community (Furuichi, 1989; Idani, 1991; Toda & Furuichi, 2020, 2022). The young immigrant females initiate social interactions with the resident females, which allows them to integrate in the new group and increase their social status (Moscovice et al., 2015; Parish, 1994; J. M. G. Stevens et al., 2006, 2008; Surbeck & Hohmann, 2013). The senior resident females might benefit from interacting with the younger immigrants through an increased number of future grand-offspring that their sons can produce (Schubert et al., 2013; Surbeck et al., 2011). The tolerance of resident females towards immigrant females depends on the costs imposed by the immigration, like for example feeding competition (Kahlenberg et al., 2008; Printes & Strier, 1999; Riveros et al., 2017). Given the age- and tenure-related female dominance hierarchy in bonobos, older females may suffer little competition, while younger resident females may need to use aggression to dominate the younger immigrant females (Furuichi, 1989, 1997; Furuichi & Ihobe, 1994; Parish, 1996). This is supported by the fact that older resident females show lower rates of aggression against immigrant females than younger resident females (Toda & Furuichi, 2020). Thus, while bonobos prefer to bond with similar others in some situations, they might also benefit from associating with more dissimilar individuals. This could also explain the variation in relationship value and incompatibility in my study (Chapter 4). Especially in a context where certain attributes of a partner, like the dominance rank position or the strength in a fight, impact the outcome of cooperative acts, individuals may benefit from choosing the most competent individual rather than individuals that are more similar in certain traits (Chapais, 2006). In this case, individuals should be able to identify and recruit the most valuable partners, which can be done by selectively investing in relationships with potentially valuable conspecifics (Gerber et al., 2021).

Indifferent hippies behave out of self-interest

As food sharing has been suggested to be the best candidate for prosocial behaviour in naturalistic conditions (Jensen, 2016b), food sharing experiments have been used to investigate prosociality and cooperation in many animal species (Dale, Despraz, et al., 2019; Feistner & McGrew, 1989; Horn et al., 2020; Jensen, 2016b; Yamamoto & Furuichi, 2017). Also in bonobos, previous studies focused mainly on food sharing as a proxy for prosocial behaviour, leading to popular notion that bonobos are more tolerant compared to chimpanzees, and that self-domestication has lead to tolerance, food sharing and prosociality in bonobos, perhaps similar to what happened in humans (Hare, 2017; Hare et al., 2012; Hare & Wrangham, 2017 - see Chapter 1). To provide additional information about prosocial behaviour in bonobos, I used three provisioning paradigms with a different experimental context (Chapter 5 and 6). They were all free choice group experiments, allowing for more naturalistic social interactions (Cronin et al., 2017).

First, in Chapter 5, I used a novel juice provisioning experiment in a group of nine bonobos, which had previously been used to study prosociality in sanctuary housed chimpanzees (van Leeuwen et al., 2021). I found that the bonobos provisioned fruit juice to group members throughout the experiment. Most pushing was done by the dominant female, who monopolised the provisioning side of the set-up and who obtained juice herself in in more than half of the pushing acts, indicating the potentially selfish nature of her pushing. Together with two other high-ranking females, which had the highest quality relations with the alpha female, this trio monopolised the fountain, impeding the participation of other individuals, including the alpha male, who was the son of the alpha female. Altogether this resulted in pushing frequencies that were lower than what was reported for an intolerant chimpanzee group (van Leeuwen et al., 2021). I suggested that the differential participation of female and male bonobos was not simply the result of their dominance rank, but might reflect the sex-specific association and cooperation patterns of wild bonobos (Moscovice et al., 2017, 2019; Nurmi et al., 2018; Surbeck, Girard-Buttoz, et al., 2017). The gregariousness of the female bonobos allowed them to aggregate around the limited resource, which may have hindered participation by the alpha male. In this case, the affiliative bonds among females may enable them to tolerate one another around the resource, in this case the set-up (Parish, 1994, 1996). Surprisingly, I found the most Valuable relationships among females, which corresponds to previous studies that have emphasized female-female bonding in bonobos (Parish, 1994, 1996). However, other studies, that included more and larger study groups, have shown that bonds among females are indeed strong but that female-male bonds, and especially between mothers and their sons, are stronger (Furuichi & Ihobe, 1994; T. Kano, 1992; J. M. G. Stevens et al., 2006, 2015). Several explanations have been provided for these contrasting conclusions (J. M. G. Stevens et al., 2006). The studies that have emphasized female-female bonding in captive bonobos included bonobo groups where only one adult male and several adult females, including mother-daughter pairs, where present (Parish, 1994, 1996). Female bonobos were therefore more likely to choose other females as bonding partners. Other study groups were recently formed, which may have overemphasised female bonding, because when females migrate to new communities in the wild, they engage in interactions with resident females (J. M. G. Stevens et al., 2006). Also in my study, the instable group composition during the collection of the relationship quality data could explain the higher relationship Values among female bonobos. At the time of behavioural data collection in Zoo Planckendael, the bonobo group was small because of the delayed construction of the new bonobo building and thus the delayed arrival of new bonobo families and because the group was split in two subgroups because of an aggressive conflict. Thus, the higher relationship Values among females in my study may also reflect the frequent interactions during the instable social context. Interestingly, the female aggregation around the set-up and the lack of participation by the males in my study are also similar to the findings of the previous studies that used an artificial “fishing” site in bonobos to investigate the role of female bonds to occupy valuable resources (Parish, 1994, 1996). The authors stated that the strong social relationships among female bonobos result in coalition formation and successful cooperation, allowing them to control the highly desirable food. Although these results are based on atypical bonobo groups, the affiliative and tolerant bonds among females seem to reflect the behaviour of females in specific contexts the wild. Frequent affiliative interactions among females are also observed between newly immigrated females and the resident females of the new community and during intergroup encounters group (Furuichi, 2011; Idani, 1991; Toda & Furuichi, 2020, 2022). Thus, the findings of Chapter 5 show that the bonobos in my study behaved out of self-interest but also show the impact of a limited sample size and the social context on the outcome of experimental studies. At the time of this experiment, the Planckendael group was small (see above) and not all individuals learned how to operate the juice fountain. Out of the five individuals that knew how to handle the device, only four subjects participated and more than 90% of the pushing was done by the most dominant female. This study shows the importance of appropriate study designs. While all bonobos were familiar with drinking apple juice, which they had received previous to this experiment during eye tracking tasks (Lewis et al., 2021), and had the opportunity to interact with the pushing box before, only five individuals showed sufficient interest in and understanding of the set-up to pass the training phase. One of the major difficulties in this study, was to activate the bonobos to push the button. Interestingly, in a study where great apes could obtain a food reward by either pushing or raking the reward, subjects overwhelmingly chose the latter, as raking is a behaviour they daily use to obtain out-of-reach food items (Mulcahy & Call, 2006). This suggests that experimental paradigms should preferably include set-ups that require subjects to pull food rewards towards themselves rather than to push and should maximize the ecological validity of the set-up (see below). Ideally, this juice experiment should be replicated in a larger bonobo group and over a longer period of time, including the necessary controls and an adjusted set-up. Also, to investigate how the presence of certain individuals influences the occurrence of prosocial acts in a free-choice group setting, future studies could remove certain individuals, like the most dominant females, from the experimental test to investigate the socio-ecological hypotheses. Alternatively multiple set ups could be used in larger groups, spaced out throughout the enclosure so that individuals cannot monopolise all access to a single button or juice fountain.

After trying this novel set up to induce prosocial food sharing, in Chapter 6, I used two other prosociality paradigms with different payoff structures, which are more commonly used in various species: the prosocial choice task (PCT) and the group service paradigm (GSP) (Burkart & van Schaik, 2013; Silk et al., 2005). In a group of 13 bonobos, I showed that in both food provisioning experiments, adult bonobos were highly motivated to obtain rewards for themselves, but not to provide food to group members. In the PCT, the bonobos chose the prosocial option by chance and did not discriminate between control and test trials, which supports previous studies that showed a lack of prosociality in bonobos in the horizontal and token PCT (Amici et al., 2014; Tan et al., 2015). This suggests that, like chimpanzees, bonobos behaved indifferently to the welfare of conspecifics (Silk et al., 2005). In the GSP, only subadult bonobos provisioned food items at a rate that was much lower than the previously reported rates for chimpanzees (Burkart et al., 2014). Interestingly, the two females that obtained all grapes during the motivation trials of the GSP, only rarely pulled the set-up during the actual test trials. The purpose of these motivation trials was to make sure that the subjects remained interested in the reward and the set-up until the end of the session. This was to some extent successful, as these females stayed around the set-up and continued pulling during some test trials. On the other hand, the very limited number of pulls in the actual test trials contrasts sharply with the frequent pulling during the motivation trials. Thus, bonobos seem selfish, and are motivated to obtain food rewards for themselves, irrespective of the outcome for social partners. Thus, these motivation trials successfully attract subjects towards the set-up, but they seem to increase competition around the highly valuable food rewards, which might stimulate selfish motivations rather than prosocial behaviour during the test trials (see also below). Thus, based on these two experimental paradigms in de Planckendael group, bonobos, the hippies of the primate world, were indifferent toward their conspecifics, in a degree that is similar to what has been reported for (adult) chimpanzees (Jensen et al., 2006; Silk et al., 2005; Vonk et al., 2008) which contrasts with previous statements about the prosocial bonobos that are eager to share food, even with strangers.

Thus, the absence of prosociality in the Planckendael bonobos contradicts the self-domestication hypothesis, which predicted that high levels of prosociality evolved in bonobos as a result of sexual selection against male reactive aggression, and that proactive prosociality should be considered part of the self-domestication syndrome (Hare, 2017; Hare et al., 2012; Hare & Wrangham, 2017), but do correspond to the human uniqueness hypothesis, which predicted that bonobos would show lower prosociality levels than humans (Burkart et al., 2014; Henrich et al., 2005; Jaeggi, Burkart, & Van Schaik, 2010). Indeed, the level of bonobo prosociality in the three different paradigms was much lower than previously reported prosociality results in humans (e.g. Burkart et al., 2014). My results also fit the cooperative breeding hypothesis, since the independently breeding bonobos are expected to show low levels of proactive prosociality (Burkart et al., 2009; Burkart & van Schaik, 2010). Based on the experiments in this PhD, the empathy hypothesis cannot be confirmed nor contradicted since food sharing is not necessarily associated with empathy (J. R. Stevens & Gilby, 2004).

How can we explain this stark difference between what I observed in Planckendael and the popular notion of the prosocial bonobos, and how do my results contribute to the proposed scenarios of prosociality in humans and bonobos?

First it seems that tolerance around food in bonobos is often exaggerated. While bonobos are seen as non-competitive species, living in a food-rich paradise, intragroup food competition is observed among bonobos in the wild and during the feeding frenzy in some captive groups (Cronin et al., 2015; Nurmi et al., 2018; Surbeck et al., 2015; Vervaecke et al., 1999). Food sharing in the wild is often relatively passive (Fruth & Hohmann, 2018; Yamamoto, 2015; Yamamoto & Furuichi, 2017) and intolerant compared to chimpanzees, as reported in experiments in captivity (de Waal, 1989; Cronin et al., 2015; Jaeggi, Stevens, et al., 2010). This already suggests that bonobos are not expected to show high levels of (proactive) food provisioning of highly preferred food items. In this respect measuring individual and group level food preferences (Chapter 2) is relevant for understanding and interpreting results of food-sharing and food-delivery studies in captivity. This food competition may further be responsible for indifference towards conspecifics, in the food provisioning paradigms where the subjects can see the food and therefore become competitive around the highly preferred food items, like peanuts, grapes or other fruits (e.g. Jaeggi, Burkart, & van Schaik, 2010; Jensen, 2016b; Melis, Warneken, et al., 2011). Typically such high-value food rewards are used to keep apes motivated, but the visibility of food has been shown to obscure prosocial tendencies, possibly because subjects may treat food-related paradigms as competitive situations or due to the lack of inhibitory control in food provisioning contexts (Hirata, 2007; Jaeggi, Stevens, et al., 2010). Subjects may behave indifferently to others' desires to obtain food as a consequence of the intra-group competition over resources, i.e. the food competition hypothesis (Melis, Warneken, et al., 2011). This hypothesis suggests that the lack of prosociality in food-based studies in bonobos, and likely other species, may be the result of the competition around the highly preferred food items, which might even be intensified during the self-benefitting motivation trials of the GSP.

Second, studies stressing "prosociality" in bonobos, have used alternative definitions than the strict definition I used. In fact, the original fox study (Trut, 1980; Trut et al., 2009) and a more recent review about self-domestication in bonobos defined prosociality as "positive and affiliative behaviour and does not imply whether these behaviours are selfishly or unselfishly motivated" (Hare

& Woods, 2017) (see also my comment on how to define prosociality in Box 1 p11). The field of prosociality is plagued with ambiguity resulting in disagreements and confusion about how to define prosocial behaviour but also about its existence across the animal kingdom (Pfattheicher et al., 2022; see also Chapter 1). Because researchers often miss out on providing definitions of their term, they risk using the same term for different concepts and different terms for the same concept, i.e. the jingle and jangle fallacies (Block, 1995). In addition to providing a definition, researchers should acknowledge the multidimensional nature of prosociality and should aim to investigate the different facets of prosocial behaviour using the appropriate paradigms (Decety et al., 2016; Pfattheicher et al., 2022; Tomasello & Vaish, 2012).

Third, I proposed that the prosociality results of previous studies that are considered to be supporting evidence for the bonobo self-domestication hypothesis may rather be the result of an age effect (Chapter 6). The GSP results at Planckendael indeed show that subadult bonobos showed higher food provisioning rates than adult bonobos, potentially because of their lower inhibitory control (Clay & de Waal, 2013b). Most subjects in previous studies that found evidence for prosociality in food delivery tasks were within the age range of 4 – 16 (see Chapter 6 - table 6.6 p 103) (Hare et al., 2007; Hare & Kwetuenda, 2010; Krupenye, Tan, et al., 2018; Tan & Hare, 2013). Thus, the positive prosociality results in these studies may to a large extent reflect the lack of inhibitory control of subadult bonobos. Also, pulling and letting go of a counterweighted apparatus may be a fun and enriching activity, which is perhaps more prominent in younger, more playful individuals. Especially for the subadult subjects, this could be an additional explanation for the higher number of pulls that did not result in food deliveries. Interestingly, the same might be true for the paradigms in which mainly subadult subjects preferred to open doors for conspecifics (e.g. Hare & Kwetuenda, 2010; Tan & Hare, 2013). In addition, the age range of these previous studies include the age range (6-14 years old) that wild female bonobos typically leave their natal group, emigrate to other communities and show high levels of social interactions with adult and subadult residents (Furuichi, 2011). Also in captivity, younger individuals are more likely to interact with newly immigrated individuals (Pfalzer et al., 1995). Also, the observed food sharing with strangers during the experimental studies at Lola Ya Bonobo sanctuary (Tan et al., 2017; Tan & Hare, 2013), may actually correspond to the high motivation of young bonobos to interact with newly immigrated group members (Pfalzer et al., 1995). It is noteworth6y that the orphans in Lola Ya Bonobo are in spatial proximity with other groups, have acoustic and visual contact with individuals that were considered “unfamiliar” in the study, and in a number of cases had even shared the same group before. It has been demonstrated that bonobos have a good social memory of previous group members (Keenan et al., 2016). The interactions between neighbouring groups in the sanctuary likely create a degree of familiarity and motivation to interact, that exceeds that of neighbouring bonobo communities in the wild (Fruth & Hohmann, 2018). This means that the xenophilic prosocial tendencies that have been reported for the bonobos at Lola Ya Bonobo (Tan et al., 2017) warrant cautious interpretation. Altogether, these conclusions provide evidence for the need of a more nuanced view on bonobo tolerance and prosociality.

Indifferent maximisers

My study shows that bonobos might not be the prosocial species as they are usually portrayed, but still, they do show interesting cooperative interactions in the wild. In chimpanzees, cooperation is usually observed during hunting, intergroup territorial defence and within group coalitions and alliances (Mitani & Watts, 2001; Muller et al., 2005, 2011; Surbeck, Boesch, et al., 2017; Wrangham et al., 2006). In bonobos, most hunting seems individualistic (Hohmann & Fruth, 2002, 2008; Surbeck et al., 2009) although some forms of group hunting have been inferred in some populations (Sakamaki et al., 2016; Surbeck & Hohmann, 2008). Intergroup territoriality seems reduced (Badrlan & Badrian, 1984; L. Cheng et al., 2021; Idani, 1990b; T. Kano, 1992; Lucchesi, Cheng, Janmaat, et al., 2021) and bonobos mainly cooperate through coalitionary support, which is reciprocally exchanged between group members (J. M. G. Stevens et al., 2005; Vervaecke, Van Elsacker, et al., 2000) and often occurs between mothers and their sons as well as between unrelated females (Furuichi & Ihobe, 1994; J. M. G. Stevens et al., 2006; Surbeck et al., 2011; Surbeck & Hohmann, 2013; Tokuyama & Furuichi, 2016). Successful cooperative interactions happen between related and unrelated individuals, making bonobos an interesting study species to investigate the stabilising mechanism of cooperation: inequity aversion (IA). In addition to previously established standard behavioural measures, I aimed to investigate the emotional component of IA, using endocrinological measures as a novel approach in Inequity Aversion research (Chapter 7). I found that the bonobos reacted behaviourally to receiving less than a partner, by refusing to exchange tokens and by leaving the experimental area. This confirms the hypothesis that IA is present in bonobos, a species with habitual cooperation mostly with kin and non-kin (reviewed in Massen et al., 2019; Price & Brosnan, 2012). I proposed that within-species variation in the inequity response can be explained by the level of cooperation between partners and found that indeed the variation between dyads in their inequity response, could be explained by characteristics of the tested dyads.

Surprisingly, I did not find a difference in the IA levels between the sex combinations of subjects. Successful cooperation in bonobos is mostly found between mothers and their sons, and in agonistic coalitions among females (Parish, 1994; J. M. G. Stevens et al., 2006; Surbeck & Hohmann, 2013). Cooperative interactions among male bonobos and between males and unrelated females occur much less frequently and are very context dependent (Hohmann & Fruth, 2003b; Surbeck & Hohmann, 2013), which likely relates to limited benefits gained through these coalitions. Within-group coalitions between bonobo males are rare, seldom injure there opponent and are never directed towards females (J. M. G. Stevens et al., 2006; Surbeck, Boesch, et al., 2017; Surbeck, Langergraber, et al., 2017; Tokuyama et al., 2019; Vervaecke, de Vries, et al., 2000a). Based on these differences in successful cooperation between the sex combinations, I expected that the tolerance to inequity would vary accordingly. However, rather than the sex combinations, I showed that the level of IA was influenced by the relationship value between individuals. Although mother-son and female-female dyads had the strongest social bonds, the relationship values within these sex combinations also showed some level of variation (Chapter 4). The tolerance towards inequity decreased with increasing social bond, which fits the hypothesis that, like in humans, closely bonded bonobos tolerate inequity while weaker bonded pairs prefer more equal distributions (Clark & Mills, 2004; Loewenstein et al., 1989). Thus, my results corroborate the suggestion that the relationship between partners has an important impact on the different aspects of cooperation (Burkart et al., 2014; Dale et al., 2020; de Waal & Suchak, 2010; Mcauliffe & Thornton, 2015; Molesti & Majolo, 2016; Range et al., 2012; Suchak et al., 2014).

While the bonobos reacted to receiving less than a partner, they never responded when receiving the more preferred reward. Although the bonobos might have been able to recognize that they received more than a partner during the experiments, they continued to exchange with the experimenter and to accept the more valuable rewards. Thus, I did not observe any negative behavioural response to advantageous inequity. It is likely that the mechanisms that allow individuals to compare their payoffs to those of others and to notice when they receive less, should also allow them to recognize situations in which they receive more (Brosnan, 2011). Note that this is the point where the two proximate mechanisms of cooperation in my study come together. On the one hand, bonobos focused on their own gain by self-benefitting from prosocial acts and by reacting to receiving less than a partner. On the other hand, they did not provide benefits to group members, even though they could have done so without any cost for themselves (PCT), and never reacted to receiving more than their partners. This suggests that, at least in in food-based paradigms, the Planckendael bonobos can be considered to behave as indifferent maximisers.

Considering the affective component of IA, surprising results were found. The results on the salivary cortisol levels show that subjects were more aroused after the advantageous inequity sessions but not after the disadvantageous inequity sessions. Thus, even though the bonobos did not react behaviourally to being overcompensated, they were more aroused when receiving the more valuable reward. The state of frustration across trials, which is considered to be the explanation for the trial refusals in the token exchange task (Massen et al., 2019), was not reflected in the measures of arousal. Further, salivary cortisol levels increased in subjects that were absent longer and in subjects that were paired with close friends. The frequency of rough self-scratching in females seemed to be lower in the disadvantageous condition than the other conditions, while in males scratching frequencies were very similar across conditions. I concluded that these inconsistent conclusions are possibly the result of the relatively small sample size, the limited effect of the unequal treatment on the level of arousal and the short sampling interval between the end of the test sessions and the post-test saliva sample. An additional shortcoming of this study is that all experimental sessions were conducted between 10:45 and 11:45 in the morning. Because of the diurnal variation in salivary cortisol (see Chapter 3), cortisol responses are more difficult to detect in the morning, when levels naturally decrease, than in the afternoon (Czekala et al., 1994). The evidence of the importance of emotions in inequity responses in humans (Cubitt et al., 2011; Matsuzawa & Tanimoto, 2018; McAuliffe et al., 2014) and the differing cortisol results in my study do suggest that future studies should include measures on the emotional component of IA. Given that the salivary cortisol levels are highly sensitive and that changes in cortisol levels can be elicited by many different factors that signal the need to mobilize energy (e.g. increased locomotion, mating, noise exposure) but also to pleasurable experiences (Anita et al., 1982; Mormède et al., 2007; Ralph & Tilbrook, 2016), studies should implement more specific and immediate measures of animals' emotional responses. One promising method to measure emotional responses is infrared thermography (Nieuwburg et al., 2021; Travain & Valsecchi, 2021). Emotions are defined as multifaceted states characterized by universal facial expressions, phylogenetic continuity of expressed behaviours, physiological activation patterns, and unconscious stimuli evaluation mechanisms (Kret et al., 2022; Massen et al., 2019; Travain & Valsecchi, 2021). Basic emotions are widespread across all mammals and even birds and can be divided based on their valence in negative and positive emotions (Jarvis et al., 2005; Reiner et al., 2004). While negative emotions like anger and fear play a crucial role in survival by inducing responses to avoid situations or to cope with stressors through the activation of the sympathetic nervous system (Levenson, 2014; Tooby & Cosmides, 1990), positive emotions such as joy facilitate social bonding through the activation of the parasympathetic nervous system (Fredrickson, 1998, 2001). In response to a stressor, activation of the HPA-axis and secretion of glucocorticoids allows for the 'fight or flight reaction' (Chapter 3), which also results in changes in internal body temperature, i.e. stress-induced hyperthermia (SIH) (Jerem et al., 2018). The parasympathetic nervous system controls the 'rest and digest' functions that cause reduction in heart rate, vasodilation and miosis (McCorryn, 2007). The internal temperature changes as a result of the 'rest and digest' and 'fight or flight' responses also result in consequent external temperature changes. These changes therefore reflect the activation of the autonomic nervous system (Travain & Valsecchi, 2021). Thus, future experimental paradigms should aim to include infrared thermography to measure the emotional responses of animals' during the inequity exchange task but also other cooperative interactions (e.g. see de Vevey et al, 2022).

Experimental testing in artificial worlds: implications for future work

With this thesis, I complemented the existing knowledge about the proximate drivers of cooperation in bonobos and I aimed to explain the findings of the different experimental paradigms from a socio-ecological perspective. Below, I will discuss some limitations of my study and suggest directions for future research.

While controlled experiments in captivity often allow for more detailed investigation of complex behaviours, two of their key shortcomings are their lack of ecological validity and their restricted social environment. The expression of a behaviour depends on the interplay between the evolved psychological predispositions (see Chapter 1) as well as the immediate social environment of the individuals, which includes elements like the group size, structure of the dominance hierarchy and the dispersal pattern of the species (Cronin & Sánchez, 2012). Each of these dimensions impacts the opportunity for cooperation but also the distribution of benefits that result from the cooperative interactions. While modern zoos strive to keep animals in naturalistic conditions, they still differ in many aspects from the situation in the wild. The smaller group sizes, the confined living spaces, the lack of inter-group interactions and the absence of any threats to survival may create social environments where the need and motivation to cooperate may have faded. Within the complex network of social living animals, benefits and services are exchanged following the market law of supply and demands, i.e. biological market (L. Barrett et al., 1999; Noë & Hammerstein, 1994, 1995). The supply and demand determine the bartering value of the exchanged commodities. Depending on factors like rank position, age and sex, the same benefit or service might have a different relative value to different individuals. As a result, the exchange of benefits can either be balanced or unbalanced but results in some sort of equilibrium likely without the need for complex and deliberate cognitive choices. In bonobos, grooming, agonistic support and sex have been suggested as commodities that are either exchanged for itself, or interchanged for one another (Anzà et al., 2021; J. M. G. Stevens et al., 2005; Surbeck & Hohmann, 2015; Vervaecke, Van Elsacker, et al., 2000). Because actors differ in the commodities they can provide, there is a market-like competition for the 'best' partners in a variety of social interactions, including cooperation (Barclay, 2016). In an attempt to maximize the biological relevance of the prosociality experiments, I used free choice group experiments. They allowed for free choice of partner and participation but were limited in time. While such studies provide information on the possible contexts that may elicit prosociality, they should be complemented with behavioural observations outside of the experimental context to fully understand how prosocial acts are exchanged for each other and other commodities in the biological market. Also, the experiments in this study involved high levels of experimenter manipulation: the experimenter was always in close proximity to the set-up, baited the platforms of the prosociality experiments and rewarded subjects after exchanging tokens. While the paradigms are designed to investigate the proximate mechanisms of cooperation, the subjects' performances might result from the combination of intraspecific and interspecific (i.e. with humans) interactions in an artificial environment. Although the Planckendael bonobos could freely choose to approach the prosociality set-ups, trial initiation and participation in the experiment was controlled by the human experimenter. From the experimenter's perspective, such free-choice group experiments allow for more free choices and interactions while from the subjects' perspective, the interventions may seem more controlling and restrictive. Subjects might have been less motivated to participate and to behave prosocially towards conspecifics because they perceived the experimental trials as experimental sessions with the experimenter. This could also explain the very limited, almost non-existent, social interactions between the bonobos during the trials. Therefore, it is crucial that experimental studies distinguish prosocial behaviour in the tasks from prosocial motivations and prosocial acts during naturalistic interactions. While such paradigms show animals' behaviours, they might not reflect the actual preferences or social motivations (House et al., 2014). Subjects might behave prosocially for reasons that do not consider other's welfare like selfish motivations, play behaviour or even as a product of conditioning (Heyes, 2012; see also below). Thus, bonobos, might lack the psychological mechanisms or the motivation to value the welfare of others independently of their own welfare in food-related experimental tasks. However, prior to investigating the psychological motives underlying prosocial behaviour, methods and paradigms should be developed to elicit it (House et al., 2014). Therefore, future studies should aim to circumvent the experimenter bias and increase the naturalistic nature of experiments that allow to investigate the proximate mechanisms of cooperation. One way to do so, is to implement a free-standing set-up with automatic bating that requires joint action of two or more individuals to obtain a reward.

Based on food provisioning experiments in a semi-artificial world, I showed that bonobos did not show proactive prosocial behaviour and behaved to maximize their own gain. While contrasting with most previous prosociality and food sharing results in bonobos, I suggest that this does correspond to the bonobos' general behaviour around food. Moreover, multiple studies showed that because of the intra- and inter-sexual competition in bonobos in the wild, grouping patterns in bonobos are largely driven by cooperation needs. This suggests that rather than food-based prosociality, bonobos may react to signals and signs of need. Agonistic support in bonobos usually do not involve clear signs of begging or asking for support and seem instantaneous and spontaneous (Vervaecke, Van Elsacker, et al., 2000). The cooperative coalitions and supports may therefore be the result of empathic concerns to closely associated individuals, potentially through high levels of contagion (but see below). The cooperation model suggests that successful cooperative interactions are also promoted by reactive prosociality, which has often an empathic basis (de Waal & Suchak, 2010; Yamamoto & Takimoto, 2012). Moreover, since bonobos reconcile and even show consolation after aggressive events, they have been suggested to be an ideal species to investigate empathy-based prosociality (Clay & de Waal, 2013b, 2013a; de Waal, 1987; Palagi et al., 2004a; Palagi & Norscia, 2013). Future studies should therefore aim to complement their food sharing studies with helping paradigms to investigate the multidimensional character of prosociality and to evaluate the predictions of the empathy hypothesis (de Waal, 2008).

When goals meet practicalities: challenges of research plans

One challenging aspect of doing (experimental) research, is the implementation of the different phases of a research plan. Although my PhD study resulted in some interesting conclusions, the initial research plan included additional elements and goals to complement the current findings.

First, one of the major drawbacks of my study, is arguably the limited sample size. Bonobos are still one of the rarer apes in captivity with no populations in research labs or facilities, and only eleven groups with a total of about 145 individuals in Europe. The median group size in European zoos in 2019 was thirteen individuals (range: 4-21 individuals, including infants and juveniles) (J. M. G. Stevens, 2020). When the new facility in Planckendael was finished in 2019, this allowed to build up a larger group of currently 21 bonobos, including 7 males and 14 females over the age of 1 to 44, which offers great potential for studies in the future. While I was able to include more bonobo subjects in the PCT and GSP than most previous studies (see table 6.6 p 103), the sample size of the juice experiment and the IA study can be considered small. This is partly due to postponed arrival of new bonobo families at Zoo Planckendael, where the start date of the construction of the new bonobo building was postponed. However, while a larger bonobo group would have resulted in more data for each of the experiments, the study would still involve one single study group. Like in other single-group studies, caution is needed in making strong interpretations and conclusions of the results of this PhD and strong generalisations about the species should be avoided since behavioral expressions, like prosociality, have been shown to depend on the group-specific social climate and may differ between populations (Bell et al., 2009; van Leeuwen et al., 2021). However, practicalities such as training the animals and building the set-ups requires a long-time investment with zoo staff, which in Zoo Planckendael has been established. While the research team works well with other zoos in doing behavioural observations, the options of doing more experimental work are often more limited. Ideally, identical paradigms should be implemented in multiple social groups. Initially, the aim of my study was to investigate within-species variability in the proximate mechanisms of cooperation among the same subjects of Zoo Planckendael by looking at factors like age, sex and personality (cfr. Dale et al., 2020; J. S. Martin et al., 2021). However, because of the limited sample size and the lack of deliberate prosocial pulling in the PCT and the GSP, this link could not be investigated in my study. With the new and larger group in Zoo Planckendael this could be a future project.

Second, I investigated the change in salivary cortisol levels to measure the affective component of IA but did not consider the affective component of prosociality. While this was originally the plan, I abandoned this idea because the prosociality experiments were done in group context and that because of practicalities and safety precautions, saliva samples could not be sampled before and after the prosociality experiments. An alternative method to study the emotional response in a group setting would be to use infrared thermography since it involves a minimal amount of manipulation, and it can be implemented from a distance (see above).

Finally, the initial plan was to investigate both testosterone and cortisol in bonobo saliva as endocrinological mechanisms underlying cooperation in bonobos. While salivary cortisol could reliably be analysed using LCMS (Chapter 3), the extraction and analytical results for salivary testosterone proved to be unreliable in bonobos (unpubl. data), and therefore have not been used. Interestingly, a previous study on food sharing in bonobos did report salivary testosterone results (Wobber et al., 2010). However, the study's method to use cotton rolls instead of salivettes to collect testosterone in saliva has been criticized because it creates unsystematic errors (Behringer, Deschner, et al., 2014; Behringer & Deschner, 2017). In addition, oxytocin (OT) and arginine vasopressin (AVP) have received increasing interest in cooperation research because of their roles in mammalian social behaviour (Baribeau & Anagnostou, 2015; Brooks et al., 2021; Caldwell & Albers, 2015; De Dreu, 2012; Rilling et al., 2012). The role of OT is conserved across mammals, and includes regulation of non-kin social bonding (Crockford et al., 2013; T. Romero et al., 2014; Wittig et al., 2014), social attention (Dal Monte et al., 2014; Guastella et al., 2008) and empathy (Burkett et al., 2016). AVP has been suggested to regulate male mammalian social behaviours like affiliation, aggression and paternal behaviours and to enhance the reward associated with social interactions (S. M. Freeman & Young, 2013). Despite their conserved roles, previous studies have shown that the role of OT and AVP even differ between closely related species, partly because of differential distributions of genes encoding for the receptors of OT and AVP in the brains (Hopkins et al., 2012; Rodrigues et al., 2009; Staes et al., 2014, 2016). Moreover, OT and AVP can be measured in urine, but proper extraction and analysis is needed to avoid interfering compounds that create artificially high values (Ziegler, 2018). Also, care is needed for storage of the urine samples because OT degrades at room temperature, requiring storage as ethanol extracts or in liquid nitrogen (Schaebs et al., 2021). There is also an ongoing debate to what degree urinary and salivary measures of OT reflect blood plasma levels and whether peripherally measured OT is indicative of central release patterns and activities within the brain (McCullough et al., 2013; Quintana & Guastella, 2020; Valstad et al., 2017). Based on this, I decided not to include measures of OT and AVP to investigate the emotional component of cooperation in my study. However, future research should aim to use the correct methodology for sampling and analyses, with a better integration of all possible confounds involved, to include multiple measures of the endocrinological aspect of cooperation.

To conclude: The proximate drivers of cooperation in bonobos

To conclude this discussion, I would like to return to the cooperation model (Fig 1.1 p 15) as the general framework of my study. Cooperation is essential for many social species, including humans, but has been considered an evolutionary puzzle. Cooperative interactions like group hunting, territorial defense and agonistic coalitions against in- or outgroup members often require coordination between multiple subjects and may involve time delays between investment and compensation. Because of this, cooperation becomes prone to cheaters. The cooperation model aims to combine the necessary proximate mechanisms with other relevant factors that help to initiate and stabilize successful cooperation. The basic mechanism suggested to contribute to the maintenance of successful cooperation, is the preference for similarity. Most successful cooperative interactions are expected between kin and friends because their relationships are based on high levels of trust, characterized by high levels of prosociality and a high tolerance towards inequity (de Waal & Suchak, 2010; Yamamoto & Takimoto, 2012). While my results showed that bonobos with high Value relationships were indeed more tolerant towards inequity (Chapter 7), I only found limited support for the higher levels of prosociality among friends. The bonobos in my study mainly behaved out of self-interest: while juice provisioning happened more frequently between individuals with higher relationship Values, more than half of the juice provisioning acts were self-benefitting (Chapter 5; see also my reflection on this study); in the PCT, subjects behaved indifferently to the outcome of others, including friends, and in the GSP, adult bonobos only obtained benefits for themselves (Chapter 6). These findings correspond to the socio-ecological characteristics of bonobos in the wild where food sharing is mainly passive and involves low quality items. Prosociality among wild bonobos may mainly be limited to coalitionary support by mothers to their adult sons and by females to other females against males (de Waal & Suchak, 2010; Yamamoto & Takimoto, 2012). Besides the indirect fitness benefits for the mother-son dyads (see above), these coordinated actions provide immediate shared benefits through reduced (feeding) competition by males and reduced male harassment (Smuts & Smuts, 1993). Participation in female coalitions is a low-risk behaviour since males do not oppose female coalitions (Tokuyama & Furuichi, 2016). Interestingly, rather than being the result of closely bonded alliances between females, these coalitions are thus the result of opportunistic collaborative actions (Nurmi et al., 2018; Surbeck & Hohmann, 2013; Tokuyama & Furuichi, 2016) and female coalitions might simply be based on 'contagious' self-serving behaviour against a common enemy, resulting in mutual benefits, i.e. (by-product) mutualism (Jerram L. Brown, 1983).

Although the cooperation model is a useful theoretical concept to link the different proximate mechanisms of cooperation with other relevant factors, it lacks convincing empirical support. The emotionally mediated reciprocity between friends, which is suggested to be based on a high level of trust, remains vulnerable to cheating. Even though cooperative interactions involve benefits for both partners, individuals are still expected to minimize their own cost at the expense of the other, i.e. the tragedy of the commons (Hardin, 1968; Lloyd, 1833). Based on this, several authors have argued that mainly two concepts can explain stable cooperation, and thus assume that cooperation is better than cheating by default (Bshary & Bronstein, 2004): 1) by-product mutualism; and 2) pseudo-reciprocity (Connor, 1986). In by-product mutualism, partners are benefitted as the result of immediately self-serving behaviour and thus no costly investment is needed on the part of the partners (Jerram L. Brown, 1983). Pseudo-reciprocity includes the cases where investment by one individual allows the partner to perform a self-serving behaviour that also benefits the investor as a by-product (Brosnan, Salwiczek, et al., 2010; Connor, 1986). In this case, investment in the partner makes cooperative behaviour the best option for the investor. Only if the investment by a partner is above a critical threshold, i.e. does not involve cheating, it is beneficial to perform an act that returns the investment. By-product mutualism and pseudo-reciprocity thus suggest that the investment in cooperative behaviour mainly yields predictable selfish benefits (Bshary & Bronstein, 2004).This suggests that most prosocial acts between unrelated individuals incur no cost to the actor but are also not performed to alleviate the needs of conspecifics (see also jingle and jangle fallacies in Box 1; p10). Thus, more than being motivated by stimuli to help others, many prosocial acts may be the result of other psychological processes than other-regarding concern (Burkart et al., 2009; Heyes, 2012; J. R. Stevens & Gilby, 2004). The desperate quest to find food-related other-regarding preferences in a variety of species has accumulated evidence of indifference to the gains of conspecifics (e.g. Amici et al., 2014, 2017; Di Lascio et al., 2013; House et al., 2014; M. L. Lambert et al., 2017; Massen et al., 2011; Silk et al., 2005; Tan et al., 2015; Vonk et al., 2008). Therefore, I recommend future research to implement paradigms that allow to investigate the link between the variation in successful cooperation and the level of by-product mutualism and pseudo-reciprocity. By varying food reward quality and cooperation effort, the variation in successful cooperative outcomes will provide information on how prosociality and inequity aversion interact during such interactions. Ultimately, a free-choice cooperation experiment that includes different choices, each with a different payoff for the participants (similar to the PCT but requiring joint action), would allow to investigate how differential rewarding affects partner choice, refusal to participate or even punishment. In addition, experimental findings should be complemented and compared with observations on similar behaviours to obtain biological meaningful conclusions and to allow phylogenetic comparisons between studies of prosociality in different species.

For decades, bonobos have been called “the hippies of the primate world”. They were said to be peaceful, food sharing, non-competitive animals that live in female-dominated societies where agonistic interactions happen very rarely and where frequent sexual interactions defuse tension. This popular image of the hippie ape was largely based on the numerous popularising articles and books (de Waal, 1987; de Waal & Lanting, 1998; J. M. G. Stevens et al., 2008). Moreover, the behavioural work that had been done only included young bonobos in very small social groups in captivity (de Waal, 1989a, 1992). Later, the experimental studies that looked for evidence of self-domestication and high levels of prosociality in bonobos, made use of this popular image to explain their results, providing additional support for the differences between the indifferent chimpanzee and the prosocial bonobo (Hare et al., 2007; Hare & Kwetuenda, 2010; Tan et al., 2017; Tan & Hare, 2013). However, the authors did not acknowledge that most of their findings were based on subadult behaviour (see above) and they often ignored previous studies in which the bonobo-chimpanzee dichotomy has been debated (de Lathouwers & van Elsacker, 2006; Fruth et al., 1999; Stanford, 1998). Later studies on more diverse bonobo groups did report findings that contrasted with the female-dominated, food sharing and non-competitive view of bonobos, providing the necessary nuance to the hippie image of our closest living relative (Cronin et al., 2015; Jaeggi, Stevens, et al., 2010; J. M. G. Stevens et al., 2007). With this PhD thesis I provide supporting evidence for this nuanced view by showing that bonobos, like chimpanzees, behave indifferently to the welfare of others in food-related tasks, resulting in mostly self-benefitting behaviour around preferred food items. Thus, the label ‘indifferent hippies’ aims to combine the nuanced view on the hippie bonobo with their behaviour during the experimental paradigms. In doing so, I hope to contribute to the continuously growing knowledge on the curious lives of one of our closest living relatives.

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[12] Definition of prosociality: any behaviour performed by one individual to alleviate the needs of other individuals or to improve their welfare, without the actor necessarily incurring extra costs to provide these benefits (Cronin, 2012; Amici et al., 2014)

Daan W. Laméris
Behavioural Ecology and Ecophysiology Research group (BECO), Department of Biology, University of Antwerp, Wilrijk, Belgium.
Antwerp ZOO Centre for Research & Conservation (CRC), Royal Zoological Society of Antwerp (RZSA), Antwerp, Belgium
Edwin J. C. van Leeuwen
Behavioural Ecology and Ecophysiology Research group (BECO), Department of Biology, University of Antwerp, Wilrijk, Belgium.
Antwerp ZOO Centre for Research & Conservation (CRC), Royal Zoological Society of Antwerp (RZSA), Antwerp, Belgium
Jeroen M.G. Stevens
Behavioural Ecology and Ecophysiology Research group (BECO), Department of Biology, University of Antwerp, Wilrijk, Belgium.
Antwerp ZOO Centre for Research & Conservation (CRC), Royal Zoological Society of Antwerp (RZSA), Antwerp, Belgium
SALTO, Agro- and Biotechnology, Odisee University College, Brussels, Belgium.
Marcel Eens
Behavioural Ecology and Ecophysiology Research group (BECO), Department of Biology, University of Antwerp, Wilrijk, Belgium.
Marina Salas
Antwerp ZOO Centre for Research & Conservation (CRC), Royal Zoological Society of Antwerp (RZSA), Antwerp, Belgium
Nicky Staes
Behavioural Ecology and Ecophysiology Research group (BECO), Department of Biology, University of Antwerp, Wilrijk, Belgium.
Antwerp ZOO Centre for Research & Conservation (CRC), Royal Zoological Society of Antwerp (RZSA), Antwerp, Belgium
Róisín Murtagh
Interim Group Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.
Tobias Deschner
Interim Group Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.
Verena Behringer
Interim Group Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.
Endocrinology Laboratory, German Primate Center, Leibniz Institute for Primate Research, Göttingen, Germany

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Table 9.1 Overview of the study subjects in Zoo Planckendael

Individual	Sex	Year of birth	In Zoo Planckendael since	CH2: Food preference	CH3: Cortisol response	CH4: Relationship quality	CH5: Juice experiment	CH6: PCT	GSP	CH7: IA
Hortense	F	1/01/1978*	6/07/2016	x	x	x	R	R	S	x
Banya	F	1/02/1990	15/03/2019			x		R	R	
Vifijo	M	23/07/1994	8/09/2009	x	x	x	S	R	S	x
Djanoa	F	27/03/1995	21/08/2002	x	x	x	S	S	S	x
Zamba	M	16/04/1998	6/07/2016	x	x	x	R	R	S	x
Busira	F	16/02/2004	12/06/2012			x	R	S	S	x
Kianga	F	17/07/2005	15/03/2019			x		S	S	x
Habari	M	29/01/2006	Birth	x	x	x	S	S	S	x
Nayoki	F	24/03/2012	Birth		x		S	S	S	
Mokonzi	M	12/04/2013	15/03/2019					S	S	
Kikongo	M	29/01/2014	6/07/2016				S	S	S	
Moko	M	16/02/2016	15/03/2019					R	R	
Sanza	F	12/06/2012	Birth				R	R	R	

Names in *italic*: individuals younger than 8 years were considered as subadults
*Estimated birth date after Pereboom & Stevens (2007)
S: Individual passed the training phase and could participate as subject and receiver
R: Individual did not pass the training phase and could only participate as receiver

Table 9.2 Overview of the study group compositions of Chapter 4

Zoo	Individual	Sex	Year of birth	Sire	Dam	Place of birth
Apenheul	Hortense	F	1/01/1978*	?	?	Wild
	Jill	F	15/07/1985	Bosondjo	Laura	Yerkes
	Zuani	F	1/01/1990*	?	?	Wild
	Bolombo	M	7/11/1997	Yenge	Kosana	Leipzig
	Zamba	M	16/04/1998	Kidogo II	Hortense	Planckendael
	Kumbuka	F	9/07/1999	Hani	Molaso	Apenheul
	Hongo	*M*	25/02/2006	Vifijo	Hortense	Planckendael
	Yahimba	*F*	7/08/2009	Zamba	Kumbuka	Apenheul
	Makasi ii	*M*	11/08/2009	Zamba	Zuani	Stuttgart
	Monyama	*F*	17/07/2010	Vifijo	Jill	Apenheul
Frankfurt	Margrit	F	1/01/1951*	?	?	Wild
	Natalie	F	1/01/1964*	?	?	Wild
	Ludwig	M	26/08/1984	Desmond	Dzeeta	Planckendael
	Kamiti	F	21/01/1987	Masikini	Kombote	Stuttgart
	Zomi	F	28/01/1998	Kidogo II	Hermien	Planckendael
	Kutu	F	29/05/1998	Masikini	Kombote	Stuttgart
	Bondo	M	17/09/1991	Mato	Lisala	Wuppertal
	Heri	M	23/01/2001	Ludwig	Natalie	Frankfurt
	Mixi	F	18/12/2001	Kirembo	Chipita	Stuttgart
	Bashira	F	30/01/2006	Bolombo	Bonnie	Köln
	Nyota ii	M	24/02/2007	Ludwig	Natalie	Frankfurt
	Bili	*M*	8/10/2008	Keke	Maringa II	Stuttgart
	Omanga	*F*	18/12/2008	Ludwig	Kamiti	Frankfurt
	Pangi	*F*	16/07/2009	Ludwig	Kutu	Frankfurt
	Panisco	M	15/12/2009	Ludwig	Zomi	Frankfurt
Planckendael	Lina	F	28/07/1985	Vernon	Loretta	San Diego Zoo
	Vifijo	M	23/07/1994	Kidogo II	Hortense	Planckendael
	Djanoa	F	27/03/1995	Santi	Yasa	Berlin Zoo
	Louisoko	M	19/04/1998	Masikini	Lina	Stuttgart
	Lucuma	M	29/10/2002	Kirembo	Lina	Stuttgart
	Habari	M	29/01/2006	Vifijo	Djanoa	Planckendael
	Lingoye	F	29/11/2007	Kirembo	Lina	Planckendael

Table 9.2 (continued) Overview of the study subjects of Chapter 4

Twycross	Diatou	F	21/10/1977	Masikini	Catherine	Stuttgart
	Kakowet ii	M	7/06/1980	Kakowet	Linda	San Diego Zoo
	Kichele	F	19/04/1989	Masikini	Diatou	Stuttgart
	Banya	F	1/02/1990	Clyde	Bonnie	Keulen
	Keke	M	2/01/1994	Kakowet II	Diatou	Twycross
	Cheka	F	18/03/1996	Bono	Salonga	Frankfurt
	Maringa ii	F	5/05/1998	Simon	Yala	Berlin Zoo
	Luo	M	1/12/2002	Jasongo	Diatou	Twycross
	Kianga	F	17/07/2005	Diwani	Kombote	Stuttgart
	Gemena	F	7/11/2005	Keke	Cheka	Twycross
	Winton ii	M	26/06/2010	MULT	Cheka	Twycross
	Malaika ii	F	23/07/2010	Kakowet II	Diatou	Twycross
	Lopori ii	F	6/01/2012	Kakowet II	Maringa III	Twycross
	Mokonzi	M	12/04/2013	Luo	Banya	Twycross
Wilhelma	Kombote	F	1/01/1966*	?	?	Wild
	Hermien	F	1/01/1978*	?	?	Wild
	Mobikisi	M	1/01/1980*	?	?	Wild
	Zorba	M	1/01/1980*	?	?	Wild
	Chipita	F	1/01/1993*	?	?	Wild
	Ximba	F	1/01/1995*	?	?	Wild
	Liboso	F	17/12/1997	Hani	Zuani	INRB
	Haiba	F	16/11/2001	Ludwig	Ukela	Frankfurt
	Banbo	F	3/09/2002	Keke	Banja	Twycross
	Kasai	M	27/12/2004	Diwani	Chipita	Stuttgart
	Nayembi	F	26/04/2006	Mobikisi	Liboso	Apenheul
	Huenda	F	6/07/2006	Zamba	Hermien	Planckendael
	Lubao	*M*	30/03/2013	Kasai I	Liboso	Stuttgart
	Alima	*F*	24/05/2013	Kasai I	Banbo	Stuttgart
	Bobali	*M*	5/07/2013	Kasai I	Hermien	Stuttgart
Wuppertal	Mato	M	22/12/1963	Camillo	Margrit	Frankfurt
	Lisala i	F	24/04/1980	Masikini	Catherine	Stuttgart
	Lusambo	M	21/07/1980	Masikini	Kombote	Stuttgart
	Birogu	M	11/08/1989	Mato	Catherine	Wuppertal
	Eja	F	14/07/1990	Bono	Daniela	Frankfurt
	Muhdeblu	F	15/04/2001	Erin	Marily-Lori	SD-WAP
	Busira	F	16/02/2004	Birogu	Eja	Wuppertal
	Luebo	M	18/03/2006	Birogu	Lisala	Wuppertal
	Ayubu	*M*	12/08/2011	Bondo	Eja	Wuppertal
	Azibo	*M*	12/08/2011	Bondo	Eja	Wuppertal

? Parents unknown

*Estimated birth date after Pereboom & Stevens (2007,2011)

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